A generalized mathematical model of ecosystems is developed. The model begins with the general class of systems known as state-determined systems, in which the time-derivative of each state variable is a function of some subset of the set of all system state variables and environmental parameters. A formal basis is presented for considering the steady-state behavior of such systems in terms of isoclines, drawing upon the fields of graph theory, linear algebra, and differential equations.

The simplifying capabilities of hierarchy theory are invoked to mitigate the adverse effects of model complexity. Like the theory of isocline analysis, the particular formulation of hierarchy theory presented is phrased in graph-theoretic terms, enabling the model to be developed as a technique for analyzing the steady-state behavior of
hierarchical systems. The role of inter-level time scale heterogeneity in hierarchical organization is discussed.

As an illustration of its ability to portray the behavior of spatially-nested hierarchies, the model is used to provide a perspective on data from the climax vegetation of the Great Smoky Mountains. The effects of time scale heterogeneity are also illustrated by using the model to organize data sets from several vegetation/avian communities across the United States. The vegetation is taken to behave with a lower characteristic frequency than the relatively rapidly-developing avian subcommunity, thus constraining the latter in a hierarchical fashion.

In order to understand in a more general way the role such a model might play in advancing ecological understanding, a broad framework is presented for analyzing the role of conceptual structures in science and the place of models in these structures. A view of models as scientific metaphors is advanced as an alternative to the pictorial/realist interpretation of models. Given this understanding of models in general, the proposed model and its underlying assumptions are compared and contrasted with a set of four partial conceptual structures drawn from the fields of systems ecology, plant ecology, natural resource economics, and organismic systems theory.
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# TABLE OF CONTENTS

## INTRODUCTION

- Ecological Modeling in Perspective .................................................. 1
- Overview of the Literature .................................................................... 4
- Statement of the Problem ...................................................................... 9

## DEVELOPMENT AND APPLICATION OF THE MODEL

- Isocline Theory ..................................................................................... 12
  - General Systems Theory .................................................................... 12
  - Isocline Analysis of Systems ............................................................ 15
  - Graph Theory .................................................................................... 28
  - Graph-Theoretic Analysis of Isocline Parameterization .................... 38
- Use of Isoclines in a Model of Ecological Hierarchy ......................... 46
  - A General Model of Hierarchy .......................................................... 46
  - Adapting the Model to Ecosystems ................................................... 63
  - Introduction of Time Scale Heterogeneity ...................................... 113
- Application of the Model to Selected Community Studies ................. 126
  - Choice of Studies ........................................................................... 126
  - A Hierarchical View of a Large-Scale Plant Community ................. 127
  - The Role of Time Scale in Vegetation/Avifauna Systems ............... 146

## MODEL IMPLICATIONS IN DIFFERENT CONCEPTUAL STRUCTURES

- Conceptual Structures and the Use of Models .................................... 164
  - Experience and the Development of Scientific Theories ................. 164
  - A Hierarchical View of Personal Conceptual Structures ............... 171
  - The Role of Models in Personal Conceptual Structures ................. 182
  - A View of Nature Based on Stability and Resilience ..................... 187
  - Gradient Analysis of Plant Communities ....................................... 202
  - Multiple-Use Natural Systems in an Economic Framework ........... 218
  - The Metaphor of the Multiple-Product Firm .................................. 218
  - A Simple Model of a Multiple-Use Natural System ...................... 230
  - A Conceptual Framework for Biology ............................................. 248

## REFERENCES ......................................................................................... 262

## APPENDICES

- Appendix I: Bird Species List ............................................................... 275
- Appendix II: Tree Data ........................................................................ 281
- Appendix III: Model Stability .............................................................. 282
- Appendix IV: BASIC Program for Multiple-Use Model .................... 288
LIST OF FIGURES

1. Phase planes for three-dimensional linear system............21
2. Illustration of graph-theoretic concepts........................30
3. Digraphs for the system of Figure 1...............................36
4. Strongly two-connected source digraph............................43
5. Digraphs of sample hierarchies.....................................59
6. Spatially-nested hierarchy.........................................64
7. A view of ecological hierarchy.....................................70
8. Isocline behavior for the system of Table 4.......................77
9. Isocline behavior for the system of Table 5.......................83
10. Composite equilibrium locus construction........................90
11. Composite equilibrium loci for levels 2 through 4.................94
12. Three-dimensional representation of composite equilibrium loci.........................................................101
13. Time-dependent composite equilibrium locus.......................104
14. Graphical representation of composite equilibrium locus coefficients.....................................................110
15. Behavior and organization of simple system exhibiting time-resolution heterogeneity.................................117
16. Behavior and organization of a more complex system exhibiting time-resolution heterogeneity........................122
17. Hierarchical representation of Great Smoky Mountains study areas..............................................................129
18. Domains of forest types plotted on dessication and elevation axes.............................................................131
19. Total diversity minus mesic diversity plotted against xeric diversity..........................................................135
20. Composite phase plane of Eastern Forest System forest types.................................................................137
21. Composite phase plane of Eastern Forest System sites, by forest type.........................................................140
22. Hierarchical view of Great Smoky Mountains vegetation across three levels.................................................143
23. Bird species diversity in Ravenel's Woods........................150
24. Hierarchical view of Eastern Forest System vegetation and avian subcommunities......................................153
25. Vegetation and avian phase planes for selected sites.............159
26. Hierarchical organization of conceptual structures..............174
27. Graph-theoretic view of the system/environment distinction.................................................................192
28. Another view of the system/environment distinction.............195
29. Three possible species distribution patterns..........................206
30. Gradient plots of performance indices from top row of level-four constituents in Figure 6..........................211
31. Composite phase planes of gradient behavior......................215
32. Production possibility frontiers and expansion path..............224
33. Four-quadrant diagram of steady-state yields and utilization levels..........................................................236
34. Steady-state expansion path...........................................243
LIST OF TABLES

1. Roles of six possible attributes in nine theories ................. 49
2. Transposed reachability matrix for system of Figure 6 ............. 67
3. Constituent-wise reduction of transposed adjacency matrix corresponding to Figure 6 ........................................ 73
4. Transformational behavior of C(1,1), C(2,1), C(3,1), and C(4,1) .......................................................... 76
5. Time-dependent transformational behavior of C(1,1), C(2,1), C(3,1), and C(4,1) ..................................................... 81
6. Transformational behavior for C(2,1-4) ................................ 88
7. Transformational behavior for C(3,1-4) ................................ 98
8. Transformational behavior for C(4,1-4) ................................ 100
9. Time-dependent transformational behavior for C(2,1-4) .................. 106
10. Transformational behavior of simple system illustrating effects of time scale .................................................... 116
11. Transformational behavior of more complex system incorporating effects of time scale ............................................. 121
12. Diversity data for birds and trees in different sites and seral stages ................................................................. 157
13. Classification of sites .................................................... 162
14. Transformational behavior of C(4,5-8), C(4,17-20), and C(4,21-24) ................................................................. 210
INTRODUCTION

Ecological Modeling in Perspective

Mathematical modeling of ecosystems has played a major role in the science of ecology for some time. The history of this approach has been marked with notable successes, but in other important respects ecosystem modeling has yielded disappointing results. Especially disappointing to some is the failure of mathematical modeling to give ecology the same sophistication of understanding attained in the physical sciences or even in physiology.

Importantly, the failure of ecology to attain "maturity" is not simply a matter of academic embarrassment. Rather, this failure comes at a time when natural systems around the world are being exploited to the point of irreversible damage, and managers of natural resources are looking to ecologists for aid in understanding the systems that have been placed under their care.

To understand the problem of modeling in ecology, it may be helpful to address the issue in three parts: 1) the appropriateness of mathematical modeling to the scientific endeavor in general, 2) the importance of change in
ecosystems and their environments, and 3) the extreme complexity of ecosystem organization.

The first of these three issues, the overall appropriateness of mathematical models in science, is an important question seldom addressed by scientists themselves. Admittedly, modeling efforts have been markedly successful in certain areas, but precisely why they should be so is generally left undiscussed. In fact, the relationship between mathematical models of nature and nature itself is highly problematic (Poythress 1983, Wigner 1960, Williams 1977). While it seems generally taken for granted that nature can be both mirrored and explained by mathematical equations, such a position is not uncontroversial. In the present research, a more complex perspective of the modeling process will be adopted, emphasizing the importance of the incorporating theoretical framework in determining a model's meaning.

In addressing the second issue (above), it may be observed that one of the dilemmas of ecological modeling is the essential meaningless of single ecosystem performances, or even of single trajectories of performances through time. One explanation for the failure of single ecosystem trajectories to provide the same explanatory power that similar performances provide in other sciences (e.g.
physics) is that these other sciences have been able to abstract from their systems causal-deterministic cores or their statistical equivalents without regard for their shells of contingencies, as the latter tend to be of a regular, if not constant, nature.

In simpler terms, ecosystems tend not to be of fixed organization, nor even of organization that develops according to particularly regular patterns. Neither is the structure of the system-environment relationship likely to be predictable in the case of ecosystems. Finally, even if such patterns of organization were relatively predictable, the magnitude and frequency of the environmental shifts that characteristically impact ecosystems are so great that attempts at understanding such systems through measurements of single performances would continue to be of limited value.

This does not imply that efforts at mathematical modeling of ecosystems are necessarily wasted, rather that focusing such models on particular performances obtained under particular environmental conditions is of limited interest. Therefore, instead of concentrating on such particular performances, a model will be proposed which emphasizes the steady-state behavior of ecosystems, drawing on the tradition of isocline analysis in ecology.
Finally, the staggering complexity of natural ecosystems has been a major stumbling block to attempts at mathematical modeling thereof. Various means have been proposed to circumvent the intractability of models which result from any kind of reductionist view of ecosystems. Among these are the now-familiar large-scale simulation models and the use of multivariate statistics. A somewhat less common technique involves the use of hierarchy theory to aid in understanding ecosystem organization. One of the tenets of this theory is that hierarchically-organized systems are "partially decomposable." Such a view focuses attention on those subsystems which may be regarded most easily as entities in their own right, with behaviors constrained by (not independent from) the greater system. The model proposed here will adopt a similar perspective in attempting to render ecosystem organization more understandable.

Overview of the Literature

Mathematical modeling of ecosystems dates back at least as far as the competition and predator/prey models of Lotka (1925) and Volterra (1926). Since then, and particularly since the advent of the electronic computer, mathematical modeling has assumed increasing prominence in the field of ecology. Obviously, recounting the entire history of such a
development in the present context would be a laborious exercise at best. It will, however, prove useful to examine some of the key presuppositions and approaches involved in ecological modeling, so that the present research may be viewed in proper perspective.

A necessary prerequisite to ecosystem modeling, of course, is the existence of ecosystems. The realization that ecosystems could be viewed as entities ("entitation" in the terminology of Gerard (1969)) marked a milestone in the development of ecology. It could be argued that this realization began with the recognition of natural systems existing at super-population levels of organization. A notable early example of this was the work of Mobius (1877), who viewed an oyster-bed community as a unified object of study, describing it by the term "biocoenosis." In the field of plant ecology, Clements (1916) took the metaphor of community-as-organism to its extreme. By the time Elton (1927) succeeded in defining the bounds of the "new" science of ecology, the view that ecosystems constituted legitimate objects of study was well-known.

The modern idea that the existence of ecological systems automatically validates attempts at mathematical modeling thereof can be interpreted as an application of the basic premise behind general systems theory. During its
initial development, general systems theory was envisioned as a "logico-mathematical discipline" (Bertalanffy 1968) which would use principles common to systems in general as a means to understand particular systems, even though these particular systems might occur in widely disparate fields. Thus, if such common principles exist, it should be true that ecosystems, as systems, may be understood through this type of logico-mathematical analysis.

A favorite technique in general systems theory is the use of sets of differential or difference equations to model system dynamics (Ashby 1956, 1960). In the study of ecosystems, however, particular dynamic performances tend not to be as interesting as analogous performances in systems with identified causal-deterministic cores or regular shells of contingencies (Bohm 1957). In this case, the same basic model form (sets of differential or difference equations) can be manipulated to shift attention away from particular dynamic performances of the system and toward more meaningful steady-state performances.

The dynamic nature of ecosystem organization, however, makes suspect the use of sets of constant-coefficient differential equations as appropriate models of these systems. In contrast, graph theory is one branch of mathematics which both finds application in systems analysis and obviates the need for precise specification of coefficients due to its non-metric nature (Wilson 1979, Bondy and Murty 1976, Harary et al. 1965, Roberts 1976).

The use of hierarchy theory to deal with the problems raised by ecosystem complexity has assumed increased popularity in recent years. The concept of hierarchy as an organizational principle is, of course, quite ancient, with the term apparently first appearing in the writings of Pseudo-Dionysius in the sixth century A.D. (Whyte 1969). Modern interest increased rapidly following the work of Simon (1962). Separate theories of hierarchy have been advanced by Allen and Starr (1982), Bastin (1969), Bunge (1969), Grobstein (1973), Pattee (1969, 1973), Rosen (1969), Warfield (1973), and Woodger (1954). The treatment by Allen and Starr views hierarchy theory specifically as a perspective for dealing with ecological complexity.

Significant as these tools for ecosystem modeling may be, the mere ability to construct objects called ecosystem models does not in itself determine the role such objects
ought to play in ecosystem science or management. In large part, this constitutes a problem in the philosophy of science. This fact, however, does not relieve scientists themselves of responsibility for the development and use of their models.

Understanding the meaning of models and their role in scientific theory requires first of all a view of the structure of scientific theories, or better, a view of theoretical structures. One school of thought on the nature of such structures can be termed "Weltanschauungen" or "world view" analyses (Suppe 1977). The central tenet of this approach is that the universe may be viewed from within any of a number of distinct conceptual structures (Pepper 1942).

If such distinct conceptual structures exist, and if they conflict at very significant levels of generality, then the meaning of any particular low-level theory or model may be very different when viewed from competing world views. In fact, given a literalist definition of "model," it is possible to find examples of credible world views in which mathematical models have no scientific meaning whatsoever.

A contrasting view of models is that of Black (1962), Hesse (1965), and Poythress (1983). Building on the
linguistic theory of metaphor advanced by Richards (1936), this interpretation equates "model" with scientific metaphor, wherein the meaning of the model is largely dependent on its context, i.e. its incorporating theoretical structure. In such a view, it would be extremely difficult to find a world view in which mathematical models were proscribed from significance a priori. However, with this freedom to apply mathematical models within a variety of conceptual structures comes the additional responsibility to show how such application can be made.

Statement of the Problem

The preceding paragraphs may be interpreted by some as overly-pessimistic regarding the success with which ecosystems can be successfully understood by mathematical modeling. This interpretation is not the one intended. In fact, when duly interpreted within an incorporating theoretical framework, ecosystem models constitute an indispensable facet of ecological understanding. Hints have been given regarding possible solutions to some of the problems inherent in the process of ecological modeling. In more explicit form, the general objective of the present research is to better understand the nature of ecosystem organization by modeling it in a steady-state, hierarchical
fashion, and by exploring how the resulting model might be interpreted within a number of different conceptual structures.

This general objective may be viewed as uniting two more specific objectives, one relating to model development and the other to model interpretation. In the context of the first specific objective, it will first be necessary to lay a groundwork for steady-state analysis of mathematical models in general. This groundwork will take the form of a particular formulation of isocline theory.

Next, a general model of hierarchy will be developed. This model will be developed in such a manner as to facilitate its analysis in terms of the previously-developed isocline theory. The model will then be adapted for specific application to ecosystems. Finally, the pure mechanics of the model will be illustrated by applying it to empirical data borrowed from selected studies of vegetative and avian communities from across the United States.

The second half of the general objective, pertaining to model interpretation within different conceptual structures, will involve exploration of both normative and positive implications of the model. The conceptual structures within which the model will be interpreted will vary in terms of
their level of generality and their completeness. Examples will be drawn from the fields of systems ecology, plant ecology, natural resource economics, and organismic systems theory.
DEVELOPMENT AND APPLICATION OF THE MODEL

Isocline Theory

General Systems Theory

Ashby (1956, 1960) laid the foundation for a formal theory of what he called "state-determined systems" (also referred to as "determinate dynamic systems"). In this theory, the state-determined system (hereafter referred to simply as "system") is composed of a set of "state variables" ("elements" or "subsystems" in some other terminologies). The "transformation" of a system describes how the system changes between time periods, given its initial state. The transformation corresponds to a subset of Klir's (1969) idea of behavior and will herein be referred to as the "transformational behavior" of the system.

Ashby asserts that the transformational behavior of any system of n variables may be represented by a set of n differential equations; i.e. that the time derivatives of the set of state variables \([x(1), \ldots, x(n)]\) can be specified as functions of that set. This set of n differential equations is known as the "canonical representation" of the system's transformational behavior.
In context, the terms "canonical representation" and "transformational behavior" shall be used interchangeably to describe this set of equations.

Since state variables have so far been defined simply as parts of the system (as opposed to a more specific requirement that the parts vary with time), it is conceivable that the time derivatives of some of the state variables could be identically zero. An example is shown below:

\[
\begin{align*}
\frac{dx(1)}{dt} &= f_1(x(1), x(2), x(3), x(4), x(5), x(6)) \\
\frac{dx(2)}{dt} &= f_2(x(1), x(2), x(3), x(4), x(5), x(6)) \\
\frac{dx(3)}{dt} &= f_3(x(1), x(2), x(3), x(4), x(5), x(6)) \\
\frac{dx(4)}{dt} &= 0 \\
\frac{dx(5)}{dt} &= 0 \\
\frac{dx(6)}{dt} &= 0.
\end{align*}
\]

Instead of being thought of as three members of a six-variable system, variables \(x(4), x(5),\) and \(x(6)\) could also be thought of as constants in the canonical representation of a three-member system consisting of state variables \(x(1), x(2),\) and \(x(3).\) However, it will be shown later that an important increase in understanding may be gained by affording a special status to certain such variables.
The following conventions will be adopted to help clarify these matters: A system will be taken to be composed of a set of system state variables, the time derivatives of which may be expressed as functions of at least one system state variable. Variables which appear as arguments in the functional form of the time derivative of at least one system state variable, but whose own time derivatives are not functions of any system state variable shall be designated "environmental variables." The state variables will then constitute the "system," while the environmental variables will form the system's "effective environment" (Warren et al. 1979), or, in context, simply "environment."

In the example above, variables \(x(4), x(5),\) and \(x(6)\) are environmental variables because 1) they each appear as an argument in the functional form of the time derivative of at least one state variable, and 2) their own time derivatives are not functions of any state variable. The second condition follows from the fact that the time derivatives of \(x(4), x(5),\) and \(x(6)\) are identically zero. While this fact is a sufficient condition, it is not a necessary one. It is, for example, conceivable that the time derivatives of \(x(4), x(5),\) and \(x(6)\) could be functions of some third set of variables (the "generative" environment, Warren et al. 1979). This possibility will be explored more fully in a later section.
Isocline Analysis of Systems

A state of the system which sets the derivatives of the canonical representation equal to zero is defined by Ashby (1956, 1960) as a state of equilibrium. This is not problematic when the discussion is confined to sets of equations, but if the system in question is a physical one, then use of the term "equilibrium" may be confusing. As open systems, biological systems may display states satisfying the above definition of equilibrium without satisfying the thermodynamic criterion of equilibrium. These states are more properly referred to as "dynamic equilibria" or "steady states" (Bertalanffy 1968). Here, the term "equilibrium" shall be used interchangeably with "steady state," although the reader should remain aware that in the context of a particular natural system the terminology may require restriction.

The equilibrium performance of systems is often analyzed through the use of isoclines. Isocline analysis finds its origin as a technique in the study of differential equations. The term "isocline" is a composite of two Greek terms, "iso" meaning "equal," and "cline" meaning "slope." Thus, in the analysis of differential equations, "isocline" refers to a locus of points along which some derivative is equal to a given constant.
Isocline analysis has found some use in ecology (Lotka 1925, Volterra 1926, Rosenzweig and MacArthur 1963, Rosenzweig 1969 and 1973, Reibesell 1974, Liss and Warren 1980, Walker et al. 1981). In most of this work, the derivative involved is the time derivative of some state variable, and the constant to which the derivative is set equal is zero. The isoclines are plotted in phase space, the dimensions of which correspond to the state variables of the system. A two-dimensional projection of phase space is called a "phase plane." These conventions will be adopted here as well.

Even with these conventions, however, there are in general a number of ways to define "isocline," especially if there is more than one state variable in the system. The canonical representation of a system by definition gives a single time derivative for each state variable in the system. A simple definition of a particular state variable's "isocline" would be the equation resulting from setting that variable's time derivative equal to zero, without making any substitutions involving any other equation in the canonical representation. Thus, let the "non-reduced isocline" of state variable x(i) be defined as the equation resulting from setting the time derivative of state variable x(i) equal to zero. This equation can be thought of as defining a function (perhaps implicit)
describing equilibrium values of $x(i)$ in terms of the other variables in its time derivative.

Given the definition of non-reduced isocline, other classes of isocline may be defined based upon various methods by which the non-reduced isocline may be reduced. For example, a "$k$-dimensional subsystem isocline" may be defined as follows for a system of $n$ state variables and $m$ environmental variables: For $0 < k < n+1$, define the $k$-dimensional subsystem isocline of $x(i)$ in a specified $k$-dimensional phase space to be the full reduction of the non-reduced subsystem isocline of $x(i)$ obtained by substitutions involving the non-reduced isoclines of any $x$'s distinct from all $k$ dimensions of the specified phase space except $x(i)$. The graphical algorithm developed by Booty (1976) generates this type of isocline.

For a system whose canonical representation consists only of linear equations (a "linear system"), such a reduction will be explicit. For nonlinear systems, on the other hand, such a reduction will most likely be implicit only. Subsystem isoclines are so called because they do not take the behavior of the entire system into account; specifically, they exclude the behavior of a specified $k-1$ dimensions.
Conversely, a class of isoclines may be defined which does take into account the behavior of all state variables in the system. A "\(k\)-dimensional system isocline" may be defined as follows: For a set of \(h\) environmental variables \([y(a), \ldots, y(b)]\), where \(\max(m-n,-1) < h < m+1\), and for \(k = m+1-h\), define the \(k\)-dimensional system isocline of \([y(a), \ldots, y(b)]\) in a specified \(k\)-dimensional phase space to be that isocline obtained by reducing the entire set of non-reduced isoclines to an equation defining one of the \(k\) subsystems in terms of the other \(k-1\) subsystems and the \(h\) environmental variables. Again, for nonlinear systems such a reduction may be an implicit one.

For a linear system, isoclines so defined will likewise be linear in form. The canonical representation of a linear system is often written in matrix form. If the system is homogeneous, the canonical representation appears as follows:

\[
dx/dt = Ax,
\]

where \(x\) is the vector of system variables and \(A\) is the matrix of coefficients in the canonical representation. At equilibrium, this equation takes the form \(Ax = 0\). This equation has a nontrivial solution if and only if the matrix \(A\) is singular, in which case there exist infinitely many
solutions, all but one of which are nontrivial. In other words, in the homogeneous case \( x=0 \) is always an equilibrium point, and in fact is the only equilibrium point when \( A \) is nonsingular.

However, if the canonical representation is nonhomogeneous, the phase plane behavior is quite different. The nonhomogeneous case may be represented by the equation

\[
\frac{dx}{dt} = Ax + b
\]

where \( b \) is a vector of constant terms, of the same order as the vector \( x \). By the adopted conventions, then, the \( b \) vector may be thought of as a vector representing the impact on \( x \) resulting from the state of the variables in the environment of the system. When \( A \) is nonsingular, the solution at \( \frac{dx}{dt} = 0 \) is easily obtainable algebraically. Setting \( \frac{dx}{dt} = 0 \) gives \( Ax = -b \). Premultiplying both sides of this equation by the inverse of \( A \) gives the solution.

As an example of such a system, consider a system of three state variables \( x(1), x(2), \) and \( x(3) \). Suppose that the canonical representation of the system can be written in matrix form as follows:
\[
\begin{bmatrix}
\frac{dx(1)}{dt} \\
\frac{dx(2)}{dt} \\
\frac{dx(3)}{dt}
\end{bmatrix} = 
\begin{bmatrix}
-1 & -1 & 0 \\
1 & -1 & -1 \\
0 & 1 & -1
\end{bmatrix}
\begin{bmatrix}
x(1) \\
x(2) \\
x(3)
\end{bmatrix} + 
\begin{bmatrix}
b(1) \\
b(2) \\
b(3)
\end{bmatrix},
\]

where the \( b(i) \) are all positive real numbers.

This example can be made particularly simple by making the following assumption: In addition to representing the environment's impact on the system, let the \( b \) vector also represent the state of the environment itself. The environment would thus be composed of three environmental variables \( b(1), b(2), \) and \( b(3) \). Note that \( b(1) \) and \( b(2) \) each have a simple positive effect on \( x(1) \) and \( x(2) \) respectively, while \( b(3) \) has a simple negative effect on \( x(3) \).

This system implies two families of two-dimensional subsystem isoclines on each of three possible phase planes: \([x(1),x(2)], [x(2),x(3)], \) and \([x(1),x(3)]\) (Figure 1). On the \([x(1),x(2)]\) phase plane there exist two families of two-dimensional subsystem isoclines, one family having positive slopes and the other having negative slopes. The positively-sloped family can be expressed by the equation \( x(2) = .5b(2) + .5b(3) + .5x(1) \). The negatively-sloped family can be expressed by the equation \( x(1) = b(1) - x(2) \).
Figure 1. Phase planes for three-dimensional linear system. Sample two-dimensional subsystem isoclines are shown for both variables on each of the three possible phase planes in Figures 1a-1c, and sample two-dimensional system isoclines are shown for the \([x(1), x(2)]\) phase plane.

Figure 1a. Two-dimensional subsystem isoclines for \([x(1), x(2)]\) subsystem. Isoclines for \(x(1)\) are shown as functions of \(x(2)\) and \(b(1)\), while isoclines for \(x(2)\) are shown as functions of \(x(1)\), \(b(2)\), and \(b(3)\).

Figure 1b. Two-dimensional subsystem isoclines for \([x(2), x(3)]\) subsystem. Isoclines for \(x(2)\) are shown as functions of \(x(3)\), \(b(1)\), and \(b(2)\), while isoclines for \(x(3)\) are shown as functions of \(x(2)\) and \(b(3)\).

Figure 1c. Two-dimensional subsystem isoclines for \([x(1), x(3)]\) subsystem. Isoclines for \(x(1)\) are shown as functions of \(x(3)\), \(b(1)\), and \(b(2)\), while isoclines for \(x(3)\) are shown as functions of \(x(1)\), \(b(2)\), and \(b(3)\).

Figure 1d. Two-dimensional system isoclines for \([x(1), x(2)]\) subsystem. In this phase plane, the two-dimensional system isoclines for the pair \([b(1), b(2)]\) are redundant with those for the pair \([b(1), b(3)]\). Also shown are two-dimensional system isoclines for the pair \([b(2), b(3)]\).
Figure 1.
On the \([x(2),x(3)]\) phase plane, there are again two families, one positively sloped and the other negatively sloped. The positively-sloped family is given by the equation \(x(3) = -b(3) + x(2)\). The negatively-sloped family is given by the equation \(x(2) = .5b(1) + .5b(2) - .5x(3)\).

On the \([x(1),x(3)]\) phase plane, both families of isoclines are positively sloped. One of these families is expressed by the equation \(x(1) = .5(b(1) - .5b(2) + .5x(3))\). The other is given by the equation \(x(3) = .5b(2) - .5b(3) + .5x(1)\).

An illustration of some of this system's two-dimensional system isoclines is given in Figure 1d, plotted on an \([x(1),x(2)]\) phase plane. The enumeration of distinct system isocline families is not a straightforward task, although if redundancy is not a concern the problem is greatly simplified. For given values of \(m\) and \(h\) (as specified in the definition of \(k\)-dimensional system isocline), there exists a total of

\[m!/[h!(m-h)!]\]

families of \(k\)-dimensional system isoclines. Over all admissible values of \(h\), then, the total number of families of \(k\)-dimensional system isoclines is equal to
where \( j = \max(m-n+1,0) \). However, some of the coefficients of the environmental variables in the equation describing a particular system isocline may be zero, causing redundancy, i.e. the equivalence of different families of isoclines. Thus, the number of distinct families of system isoclines may be somewhat less than the total number of families.

For example, Figure 1d shows members of each of three families of two-dimensional system isoclines in the \([x(1),x(2)]\) plane. However, there is some redundancy among system isoclines for this system, as the figure shows. For example, the \([b(1),b(2)]\) family of two-dimensional system isoclines is identical to the \([b(1),b(3)]\) family of isoclines. This family is also identical to the family of \(x(1)\) non-reduced isoclines and \(x(1)\)'s family of two-dimensional subsystem isoclines in \([x(1),x(2)]\)-space.

This system is asymptotically stable by the standard definition thereof, with eigenvalues of \(-1\) and \(-1 \pm 1.414i\). It is generally true that linear systems which are stable under this definition are also globally stable, that is to say that given the same \(b\) vector, the system will always
tend toward the same equilibrium point in phase space, regardless of the initial state of the $x$ vector.

When presented in the manner of Figure 1, an important property of globally stable nonhomogeneous linear systems becomes obvious: there exists a multiplicity of equilibrium states for the system, even though in the globally stable case only one of these will obtain for any given $b$ vector (Liss and Warren 1980). This property may be referred to as the "multiple steady state" nature of such systems. Importantly, this property is not restricted to linear systems, but applies to any system which possesses an effective environment as the term is defined here.

This section has been developed so far using the linear system as an example because of its familiarity and amenability to algebraic solution. Many natural systems, of course, are far better understood by use of nonlinear models. Like linear systems, globally stable nonlinear systems have equilibrium performances which may be displayed as families of isoclines on phase planes. However, the isoclines, like the canonical representation, are nonlinear in form, and their equations are not generally obtainable algebraically.

Solution of systems of nonlinear differential equations
by numerical means is commonplace in many areas of research, although generation of isoclines by this method is less common. Thompson (1981) presented one example of computer-assisted isocline derivation. Computer generation of isoclines by Thompson's method is based on differences between the sets of environmental variables occurring as arguments in the functional forms of subsystem isocline families.

For ease of discussion, all environmental variables which appear as arguments in the functional expression of a k-dimensional subsystem isocline family shall be called the "parameters" of the isoclines of that family, modifying Ashby's (1956) terminology somewhat. An isocline is said to be "parameterized" by its parameters. For example, in Figure 1a, the upward-sloping family of isoclines is parameterized by \( b(2) \) and \( b(3) \), while the downward-sloping family is parameterized by \( b(1) \).

Thompson's (1981) method involves solution of the canonical representation of the system for a schedule of fixed environmental states. The schedule consists in part of a series of sets of values for a specific set of environmental variables. The environmental variables which are to be included in this set are those which parameterize some isocline family different from the family containing
the isocline to be generated, but located in the same phase plane. The other part of the schedule consists of a constant set of values for the set of environmental variables which parameterize the isocline to be generated.

For example, to generate the $x(1)$ two-dimensional subsystem isocline parameterized by $b(1) = 1$ in Figure 1a, the entire set of equations in the system's canonical representation could be solved for each environmental state in the following schedule:

\[
\begin{align*}
b(1) & : 1 \ 1 \ 1 \\
b(2) & : 0 \ 1 \ 0 \\
b(3) & : 2 \ 0 \ 0 .
\end{align*}
\]

When the steady-state values of $x(1)$ and $x(2)$ have been computed (by whatever numerical algorithm is chosen), the points may be plotted in $[x(1),x(2)]$-space and connected by a curve. This locus is the $x(1)$ two-dimensional subsystem isocline in $[x(1),x(2)]$-space parameterized by $b(1) = 1$. In the case of a nonlinear isocline, the accuracy of the plot will depend on the number and distribution of points plotted. Note that this method of isocline generation requires prior knowledge of the parameterizing environmental variables for a given isocline. For nonlinear systems, determining this information can be a complex procedure in
the absence of an efficient algorithm. Such an algorithm will be presented later in this discussion.

Numerical solution is not the only means of generating isoclines for nonlinear systems. Booty (1976) presented a graphical technique for deriving two-dimensional subsystem isoclines of nonlinear systems, which he used to model the steady-state behavior of fishery systems.

Graph Theory

The more qualitative methods of systems analysis often make use of the principles of graph theory. Levins (1975) used graph-theoretic techniques to discuss potential stability and evolution of biological communities. Li and Moyle (1981) used Levins' method to discuss the stability-related effects of species introductions into biological communities. Certain qualitative properties of a system's isocline behavior can likewise be analyzed via graph-theoretic techniques, but because of the non-standard nature of graph terminology, the presentation of these techniques will have to await the definition of some basic terms. Unless otherwise noted, the following definitions are taken from Wilson (1979) and are concordant with those of Bondy and Murty (1976).
In graph-theoretic language, a "graph" G is defined as a pair \([V(G), E(G)]\), where \(V(G)\) is a non-empty finite set of elements called "vertices," and \(E(G)\) is a family of pairs of elements of \(V(G)\), where these pairs define "edges" (Figure 2a). If each element of each pair in \(V(G)\) is distinct and the family of pairs in \(V(G)\) may be properly called a set (i.e. no element occurs more than once), then the graph is called a "simple graph" (Figure 2b). If the pairs in \(V(G)\) are ordered, the graph is called a "directed graph" or "digraph," and the pairs are said to define "arcs" rather than edges (Figure 2c). An arc from vertex x to vertex y shall be written "xy." If all arcs in a digraph are distinct and there is no arc which does not join distinct vertices, the digraph is called a "simple digraph" (Figure 2d).

A "subgraph" of a (di)graph G is simply a (di)graph, all of whose vertices belong to \(V(G)\) and all of whose edges (or arcs) belong to the edge set (or arc set) of G (Figure 2e). A simple (di)graph in which the addition of any new edge (arc) would result in a (di)graph which is not simple is called a "complete (di)graph." A complete (di)graph with \(n\) vertices is denoted \(K(n)\). \(K(4)\) is shown in Figure 2f.

A finite sequence of edges or arcs of the form \([x(0)x(1), x(1)x(2), \ldots, x(m-1)x(m)]\), where \(x(0), x(1), \ldots, x(m)\)
Figure 2. Illustration of graph-theoretic concepts.

Figure 2a. A graph containing four vertices \(x(1), x(2), x(3),\) and \(x(4)\) and nine edges (curved lines connecting vertices). There is one edge connecting \(x(1)\) to \(x(2)\), and one connecting \(x(3)\) to \(x(4)\). There are three edges connecting \(x(1)\) to \(x(3)\), and two connecting \(x(1)\) to \(x(4)\). Note that there is also an edge connecting \(x(2)\) to itself, and another connecting \(x(4)\) to itself.

Figure 2b. A simple graph. This graph qualifies as a simple graph because in no case is there more than one edge connecting any two vertices, and there are no edges connecting any given vertex to itself.

Figure 2c. A digraph. Curved arrows represent arcs, the digraph equivalent of edges. Use of arrows signifies directionality of relationship.

Figure 2d. A simple digraph. Unlike simple graphs, simple digraphs can have two edges (arcs) between the same pair of vertices, but they must run in opposite directions in order for the digraph to be called simple.

Figure 2e. A subgraph of Figure 2c. This figure can be derived from Figure 2c by erasing vertices \(x(2)\) and \(x(3)\), along with all arcs involving those vertices.

Figure 2f. A complete digraph with four vertices \((K(4))\). This digraph is complete because it contains the maximum number of arcs possible while remaining simple.

Figure 2g. Adjacency matrix for Figure 2c. The number of arcs running from vertex \(x\) to vertex \(y\) in Figure 2c is shown in row \(x\), column \(y\) in this matrix. Thus, adding all the entries in this matrix gives a total of nine, the same number as the number of arcs in Figure 2c.

Figure 2h. Reachability matrix for Figure 2c. A Boolean matrix, showing those pairs of vertices between which a path exists. Note that the only pairs of vertices not connected by any path are \([x(1), x(2)]\), \([x(3), x(2)]\), and \([x(4), x(2)]\). This is because there are no arcs entering \(x(2)\) except the one which connects that vertex to itself.
Figure 2.
x(2), ..., x(m) are all vertices in a (di)graph and all involved edges (arcs) and vertices (except, perhaps, for x(0) and x(m)) are distinct is called a "path." For example, [x(2)x(1), x(1)x(4), x(4)x(3)] is a path in Figure 2d. The number of edges (arcs) in a path is termed its "length." Following Harary et al. (1965), a path in which x(0)=x(m) is called a "cycle." In a digraph, any vertex x which does not have any arc directed at it (i.e. there is no arc of the form yx) is called a "source vertex" and is defined to have "in-degree" equal to zero (x(2) is a source vertex in Figure 2d).

For a digraph D, the graph obtained from D by replacing each arc of the form xy by a corresponding edge xy is called the "underlying graph" of D (Figure 2a is the underlying graph of Figure 2c). Following Harary et al. (1965), a path in the underlying graph of a digraph D is called a "semipath" in D.

A graph G is "connected" if given any pair of vertices x and y of G, there is a path from x to y (Figures 2a and 2b are each connected, but the two taken together are not connected). A digraph is connected if its underlying graph is connected (Figure 2c is connected). A "separating set" of a connected (di)graph G is a set of vertices of G whose deletion disconnects G (x(1) is a separating set in Figures
The "connectivity" of a connected (di)graph is the size of the smallest separating set in G (thus Figures 2a-d each have a connectivity of 1).

A (di)graph G is "k-connected" if the connectivity of G is greater than or equal to k (Figures 2a-d are 1-connected, but not 2-connected). A digraph D is "strongly-connected" if for any two vertices x and y of D, there is a path from x to y (Figure 2e is strongly-connected, but Figures 2c and 2d are not). The "adjacency matrix" of a (di)graph G with n vertices is the n x n matrix A(G) in which each element a(i,j) is the number of edges (arcs) from vertex x(i) to vertex x(j). Figure 2g shows the adjacency matrix for Figure 2c.

Following Harary et al. (1965), the adjacency matrix formed according to the rules of Boolean algebra (i.e. a(i,j) = 1 if there exists an edge (arc) of the form x(i)x(j), otherwise a(i,j) = 0) is called the "Boolean adjacency matrix." (Changing a(1,3) to 1 in Figure 2g results in the Boolean adjacency matrix of Figure 1c.) Also, for a (di)graph G with n vertices, the Boolean sum of the powers one through n-1 of the Boolean adjacency matrix is called the "reachability matrix" of G. Figure 2h shows the reachability matrix for Figure 2c; note that vertex x(2) cannot be reached by any vertex except itself, while all
other vertices may be reached from any vertex.

To complete the set of graph-theoretic concepts to be used in this development, some additional terms need to be defined, although it may be noted that these terms bear a close relation to those already defined. A "source digraph" may be defined as a digraph containing at least one source vertex. A "complete source digraph" is a simple source digraph containing the maximum number of arcs possible given that the in-degree of all source vertices remains zero. A complete source digraph containing $m$ source vertices and $n$ non-source vertices will be denoted $K(m/n)$. A "strongly-connected source digraph" is a source digraph wherein there exists at least one path from each source vertex to each non-source vertex. (This modifies the definition of strong-connection for use with source digraphs, since under the standard definition no source digraph can be strongly-connected.)

A (di)graph $G$ is said to be "strongly $k$-connected" if for any two vertices $x(a)$ and $x(b)$ of $G$ and any $k-1$ vertices $[x(1), ..., x(k-1)]$ of $G$ such that all $x$'s are distinct, there exists a path from $x(a)$ to $x(b)$ which does not include any vertex $[x(1), ..., x(k-1)]$. A "strongly $k$-connected source digraph" is a source digraph which satisfies the definition for strong $k$-connection, subject to the
restrictions that \( x(a) \) be a source vertex and the other \( x \)'s be non-source vertices. This definition modifies the concept of strong \( k \)-connection for application to source digraphs in the same manner that the concept of strong-connection was modified for the same application.

Central to Levins' (1975) analysis is a graph-theoretic representation of system transformational behavior. Following Levins in principle, the following construction shall be employed: If a system's canonical representation is differentiable, the "digraph of the transformational behavior" may be defined by associating vertices with system variables on a one-to-one basis, and constructing arcs between each pair of vertices \((xy)\) according to whether the \( x \)th partial derivative of the \( y \)th equation in the canonical representation is non-zero. Such a digraph is shown for the system of Figure 1 in Figure 3a.

If the variables of the system's effective environment are added to the construction and interactions between environmental variables are ignored, the resulting digraph is called the "source digraph of the transformational behavior," since environmental variables will appear in the digraph only as source vertices. Such a digraph is shown for the system of Figure 1 in Figure 3b. One benefit of such a construction is increased visualizability of the
Figure 3. Digraphs for the system of Figure 1.

Figure 3a. Digraph for the system's state variables only. Each vertex in this digraph corresponds to a state variable in the system of Figure 1. Arcs are drawn according to the existence of non-zero cross-partial derivatives between state variables. Thus, since the partial derivative of the equation for $dx(1)/dt$ taken with respect to $x(3)$ is identically zero, no arc is drawn from $x(3)$ to $x(1)$ in the digraph. However, the partial derivative of the same equation taken with respect to $x(2)$ is not identically zero, so an arc is drawn from $x(2)$ to $x(1)$ in the digraph.

Figure 3b. Source digraph for the system. This digraph contains Figure 3a as a subgraph. The additional features of Figure 3b result from considering the environmental variables as well as the state variables. The arcs are constructed in the same manner as described above. For example, the partial derivative of the equation for $dx(1)/dt$ taken with respect to $b(1)$ is not identically zero, so an arc is drawn from $b(1)$ to $x(1)$. However, the partial derivative of the same equation taken with respect to $b(3)$ is identically zero, so no arc is drawn from $b(3)$ to $x(1)$.
Figure 3.
system/environment distinction. Once a system is defined on a digraph, its effective environment is graphically defined as the set of vertices which can be reached from the system by a semipath of length one but by no path.

It may be noted that this construction deviates from Levins' (1975) digraph in that Levins was also concerned with the sign(s) of the partial derivative(s), and only dealt with the derivative(s) at equilibrium. In context, the (source) digraph defined above will be referred to as the system's "(source) digraph," although it should be remembered that there are a number of possible digraphs which may be associated with any given system. For example, Klir (1969) uses a digraph to represent his concept of state-transition structure (resulting in a diagram equivalent to Ashby's (1956) "kinematic graph"), and Roberts (1976) develops a further modification of Levins' signed digraph.

Graph-Theoretic Analysis of Isocline Parameterization

Using these concepts, some theorems about the qualitative isocline behavior of systems may be formulated. One important aspect of the qualitative isocline behavior of systems has to do with the specific identities of the environmental parameters of a k-dimensional subsystem
isocline family. The following theorem addresses this issue:

Theorem #1: For a state variable $x$ and an environmental variable $y$, $x$'s $k$-dimensional subsystem isoclines in a specified $k$-dimensional phase space are parameterized by $y$ if and only if there is a path in the system's source digraph from $y$ to $x$ which does not involve any of the $k$ vertices dimensionalizing the specified phase space other than $x$ itself.

For example, this theorem may be used in conjunction with Figure 3b to determine which environmental variables should (and do) appear as parameters of the isoclines in Figure 2. For example, Theorem #1 can be used to test whether or not $b(2)$ should appear as a parameter of $x(1)$'s two-dimensional subsystem isoclines on the $[x(1),x(2)]$ phase plane. By Theorem #1, it should do so only if there is a path in Figure 3b from $b(2)$ to $x(1)$ which does not involve $x(2)$. As can readily be seen from inspection of Figure 3b, this is not the case. In other words, in order for $b(2)$ to affect $x(1)$, it must "go through" $x(2)$. Since $x(2)$'s non-reduced isocline cannot be used in the reduction of $x(1)$'s non-reduced isocline (by definition of subsystem isocline), $x(2)$ "cuts off" $b(2)$ from $x(1)$.
A similar argument may be followed to show in general why Theorem #1 should be true. The initial step in the step-wise reduction of a target variable's non-reduced isocline will not involve the non-reduced isoclines of any variables outside that set of state variables appearing as arguments in the target variable's non-reduced isocline. In fact, the reduction will involve only a subset of that set. This subset will exclude all variables dimensionalizing the specified phase space. The included variables can be identified in the system's source digraph as those with arcs running directly to the target vertex, excluding those vertices dimensionalizing the specified phase space.

The reduction, if it can proceed further, will do so by substituting into the non-reduced isoclines of this subset of variables the non-reduced isoclines of a second subset of variables. This second subset may be identified on the system's source digraph as those vertices with arcs running directly to members of the first subset of vertices, again excluding those dimensionalizing the specified phase space. This process is repeated until full reduction (within the limits prescribed by definition) is achieved. In terms of the system's source digraph, this means that it is impossible to "work backward" any further; the only vertices which can be reached by moving along an incoming arc are those representing variables which dimensionalize the
specified phase space.

Note that at no step may the vertices representing the variables dimensionalizing the specified phase space be traversed. If, however, the only way to reach a given source vertex in the system's source digraph is to traverse such a prohibited vertex, then the environmental variable represented by that source vertex cannot appear as an argument in the reduced form of the target variable's non-reduced isocline, which is precisely the content of Theorem #1.

Using these ideas, a different way of looking at subsystem isoclines may now be described. The k-dimensional subsystem isoclines of variable $x(i)$ may be thought of as $x(i)$'s one-dimensional system isoclines derived from a particular subgraph of the system's source digraph. The subgraph involved is that obtained by deleting all arcs terminating at any of the k dimensions in the specified phase space other than $x(i)$ itself. This increases the number of source vertices in the digraph by $k-1$.

Situations could be imagined, of course, in which a particular set of environmental variables parameterize all members of a particular set of k-dimensional subsystem isoclines. The following theorem states the conditions
under which that occurs:

Theorem #2: For any system's source digraph, if a subgraph thereof containing a set Y of source vertices and a set X of non-source vertices is a strongly k-connected source digraph, then all elements of Y parameterize the k-dimensional subsystem isoclines of any element of X in any k-dimensional subsystem phase space dimensionalized by elements of X.

This theorem follows directly from Theorem #1 and from the definitions of k-dimensional subsystem isocline and strongly k-connected source digraph. Its use may be illustrated by a simple example. Figure 4 shows a source digraph and a specified subgraph thereof. The source vertices contained in the subgraph are y(1) and y(2), and the non-source vertices contained in the subgraph are x(1), x(2), x(3), and x(4). This subgraph qualifies as a strongly three-connected source digraph (it may be noted, however, that it is not a strongly four-connected source digraph). Thus any non-source vertex x(i) may be reached from any source vertex without passing through any given set of two non-source vertices distinct from x(i). Therefore, given any set S of three state variables represented by vertices in this subgraph, the three-dimensional subsystem isoclines of any member of S will be parameterized by both y(1) and
Figure 4. Strongly two-connected source digraph. This is the digraph of a particular system containing six state variables \([x(1), \ldots, x(6)]\) and two environmental variables \((y(1)\) and \(y(2))\). The dashed lines demarcate a subgraph containing all of the system except for \(x(5)\) and \(x(6)\) (and any arcs involving those two vertices). The subgraph is a strongly three-connected source digraph, since any non-source vertex can be reached from any source vertex without going through any of the other three non-source vertices in the subgraph. The entire digraph (including vertices \(x(5)\) and \(x(6)\)) constitutes a strongly two-connected source digraph. That this source digraph is not strongly three-connected, however, may be proven by noting that neither \(x(5)\) nor \(x(6)\) can be reached by either source vertex \((y(1)\) or \(y(2))\) without going through either \(x(3)\) or \(x(4)\). It is thus possible to choose a set of three vertices (e.g. \([x(3), x(4), x(5)]\)) such that one element thereof cannot be reached by a source vertex without traversing another element of the set.
Figure 4.
Also, since any strongly \( k \)-connected source digraph is also a strongly \( j \)-connected source digraph for any positive integer \( j \) less than \( k \), it is also the case that the subgraph shown in Figure 4 is a strongly two-connected source digraph, in which case Theorem #2 can be used to talk about this subsystem's two-dimensional subsystem isoclines as well.

Theorem #2 can be extended to talk about the entire source digraph as well as some subgraph thereof, as is shown in the following theorem:

**Theorem #3:** If a system's source digraph is a strongly \( k \)-connected source digraph, then all environmental variables parameterize the \( k \)-dimensional subsystem isoclines of any state variable in any \( k \)-dimensional phase space.

This theorem is simply Theorem #2 rewritten to encompass the entire source digraph. Figure 4 can be seen to represent a strongly two-connected source digraph, (but not a strongly three-connected source digraph). Therefore, all environmental variables \([y(1)\text{ and } y(2)]\) parameterize the two-dimensional subsystem isoclines of any state variable \(x(1-6)\) in any phase plane.
A variety of source digraphs, of course, constitute strongly k-connected source digraphs. One important example is given in the following theorem:

Theorem #4: If D is a digraph with exactly m source vertices and n non-source vertices, and D contains K(m/n) as a subgraph, then D is a strongly n-connected source digraph.

This theorem follows from the definition of K(m/n), which requires in part that an arc exist from each source vertex to each non-source vertex. Therefore, a path always exists between each source vertex of K(m/n) and each non-source vertex such that no other vertex is traversed. This will also necessarily hold for any digraph obtained by adding arcs to K(m/n) which do not transform any source vertex into a non-source vertex. Thus, for any system whose source digraph is complete, all environmental variables parameterize all k-dimensional subsystem isoclines for all values of k from one to n.

Use of Isoclines in a Model of Ecological Hierarchy

A General Model of Hierarchy

As stated in a previous section, formal definitions of "hierarchy" have taken a variety of forms. Central to all
definitions is the idea of "levels," but beyond this consensus there is considerable disagreement, generally focusing on the nature of levels and the relationships between them. Specifically, six defining characteristics of hierarchy may be chosen from various definitions in the literature. These are listed and explained below; the explanations are of necessity somewhat informal, since to define the criteria precisely may commit one to a particular formal system which may in turn bias the explanation of the criteria being defined. Once a general understanding of these concepts is attained and a formal definition adopted, certain criteria will take on more precise meaning.

1) Control: the relationship between levels is one of domination or dynamic constraint, as opposed to, e.g. mere spatial position.

2) Nestedness: subsystems at a given level are controlled or spatially subsumed by one subsystem at the next higher level.

3) Time-frequency difference: lower levels in the hierarchy have a behavioral frequency distinct from (in fact, usually specified to be higher than) that of higher levels.
4) Intra-level interactions: pertaining to whether subsystems at a given level interact.

5) Feedback: the relationship between high and low levels is two-way, i.e. high levels may affect low levels and vice-versa.

6) Descriptive duality: distinction between levels requires different descriptions of the system's behavior.

The roles of these six criteria in a number of definitions of hierarchy are displayed in Table 1. The treatment by Warfield (1973) is significant in its explicit connection of hierarchy theory to graph theory. Having made the connection between isocline theory and graph theory in a previous section, it will prove prudent to utilize some of Warfield's terminology, although his definition of hierarchy per se will not be adopted without some modification.

Warfield's development uses the concepts of the adjacency and reachability matrices of a system. His treatment is somewhat more general than that adopted here, in that he only requires that some directional "relation" hold between vertices linked by an arc, as opposed to the more specific requirement that has been adopted in the present discussion of state-determined systems. Warfield
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<th>FEED</th>
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Table 1. Roles of six possible attributes in nine theories.

Symbols:
- CONT = control
- NEST = nestedness
- TIME = time-frequency difference
- INTR = intra-level interactions
- FEED = feedback
- DUAL = descriptive duality
- LEVL = levels
- Reqd = attribute required by this definition of hierarchy
- Alld = attribute allowed by this definition of hierarchy
- Excd = attribute excluded by this definition of hierarchy
notes that the adjacency or reachability matrix of a system may generally be written in a number of different ways, simply by changing the order of indexing. For example, the two matrices shown below represent the same system, differing only in the order of indexing:

\[
\begin{array}{cc}
A & B \\
A & 0 & 1 \\
B & 0 & 0 \\
\end{array}
\quad
\begin{array}{cc}
B & A \\
B & 0 & 0 \\
A & 1 & 0 \\
\end{array}
\]

where A and B represent two subsystems.

Keeping the requirement that column order of indexing must correspond to row order of indexing, there are \( n! \) different ways to write the reachability matrix for a system containing \( n \) subsystems.

The concept of a matrix "partitioning" is introduced as a device by which a matrix is divided geometrically into a number of "submatrices." The following matrix (1) has been partitioned into four submatrices:
1) \[
\begin{bmatrix}
A & B & C \\
A & 0 & 1 & 0 \\
B & 1 & 0 & 0 \\
C & 1 & 1 & 1 \\
\end{bmatrix},
\]

where the following are the submatrices:

\[
\begin{bmatrix}
A & B & C \\
A & 0 & 1 & A & 0 & C & 1 & 1 & C & 1 \\
B & 1 & 0 & B & 0 \\
\end{bmatrix}
\]

A matrix "condensation" consists of a matrix composed of elements which are in turn submatrices of a partitioned matrix. For example, let the following relationship hold:

\[
K = 0 & 1, L = 0, M = 1 & 1, N = 1. \\
1 & 0 & 0 \\
\]

Then the following matrix represents a particular condensation of matrix (1):

\[
K & L \\
M & N \\
\]

A "diagonal submatrix" is a square submatrix which
forms a diagonal element on the relevant condensation of the partitioned matrix. Thus, in the above example, K and N are diagonal submatrices.

Now, suppose that a particular system's reachability matrix may be transposed and written in a manner such that a partition may be made wherein only zeros obtain in all submatrices above the diagonal submatrices. The transposed reachability matrix is then said to be written in "block triangular" form. It may be noted that if the transposed reachability matrix of a system can be written in block triangular form, then its transposed adjacency matrix can be written in block triangular form as well.

These concepts from Warfield's (1973) theory provide the basis for the definition of hierarchy to be adopted here: A state-determined system is said to be a hierarchy if and only if the transpose of the reachability matrix corresponding to the system's digraph can be written in block triangular form.

This definition of hierarchy facilitates a straightforward definition of "level," again following Warfield: Suppose that a particular system's transposed reachability matrix can be written in block triangular form. Suppose that the matrix is then partitioned by creating the
smallest diagonal submatrices possible while preserving the criterion that only zeros obtain in all submatrices above the diagonal submatrices. It will be useful to define a "constituent" as the set of subsystems indexing a diagonal submatrix in such a partitioning. Now, the condensation of such a partitioned matrix can in turn be partitioned by creating the largest possible diagonal submatrices that contain only zeros as their off-diagonal elements. The set of subsystems indexing a diagonal submatrix resulting from such a partitioning defines a "level." For example, suppose the following matrix (2) represents a particular system's reachability matrix:

\[
\begin{array}{cccccc}
A & B & C & D & E & F \\
A & 0 & 1 & 0 & 0 & 0 & 0 \\
B & 1 & 0 & 0 & 0 & 0 & 0 \\
C & 1 & 1 & 0 & 1 & 0 & 0 \\
D & 1 & 1 & 1 & 0 & 0 & 0 \\
E & 1 & 1 & 0 & 0 & 0 & 1 \\
F & 1 & 1 & 0 & 0 & 1 & 0 \\
\end{array}
\]

This matrix may be partitioned constituent-wise as follows (note that this partitioning makes clear the fact that the matrix is written in block triangular form):
The constituents of the system are thus (A,B), (C,D), and (E,F). Let these be denoted X, Y, and Z, respectively, and let the following relationships hold:

\[
M = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}, 
N = \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}, 
O = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}
\]

The constituent-wise condensation of matrix (2) may now be written as follows:

(3) \[
\begin{array}{ccc}
M & O & O \\
N & M & O \\
N & O & M \\
\end{array}
\]

This matrix may then be partitioned level-wise as shown below:
The levels of the system are thus \((X)\) and \((Y,Z)\). Note that each level contains a whole number of constituents.

So far, then, three classes of subsystem have been defined: 1) levels, which are made up of whole numbers of 2) constituents, which are made up of whole numbers of 3) state variables, represented in the above example by \(A, B, C, D, E,\) and \(F\).

 Those definitions of hierarchy which adhere most closely to the historic usage of the term (e.g. Bunge 1969) generally require that the hierarchy be nested, either spatially or in terms of control (Table 1). In the terminology developed so far, this means that a constituent at a given level is entirely contained or controlled by a single constituent at the next level up. The nestedness criterion also implies that the system is only allowed to have a single constituent at the top level. A formal way of defining a nested hierarchy using the terminology developed here is as follows: A hierarchy is said to be "nested" if
and only if there is no more than one non-zero off-diagonal element in any row of the constituent-wise condensation of the hierarchy's transposed adjacency matrix, written in block triangular form. Or, more simply, a hierarchy is nested if and only if the in-degree of each constituent in the hierarchy's constituent-condensed digraph is equal to 1.

The first definition of nestedness (above) involves the system's adjacency matrix. Matrix (2), it may be remembered, represented the transposed reachability matrix of a particular system. Suppose that matrix (2) also happens to represent the same system's transposed adjacency matrix. It is then clear that the system in question is a nested hierarchy, since there is no more than one non-zero off-diagonal element in any row of matrix (3).

An example of a hierarchy which is not nested is easily described. Suppose that the following matrix [like matrix (2)] represents both the transposed reachability and adjacency matrices of a particular system:

\[
\begin{array}{ccc}
A & B & C \\
A & 0 & 0 & 0 \\
B & 0 & 0 & 0 \\
C & 1 & 1 & 0 .
\end{array}
\]
The constituent-wise partitioning of this matrix appears as follows:

\[
\begin{array}{ccc}
A & B & C \\
A & 0 & 0 & 0 \\
B & 0 & 0 & 0 \\
C & 1 & 1 & 0 \\
\end{array}
\]

The constituent-wise condensation will thus be identical to the original matrix, since each submatrix of the constituent-wise partitioning consists of exactly one element.

This system qualifies as a hierarchy because its transposed reachability matrix may be written in block triangular form, but it does not qualify as a nested hierarchy because there appear two "one's" in the third row of the above matrix, neither of which lies on the diagonal. In other words, C is subordinate to both constituents A and B at the upper level of this two-level hierarchy.

Recall that there is a one-to-one correspondence between an adjacency matrix and its associated digraph. That is, for any adjacency matrix there corresponds a unique
digraph, and for any digraph there corresponds a unique adjacency matrix. However, it is not generally true that a unique digraph corresponds to a given reachability matrix, although a unique reachability matrix always corresponds to a given digraph. It is clearest, then, to work from a digraph to its associated adjacency and reachability matrices, at which point it can be determined whether or not the system is a hierarchy, and if so, whether or not it is nested.

For example, the digraph shown in Figure 5a corresponds to the transposed reachability matrix (2). If boundaries are drawn around the subsystems corresponding to each of the three constituents, as in Figure 5b, it will be noted that no cycle exists which involves elements of different constituents (Warfield 1973). If the hierarchy is nested, then there will be arcs entering a constituent from no more than one other constituent. Such is the case for this system. Note also that inter-constituent arcs reflect difference in level. An inter-constituent arc means that the initial vertex is part of a higher level than that containing the terminal vertex.

In contrast, Figure 5c shows a digraph which has a transposed reachability matrix identical to matrix (4). Recall that each elementary subsystem is also a constituent
Figure 5. Digraphs of sample hierarchies.

Figure 5a. Digraph corresponding to reachability matrix (2). Vertices A and B form a constituent, as do vertices C and D, and vertices E and F. The (A,B) constituent forms its own level, while the (C,D) and (E,F) constituents constitute the lower level in this system.

Figure 5b. The same digraph, showing boundaries between constituents. Note that no cycle exists which involves elements of different constituents (although cycles may exist involving vertices within a constituent). This is a nested hierarchy, since neither lower-level constituent has arcs entering from more than one higher-level constituent, since the higher level consists of only a single constituent.

Figure 5c. Digraph corresponding to reachability matrix (4). This is a non-nested hierarchy, since the vertex representing the lower-level constituent (C) is entered by arcs originating in vertices representing two distinct higher-level constituents (A and B).
Figure 5.
in this system. It may be noted that C has arcs entering it from both constituents A and B, indicating again that this is not a nested hierarchy.

Having found that certain principles of graph theory form a common bond between a particular model of hierarchy on one hand and isocline theory on another, it is now possible to examine the implications of isocline theory for the proposed model of hierarchy. Recall by the adopted definition that a system's environment consists of those variables which can be reached from the system by a semipath but by no path. This poses an interesting question of definition in the case of hierarchies, namely that there are as many ways to draw the line between system and environment as there are levels in the hierarchy. In the example of Figure 5a, it is possible to consider the set \([C,D,E,F]\) as the system, and the set \([A,B]\) as the environment. Or, the set \([A,B,C,D,E,F]\) could be defined as the system of interest, with either no environment or some unshown quantities defined as the environment.

to phrase this concept is to say that what operates as the environment of a system from one perspective may function as a part of the system when viewed from another perspective. The idea of complementary definitions serving as the basis for a philosophy of biology is discussed by Levins and Lewontin (1980).

If such complementary system/environment distinctions are allowed, some useful implications arise regarding isocline analysis of hierarchies. One of the implications stems from the fact that the environment of any constituent can always be defined by a set of constituents at the next higher level. If the hierarchy is nested, the situation is simplified even further, in that this set will always consist of a single constituent. Also, if the variables of a constituent are maximally connected to their environment (subject to the system/environment distinction), then all subsystem isoclines in any phase space composed of variables in that constituent will be parameterized by all variables in the set of environmental constituents.

For example, in the case of Figure 5a, the subgraph corresponding to the (C,D) constituent is maximally connected to its one and only environmental constituent (A,B). Therefore, all subsystem isoclines in (C,D)-space will be parameterized by both A and B. An analogous
situation is found for the \((E,F)\) constituent.

Adapting the Model to Ecosystems

In ecosystem classification, ecosystem organization is often viewed (informally) as a spatially-nested hierarchy, as in the classifications of Bailey (1976) and Warren (1979, Gregor 1982). Figure 6 represents an idealized system organized in a spatially-nested fashion. Each square in Figure 6 is intended to represent one constituent. In this system there are four levels, with a single constituent at level one, and each constituent at levels one through three consisting of four constituents at the next level down. Thus there are four constituents at level two, 16 constituents at level three, and 64 constituents at level four. The constituents at each level are numbered in reading order and according to their incorporating constituent at the next level up (the "constraining constituent").

In order to standardize notation, the following conventions will be observed: a subsystem \(X\) of constituent \(K\) at level \(L\) will be denoted \(X(L,K)\). If \(X\) itself is a constituent, it will be denoted by a "C," e.g. \(C(2,1)\) denotes constituent 1 at level 2.
Figure 6. Spatially-nested hierarchy. The hierarchy depicted in this figure consists of a total of four levels, with one constituent at level one, four at level two, 16 at level three, and 64 at level four. Each constituent at a given level consists of four constituents at the next lower level. The constituents at each level are numbered in reading order and according to their constraining constituent; e.g. the four level-three constituents constrained by constituent number one at level two are numbered one through four in reading order.
Figure 6.
To confirm that the system of Figure 6 is a hierarchy, it may be observed from Table 2 that the transposed reachability matrix of this system may be written in block triangular form. It will be noted that Figure 6 only shows constituents, not the variables that make up those constituents. Using Bailey's (1976) terminology, the constituent at level one might correspond to a division, a constituent at level two might correspond to a province, a constituent at level three might correspond to a section, and a constituent at level four might correspond to district. While Bailey's method provides a neat breakdown of ecosystems in physical space, it does not speak to ecosystem components that express themselves throughout a physical area. In contrast, Gregor (1982) decomposes ecosystems into a set of five subsystems: climate, culture, substrate, water, and biota. These subsystems may be expressed at any level of Bailey's hierarchy; i.e. it may be possible to identify climate, culture, substrate, water, and biota at the division level, at the province level, or at any other level in the spatial hierarchy.

Note that by declaring each square in Figure 6 to represent one constituent, it is implicitly stated that any subsystem represented by a square does not interact with neighbor subsystems except to the extent that each neighbor subsystem forms part of that subsystem's environment at a
Table 2. Transposed reachability matrix for system of Figure 6. The dots running diagonally down the lower right portion of the table represent 1's along the main diagonal. All elements of the matrix not filled in by 1's are implicitly filled by 0's. Since no 1's appear above the diagonal, this matrix is in block triangular form, meaning that the system of Figure 6 qualifies as a hierarchy. The lack of any 0's in the column indexed by C(1,1) means that C(1,1) incorporates or affects all other constituents. Likewise, examining the column indexed by C(2,1) reveals that C(2,1) incorporates or affects C(3,1-4) and C(4,1-16). See Figure 6 for comparison.
higher level. However, no restriction is placed on the extent to which subsystems below the constituent level interact. In Gregor's (1982) scheme, the five subsystems (climate, culture, substrate, water, and biota) are fully interconnected, i.e. the corresponding digraph contains $K(5)$ as a subgraph. Such a scheme would be fully consistent with the type of organization depicted in Figure 6.

To simplify matters for the present, however, Gregor's scheme will be collapsed into two dimensions: 1) habitat (representing the equivalent of climate, culture, substrate, and water), and 2) biota. The digraph of this system will be drawn as $K(2)$ with unit-length cycles at both vertices. Furthermore, it will be assumed that each variable at a given level reacts with all (in this case both) of the variables in its environment. This represents a generalization of Gregor's model, which placed some restrictions on system/environment interaction.

This arrangement may be symbolized by Figure 7. In this figure, there is an environment at level zero $[E(0,1)]$ constraining a level-one biotic subsystem $[B(1,1)]$ and habitat subsystem $[H(1,1)]$. In turn, part of each $[B(1,1)$ and $H(1,1)]$ becomes a subsystem at level two $[B(2,1)$ and $H(2,1)$, respectively]. These subsystems are constrained by an environment $[E(1,1)]$ consisting of the entire system at
Figure 7. A view of ecological hierarchy. Here, an ecosystem is depicted as a nested hierarchy. At a given level, the ecosystem consists of a single constituent consisting of biotic and habitat subsystems, constrained by the state of the entire system at the next higher level (the environment). In turn, a portion of each subsystem (biota and habitat) constitutes a particular subsystem at the next lower level. Thus, a portion of $B(1,1)$ becomes $B(2,1)$, and a portion of $H(1,1)$ becomes $H(2,1)$. This pair of level-two subsystems form a constituent at that level ($C(2,1)$). This constituent is then constrained by the state of the system at level one ($C(1,1)$). Likewise, a portion of $B(2,1)$ becomes $B(3,1)$, a portion of $H(2,1)$ becomes $H(3,1)$, and so on.
Figure 7.
level one \([B(1,1) \text{ and } H(1,1)]\). Similarly, \(B(2,1) \text{ and } H(2,1)\) join together to act as \(E(2,1)\), with part of each becoming \(B(3,1)\) and \(H(3,1)\). This procedure is repeated once again for level four.

Since the source digraph of any constituent contains \(K(2/2)\) as a subgraph (remembering that by convention any constituent may be considered as a target system), both subsystem isoclines are parameterized by both environmental variables on all phase planes. In general, the number of constituents represented by the environmental variables of a particular (lower level) constituent depends on whether or not the hierarchy in question is nested. Table 3 shows the constituent-wise reduction of the transposed adjacency matrix corresponding to the system of Figure 6. It may be noted that since there is no more than one non-zero off-diagonal element in any row therein, the system of Figure 6 is nested. Therefore, the environmental variables of any constituent will be found in a single constituent at the next level up. So, on any \([H(L,K),B(L,K)]\) phase plane, all subsystem isoclines will be parameterized by the environmental variable set \([H(L-1,K*),B(L-1,K*)]\), where \(K*\) is the index of the constraining constituent. For the system of Figure 6, \(K* = (\text{int}[((K-1)/4)]+1\).

The canonical representation of a constituent
Table 3. Constituent-wise reduction of transposed adjacency matrix corresponding to Figure 6. This matrix shows which constituents directly incorporate or affect other constituents. For example, $C(1,1)$ directly incorporates (affects) all four level-two constituents. Likewise, $C(2,1)$ directly incorporates (affects) $C(3,1-4)$, and $C(3,1)$ directly incorporates (affects) $C(4,1-4)$. 
Table 3.
subsystem's transformational behavior takes the following form:

\[
\begin{align*}
\frac{dB(L,K)}{dt} &= b(L,K)[B(L,K),H(L,K),B(L-1,K^*),H(L-1,K^*)] \\
\frac{dH(L,K)}{dt} &= h(L,K)[B(L,K),H(L,K),B(L-1,K^*),H(L-1,K^*)],
\end{align*}
\]

where \(b(L,K)\) and \(h(L,K)\) are level- and constituent-specific functions.

Specific equations may now be inserted in place of the generic functions above. All constituent subsystems of Figure 6 will be assumed to have canonical representations which display asymptotically stable steady states. Table 4 gives the canonical representation of \(C(1-4,1)\). Note that the equations for \(C(1,1)\) include terms for \(C(0,1)\). These are included to imply that the level one system has an environment as well, which will be referred to here as the level zero system or "ultimate environment."

These equations can be solved to generate the two-dimensional isocline families in \([H(L,1),B(L,1)]\)-space. Sample isoclines are shown in Figure 8. The multiple steady state behavior of the system may be illustrated by tracing through the steady states corresponding to given conditions in the ultimate environment. Note, for example, that fixing the state of the ultimate environment at a value
\[
\left[ \frac{dH(1,1)}{dt} \right] = \begin{bmatrix} 2.00 & -1.00 \\ 2.00 & -2.00 \end{bmatrix} \left[ H(1,1) \right] + \begin{bmatrix} 1.25 & 1.75 \\ 1.00 & 1.00 \end{bmatrix} \left[ H(0,1) \right]
\]

\[
\left[ \frac{dB(1,1)}{dt} \right] = \begin{bmatrix} 1.00 & -2.00 \\ 2.00 & -3.00 \end{bmatrix} \left[ B(1,1) \right] + \begin{bmatrix} 0.75 & 0.50 \\ 1.50 & 1.25 \end{bmatrix} \left[ B(0,1) \right]
\]

\[
\left[ \frac{dH(2,1)}{dt} \right] = \begin{bmatrix} -1.00 & -0.25 \\ 2.00 & -3.00 \end{bmatrix} \left[ H(2,1) \right] + \begin{bmatrix} 0.75 & 0.50 \\ 1.50 & 1.25 \end{bmatrix} \left[ H(1,1) \right]
\]

\[
\left[ \frac{dB(2,1)}{dt} \right] = \begin{bmatrix} -2.50 & -0.50 \\ 0.50 & -4.00 \end{bmatrix} \left[ B(2,1) \right] + \begin{bmatrix} 0.75 & 0.50 \\ 1.50 & 1.25 \end{bmatrix} \left[ B(1,1) \right]
\]

\[
\left[ \frac{dH(3,1)}{dt} \right] = \begin{bmatrix} -2.50 & -0.50 \\ 0.50 & -4.00 \end{bmatrix} \left[ H(3,1) \right] + \begin{bmatrix} 2.00 & 2.00 \\ 1.00 & 0.50 \end{bmatrix} \left[ H(2,1) \right]
\]

\[
\left[ \frac{dB(3,1)}{dt} \right] = \begin{bmatrix} -3.00 & -0.50 \\ 1.00 & -3.50 \end{bmatrix} \left[ B(3,1) \right] + \begin{bmatrix} 2.50 & 2.00 \\ 0.50 & 1.00 \end{bmatrix} \left[ B(2,1) \right]
\]

Table 4. Transformational behavior of C(1,1), C(2,1), C(3,1), and C(4,1).
Figure 8. Isocline behavior for the system of Table 4. The states of H(0,1) and B(0,1) (the ultimate environment) determine the steady states of all lower-level subsystems.

Figure 8a. [H(1,1),B(1,1)] phase plane. Fixing the state of the ultimate environment [H(0,1),B(0,1)] at a level of (5,3) sets the steady state of the [H(1,1),B(1,1)] subsystem at a value of (2.5,6.5), indicated by the solid circle in the figure. If the state of the ultimate environment were different, however, the implied steady state of the [H(1,1),B(1,1)] subsystem would be different as well. For example, if the ultimate environment were fixed at a level of (1,3), the steady state point on this phase plane would be moved to the location marked by the solid square (1.5,3.5).

Figure 8b. The [H(2,1),B(2,1)] phase plane. The isoclines on this phase plane are parameterized by states of the variables in the constraining constituent: H(1,1) and B(1,1). The steady state associated with the circle in Figure 8b corresponds to an H(1,1) value of 2.5 and a B(1,1) value of 6.5. The steady state on this phase plane is thus located at the intersection of the isoclines parameterized by H(1,1) = 2.5 and B(1,1) = 6.5. This point is marked by the solid circle in this figure, and is located at (3.55,6.32). However, if the constraining constituent were moving toward the steady state associated with the square in Figure 8a, the steady state implied for the level-two subsystem would be different, corresponding instead to the point marked by the square (1.99,3.54). This point is located at the intersection of the isoclines parameterized by the steady state associated with the square in Figure 8a (H(1,1) = 1.5, B(1,1) = 3.5).

Figure 8c. The [H(3,1),B(3,1)] phase plane. This phase plane is the level-three analogue of Figure 8b. Just as the C(1,1) steady state parameterized the steady state of the level-two subsystems, so the level-two subsystems parameterize the steady state of the level-three subsystems. Thus, the steady-state values of H(2,1) and B(2,1) associated with the circle and square in Figure 8b parameterize the steady-state values of H(3,1) and B(3,1) associated with the circle and square in this figure.

Figure 8d. The [H(4,1),B(4,1)] phase plane. This is the level-four projection of the overall system steady state implied by fixing the ultimate environment at the two values described in Figure 8a. The steady states associated with the circle and square in this figure correspond to the steady states parameterized by the same symbols in the other three phase planes.
Figure 8.
of (5,3) fixes the steady state of the level one constituent at a value of (2.5,6.5) (circle in Figure 8a). Moving to Figure 8b, the two-dimensional system isoclines in $[H(2,1),B(2,1)]$-space are parameterized by $B(1,1)$ and $H(1,1)$. The circle in Figure 8b is the steady state resulting from fixing the value of the $[H(1,1),B(1,1)]$ constituent at (2.5,6.5). The value of this steady state is (3.55,6.32). This point (circle, Figure 8b) is the projection into $[H(2,1),B(2,1)]$-space of the same steady state represented by the circle in Figure 8a.

In Figure 8c, the two-dimensional system isoclines in $[H(3,1),B(3,1)]$-space are parameterized by $B(2,1)$ and $H(2,1)$. The circle in Figure 8c is the steady state resulting from fixing the value of $[H(2,1),B(2,1)]$ at (3.55,6.32). The value of this steady state is (7.38,2.60). Again, this steady state is the projection into $[H(3,1),B(3,1)]$-space of the same steady state represented by the circles in Figures 8a and 8b. Finally, Figure 8d shows some two-dimensional system isoclines in $[H(4,1),B(4,1)]$-space. The isoclines on this phase plane are parameterized by $H(3,1)$ and $B(3,1)$. The circle represents the steady state generated by holding $H(3,1)$ and $B(3,1)$ at values of 7.38 and 2.60, respectively. This point, then, is the projection into $[H(4,1),B(4,1)]$-space of the same steady state represented by the circles in Figures
8a, 8b, and 8c.

Of course, any set of values for \( H(0,1) \) and \( B(0,1) \) could have been selected for the state of the ultimate environment. Instead of \( (5,3) \), the value which generated the steady state represented by the circles in Figure 4, the value \( (1,3) \) could have been chosen. This value would result in a steady state in \([H(1,1),B(1,1)]\)-space of \( (1.5,3.5) \), represented by the square in Figure 8a. The corresponding steady states in \([H(2,1),B(2,1)]\)-, \([H(3,1),B(3,1)]\)-, and \([H(4,1),B(4,1)]\)-space are represented by the squares in Figures 8b, 8c, and 8d, respectively. As with the steady states represented by the circles, the steady states denoted by the squares are each different projections of the same co-determined steady state.

Given that ecosystems can be talked about as though they behaved like state-determined systems, it must surely be fair to state that the transformational behavior of ecosystems is constantly changing. Thus, at any given instant, the system has a particular transformational behavior, and therefore a particular implicit isocline behavior. For example, in the system of Table 4, one could imagine that the coefficients of the canonical representation were themselves linear functions of time. Such a possibility is realized in Table 5. Note that the
\[
\begin{align*}
\frac{dH(1,1)}{dt} &= \begin{bmatrix} 2.00-1.50t & -1.00-1.00t \\ 2.00+1.50t & -2.00-2.00t \end{bmatrix} \begin{bmatrix} H(1,1) \\ B(1,1) \end{bmatrix} + \\
\frac{dB(1,1)}{dt} &= \begin{bmatrix} 1.25+1.25t & 1.75+1.75t \\ 1.00+1.00t & 1.00+1.00t \end{bmatrix} \begin{bmatrix} H(0,1) \\ B(0,1) \end{bmatrix} \\
\frac{dH(2,1)}{dt} &= \begin{bmatrix} 1.00-2.00t & -0.25-0.25t \\ 2.00+1.00t & -3.00-2.00t \end{bmatrix} \begin{bmatrix} H(2,1) \\ B(2,1) \end{bmatrix} + \\
\frac{dB(2,1)}{dt} &= \begin{bmatrix} 0.75+0.50t & 0.50+1.00t \\ 1.50+1.25t & 1.25+1.50t \end{bmatrix} \begin{bmatrix} H(1,1) \\ B(1,1) \end{bmatrix} \\
\frac{dH(3,1)}{dt} &= \begin{bmatrix} 2.50-2.50t & -0.50-1.00t \\ 0.50+0.50t & -4.00-3.00t \end{bmatrix} \begin{bmatrix} H(3,1) \\ B(3,1) \end{bmatrix} + \\
\frac{dB(3,1)}{dt} &= \begin{bmatrix} 2.00+1.50t & 2.00+2.50t \\ 1.00+0.50t & 0.50+0.50t \end{bmatrix} \begin{bmatrix} H(2,1) \\ B(2,1) \end{bmatrix} \\
\frac{dH(4,1)}{dt} &= \begin{bmatrix} 3.00-2.50t & -0.50-0.50t \\ 1.00+1.00t & -3.50-4.00t \end{bmatrix} \begin{bmatrix} H(4,1) \\ B(4,1) \end{bmatrix} + \\
\frac{dB(4,1)}{dt} &= \begin{bmatrix} 2.50+2.00t & 2.00+1.50t \\ 0.50+1.00t & 1.00+0.50t \end{bmatrix} \begin{bmatrix} H(3,1) \\ B(3,1) \end{bmatrix}
\end{align*}
\]

Table 5. Time-dependent transformational behavior of C(1,1), C(2,1), C(3,1), and C(4,1). The elements of the coefficient matrices are functions of time. The equations of Table 4 obtain when t = 0.
equations of Table 4 obtain when \( t = 0 \). For the system of Table 5, a different isocline behavior is implied at every value of \( t \). Sample isoclines are shown in Figure 9 for two values of \( t \), namely zero and the limit as \( t \) approaches infinity.

In Figure 9a, the point denoted by the open circle corresponds to the same steady state denoted by the circle in Figure 8a, in which the state of the ultimate environment is fixed at \((5,3)\) and the \([H(1,1),B(1,1)]\) system moves toward \((2.5,6.5)\). Moving through time, one would expect the state of the ultimate environment to change. However, even if it did not, Figure 9a shows how the implied steady state of the \([H(1,1),B(1,1)]\) system would change through time, converging on a value of \((3.33,6.5)\) as \( t \) approached infinity (solid circle, Figure 9).

From the perspective of the \([H(2,1),B(2,1)]\) system, two things are happening. First, the environment is changing from an implied steady state of \((2.5,6.5)\) to an implied steady state of \((3.33,6.5)\). Second, its own transformational behavior is changing as a function of time. Thus the shift in the system's implied steady state is due to two factors. If only the first factor obtained, i.e. if the situation involved only a change in environment with no change in transformational behavior, then the steady state
Figure 9. Isocline behavior for system of Table 5. When the transformational behavior of the system is itself a function of time, the system's isoclines also become functions of time. The intersections of isocline pairs then represent only implied steady states, i.e. the steady states that would obtain were the system's transformational behavior to remain constant.

Figure 9a. \([H(1,1), B(1,1)]\) phase plane. The state of the ultimate environment \([H(0,1), B(0,1)]\) is fixed at a value of \((5,3)\). At \(t = 0\), the transformational behavior implies a pair of isoclines intersecting at the point associated with the solid circle \((2.5, 6.5)\). However, since the transformational behavior of the system changes with time, so do the implied isoclines and steady states. Under the equations given in Table 5, the isoclines converge on a limit as \(t\) approaches infinity. The isocline pair for \(H(0,1) = 5\) and \(B(0,1) = 3\) is shown in the figure. The open circle indicates the steady-state point at the intersection of these isoclines.

Figure 9b. \([H(2,1), B(2,1)]\) phase plane. This figure indicates the combined effects on \(C(2,1)\) steady-state behavior resulting from changing environmental conditions combined with changing transformational behavior. The point marked by the solid circle in this figure corresponds to the steady state implied by the transformational behavior at \(t = 0\). Because of changing transformational behavior at level one, however, the environment of \(C(2,1)\) will not remain at the levels which parameterize this steady state. Instead, \(C(2,1)\)'s environment will move toward a value of \((3.33, 6.5)\). Given this environment, the transformational behavior of \(C(2,1)\) at \(t = 0\) would imply a steady state at the point marked by the cross-hatched circle in this figure. However, the transformational behavior of \(C(2,1)\) is also changing, causing the steady state parameterized by \(H(1,1) = 3.33\) and \(B(1,1) = 6.5\) to converge on the point marked by the open circle in this figure as \(t\) approaches infinity.

Figure 9c. \([H(3,1), B(3,1)]\) phase plane. This figure is the level three analogue of Figure 9b. The solid circle marks the steady state implied by \(C(3,1)\)'s transformational behavior at \(t = 0\). The cross-hatched circle marks the steady state implied by the environment resulting from the change in \(C(1,1)\)'s transformational behavior. The open circle marks the steady-state limit implied by the changes in the transformational behaviors of both \(C(1,1)\) and \(C(2,1)\) as \(t\) approaches infinity.

Figure 9d. \([H(4,1), B(4,1)]\) phase plane. Analogous to Figures 9b and 9c.
Figure 9.
would shift in Figure 9b from the point denoted by the open circle to that denoted by the cross-hatched circle [where the isoclines parameterized by \( H(1,1) = 3.33 \) and \( B(1,1) = 6.5 \) cross]. However, the transformational behavior of the \([H(2,1),B(2,1)]\) system is changing as well, so as time approaches infinity, the steady state for this set of environmental conditions will converge on the point associated with the solid circle \((3.02,8.47)\).

Likewise, from the perspective of the \([H(3,1),B(3,1)]\) system, the implied steady state shifts due to both a change in environment and a change in transformational behavior. The open circle in Figure 9c represents the same steady state as that in Figure 8c. The cross-hatched circle represents the steady state that would obtain if all that were involved were a shift in environment from the open circle to the cross-hatched in Figure 9b. The solid circle represents the steady state upon which the system will tend to converge given this environmental shift and the change in transformational behavior described in Table 5. The point denoted by the solid circle represents the projection into \([H(3,1),B(3,1)\]-space of the same steady state denoted by the solid circles in Figures 9a and 9b. An analogous projection is shown in Figure 9d for the \([H(4,1),B(4,1)]\) system.
The isocline behavior of the systems of Tables 4 and 5 illustrates an important point: Even when transformational behavior is held constant, a change in environment may cause a system's trajectory through phase space to display no understandable pattern independent of that change in environment. The complexity of the situation increases dramatically when the system not only pursues a changing steady state through phase space, but pursues it according to changing rules of behavior.

So far, isocline analysis of the system of Figure 6 has been limited to four constituents, namely C(1,1), C(2,1), C(3,1), and C(4,1). If these were the only constituents in the hierarchy, they would be an example of a particular type of hierarchy which may be usefully termed "lineal." Following Rescigno and Segre (1964), let a lineal hierarchy be defined in the following manner: A hierarchy is said to be lineal if and only if the number of levels in the hierarchy is equal to the number of constituents in the hierarchy. Such a hierarchy is said to be lineal because it is possible to construct the hierarchy's digraph so that each vertex is associated with a constituent, all the vertices fall along a straight line, and each arc takes the form of a straight line as well.

It may be noted that all lineal hierarchies are nested,
but not all nested hierarchies are lineal. Obviously, the full system represented by Figure 6 does not qualify as a lineal hierarchy, although it is nested. There are only four levels in the hierarchy of Figure 6, although there are 85 constituents. To analyze the isocline behavior of this system in a manner such that each constituent's behavior were illustrated on its own unique phase plane would require 85 phase planes.

The difficulty of truly understanding a set of 85 phase planes would be enormous. However, it is possible to devise a methodology whereby the number of entities required to fully represent the system's isocline behavior is considerably reduced. The method can be illustrated by constructing what will be termed "composite equilibrium loci." This may be accomplished by a graphical technique which constructs loci from the intersections of appropriate pairs of two-dimensional system isoclines, where the intersections to be connected will involve isoclines of different constituents.

The constituents C(2,1), C(2,2), C(2,3), and C(2,4) of Figure 6 will be used to generate an example. The transformational behavior of each of these constituents is given in canonical form in Table 6. It may be noted that these four constituents are all constrained by the same
Table 6. Transformational behavior for C(2,1-4). The equation for C(2,1) is the same as the C(2,1) equation in Table 4.
environmental constituent, C(1,1). By setting the values of H(1,1) and B(1,1) equal to some pair of constants, two-dimensional system isoclines may be determined for the habitat and biota subsystems of each of the level-two constituents [C(2,1), C(2,2), C(2,3), C(2,4)]. Superimposing these isoclines onto a single phase diagram results in a display of four pairs of intersecting isoclines, with each pair parameterized by the same values of H(1,1) and B(1,1), but corresponding to a different level-two constituent. Connecting the four intersections by a single curve yields the composite equilibrium locus for those four constituents under that particular set of environmental conditions. Two such loci and their underlying two-dimensional system isoclines are depicted in Figure 10.

The dashed lines in Figure 10 represent two-dimensional system isoclines for each of the four level-two constituents under consideration. Four of these lines are isoclines parameterized by B(1,1) = 3 (one for each of the four constituent subsystems). There are also four isoclines parameterized by H(1,1) = 5. The two solid lines represent general equilibrium loci, one of which is parameterized by C(1,1) = (5,3). This general equilibrium locus incorporates the steady states of each of the four target constituents for an environmental [H(1,1),B(1,1)] value of (5,3), and is
Figure 10. Composite equilibrium locus construction. Composite equilibrium loci are constructed for level two of this system by connecting steady-state points of commonly-constrained constituents \([C(2,1), C(2,2), C(2,3),\text{ and } C(2,4)]\). Two-dimensional system isoclines are represented for each of these four constituents by the dashed lines. Isoclines are shown for \(B(1,1) = 5\), and for two different values of \(H(1,1) (3 \text{ and } 5)\), resulting in a total of 12 isoclines defining eight steady states (two for each constituent). Connecting appropriate steady states results in a composite equilibrium locus. For example, the locus parameterized by \(H(1,1) = 5\) and \(B(1,1) = 3\) is constructed by connecting the four level-two steady states parameterized by those values. The locus parameterized by \(H(1,1) = 3\) and \(B(1,1) = 3\) is likewise constructed by connecting the four level-two steady states so parameterized.
Figure 10.
constructed simply by connecting those steady states with a curve.

Also shown in Figure 10 is the construction of the (3,3) general equilibrium locus. It connects the intersections of the four pairs of two-dimensional system isoclines parameterized by \( H(1,1) = 3 \) and \( B(1,1) = 3 \). This locus summarizes the steady-state values of the four target constituents under environmental values of \( H(1,1) = 3 \) and \( B(1,1) = 3 \).

Since intersecting subsystem isoclines and intersecting system isoclines in general define the same steady state, it is true that a general equilibrium locus may be defined by intersecting subsystem isoclines as well as by intersecting system isoclines. The utility of employing system isoclines over subsystem isoclines becomes apparent, however, when comparing composite equilibrium loci parameterized by partially similar environmental conditions, as is the case in Figure 10. Here, the only difference in parameterization between the two composite equilibrium loci is that one is parameterized by \( H(1,1) = 5 \) and the other is parameterized by \( H(1,1) = 3 \); both are parameterized by \( B(1,1) = 3 \).

The graphical relationship between the two loci becomes clear as it is noted that they are both formed by connecting
intersections of $H(1,1)$ system isoclines with the same set of four $B(1,1)$ system isoclines, namely those parameterized by $B(1,1) = 3$. Were the general equilibrium loci to have been constructed from subsystem isoclines instead of system isoclines, sixteen dashed lines would have appeared in Figure 10 instead of twelve (a unique pair for each constituent under each set of environmental conditions), and there would have been no graphical connection between the two composite equilibrium loci.

The utility of the composite equilibrium locus lies largely in that it reduces the dimensionality of the isocline behavior of the system, thus increasing its tractability. The key here is that while formerly there were four entities to keep track of in the example of Figure 10 (the four steady states of each of the four constituents), with the construction of the composite equilibrium locus there is only one (a single steady-state curve). The abstraction involved in constructing the composite equilibrium locus both unifies and simplifies the steady-state behavior of the hierarchy. In a very rich sense, the family of composite equilibrium loci captures the organization of the hierarchy at the next level up.

In a nested hierarchy, the state of a constraining constituent will appear as the sole parameter of the
Figure 11. Composite equilibrium loci for levels two through four.

Figure 11a. Composite equilibrium loci for level two. The two loci constructed in Figure 10 are reproduced here, along with loci parameterized by \( [2.5H(1,1), 6.5B(1,1)] \) (solid circle) and by \( [1.5H(1,1), 3.5B(1,1)] \) (solid square). The latter two loci correspond to the steady states that obtain in Figure 8; i.e. the point labeled #1 on the locus marked by the solid circle is the same point marked by the solid circle on the phase plane for \( C(2,1) \) (Figure 8b). In addition, the parameterizing values of this locus are those that obtain in Figure 8a (circle) when \( H(0,1) = 5 \) and \( B(0,1) = 3 \). However, the points labeled #2, #3, and #4 have no counterparts in Figure 8, since each phase plane in Figure 8 represents the behavior of only a single \( (K=1) \) constituent.

Figure 11b. Composite equilibrium loci for level three. The loci marked by the square and circle have corresponding steady states in Figure 8. The parameterizing values of these loci are those that obtain for \( C(2,1) \) in Figure 8b (square and circle, respectively). Also, the points labeled #1 on these two loci are the same steady states marked by the square and circle in Figure 8c.

Figure 11c. Composite equilibrium loci for level four. The loci marked by the square and circle are the level-four analogues of the similarly labeled loci in Figures 11a and 11b.
Figure 11.
composite equilibrium locus of those constituents which it (uniquely) constrains. Figure 11 illustrates this principle. In Figure 11a, the two composite equilibrium loci shown in Figure 10 ((5,3) and (3,3)) are reproduced as references, and two additional loci are shown as well: (2.5,6,5) and (1.5,3.5) (circle and square, respectively). These loci are positioned in phase space according to the state of the constraining constituent, namely C(1,1).

The values parameterizing these two loci, as well as their reference symbols, were purposely chosen to correspond to the values and symbols of Figure 8. Thus, when the state of the ultimate environment \( [H(0,1), B(0,1)] \) is fixed at (5,3), C(1,1) moves toward a steady state of (2.5,6.5), as shown in Figure 8a. This in turn causes the constituents constrained by C(1,1) [i.e. C(2,1), C(2,2), C(3,2), and C(4,2)] to move toward steady states located along the composite equilibrium locus in Figure 11a parameterized by \( H(1,1) = 2.5 \) and \( B(1,1) = 6.5 \) (circle, Figure 11a). As confirmation, it may be noted that the point labeled K=1 on this locus corresponds to the point identified by the circle in Figure 11b, the steady state for C(2,1).

Alternatively, if the state of the ultimate environment were fixed at \( H(0,1) = 1 \) and \( B(0,1) = 3 \), C(1,1) would move toward a steady state of (1.5,3.5) (square, Figure 8a).
This, in turn, implies that the constituents constrained by C(1,1) will come to steady state along the composite equilibrium locus in Figure 11a parameterized by H(1,1) = 1.5 and B(1,1) = 3.5 (square, Figure 11a). It may be noted that the point labeled K=1 on this locus is the same as that identified by the square in Figure 8b.

Just as C(1,1) constrains C(2,1), C(2,2), C(2,3), and C(2,4), so C(2,1) constrains C(3,1), C(3,2), C(3,3), and C(3,4). Table 7 shows the transformational behavior of each of these constituents in canonical form. Operating in a manner analogous to that used to derive composite equilibrium loci for Figures 10 and 11a, composite equilibrium loci may be generated for the constituents constrained by C(2,1). Samples of such loci are shown in Figure 11b. The locus denoted by the circle is parameterized by H(2,1) = 3.55 and B(2,1) = 6.32, and is the composite equilibrium locus which obtains when C(2,1) reaches the steady state identified by the circle in Figure 8b. The point labeled K=1 on this locus is the same point denoted by the circle in Figure 8c. The locus labeled with the square in Figure 11b is parameterized by H(2,1) = 1.99 and B(2,1) = 3.54. These are the values of H(2,1) and B(2,1) which obtain when the ultimate environment is set at values of H(0,1) and B(0,1) equal to 1 and 3, respectively. The point labeled K=1 on this locus corresponds to the point
\[ \begin{align*}
\frac{dH(3,1)}{dt} &= \begin{bmatrix} -2.50 & -0.50 \\ 0.50 & -4.00 \end{bmatrix} H(3,1) + \begin{bmatrix} 2.00 & 2.00 \end{bmatrix} B(2,1) \\
\frac{dB(3,1)}{dt} &= \begin{bmatrix} -2.50 & -0.50 \\ 0.50 & -4.00 \end{bmatrix} B(3,1) + \begin{bmatrix} 1.00 & 0.50 \end{bmatrix} B(2,1) \\
\frac{dH(3,2)}{dt} &= \begin{bmatrix} -3.50 & -0.50 \\ 1.50 & -5.00 \end{bmatrix} H(3,2) + \begin{bmatrix} 3.00 & 3.00 \end{bmatrix} B(2,1) \\
\frac{dB(3,2)}{dt} &= \begin{bmatrix} -3.50 & -0.50 \\ 1.50 & -5.00 \end{bmatrix} B(3,2) + \begin{bmatrix} 1.50 & 0.50 \end{bmatrix} B(2,1) \\
\frac{dH(3,3)}{dt} &= \begin{bmatrix} -4.50 & -0.50 \\ 2.50 & -6.00 \end{bmatrix} H(3,3) + \begin{bmatrix} 4.00 & 4.00 \end{bmatrix} B(2,1) \\
\frac{dB(3,3)}{dt} &= \begin{bmatrix} -4.50 & -0.50 \\ 2.50 & -6.00 \end{bmatrix} B(3,3) + \begin{bmatrix} 2.00 & 0.50 \end{bmatrix} B(2,1) \\
\frac{dH(3,4)}{dt} &= \begin{bmatrix} -5.50 & -0.50 \\ 3.50 & 7.00 \end{bmatrix} H(3,4) + \begin{bmatrix} 5.00 & 5.00 \end{bmatrix} B(2,1) \\
\frac{dB(3,4)}{dt} &= \begin{bmatrix} -5.50 & -0.50 \\ 3.50 & 7.00 \end{bmatrix} B(3,4) + \begin{bmatrix} 2.50 & 0.50 \end{bmatrix} B(2,1)
\end{align*} \]

Table 7. Transformational behavior for C(3,1-4). The equation for C(3,1) is the same as C(3,1)'s equation in Table 4.
identified by the square on Figure 8c.

Figure 11c shows sample composite equilibrium loci for the constituents constrained by C(3,1), namely C(4,1), C(4,2), C(4,3), and C(4,4). The canonical representations of these constituents are shown in Table 8. The locus identified by the circle contains the steady-state values of these constituents which obtain when C(3,1) attains the steady state associated with the circle in Figure 8c. The locus identified by the square contains the steady-state values of the constituents which obtain when C(3,1) attains the steady state associated with the square in Figure 8c. The points labeled K=1 on the loci identified by the circle and square in Figure 11c correspond to the points in Figure 8d identified by the circle and square, respectively.

The relationships between composite equilibrium loci across levels may be examined in a three-dimensional phase diagram in which "level" is used to index the third axis. Such a diagram is shown in Figure 12. The loci shown here are those containing the steady states toward which each level's constituents (K = 1, 2, 3, 4) will tend given an ultimate environment of H(0,1) = 5 and B(0,1) = 3 (of course there is only one constituent at level one, so a single point obtains there, instead of an entire locus). The points labeled K=1 at each level correspond to the points
\[
\begin{bmatrix}
\frac{dH(4,1)}{dt} \\
\frac{dB(4,1)}{dt}
\end{bmatrix} =
\begin{bmatrix}
3.00 & -0.50 \\
1.00 & -3.50
\end{bmatrix}
\begin{bmatrix}
H(4,1)
\end{bmatrix} +
\begin{bmatrix}
2.50 \\
1.00
\end{bmatrix}
\begin{bmatrix}
H(3,1)
\end{bmatrix}
\]

\[
\begin{bmatrix}
\frac{dH(4,2)}{dt} \\
\frac{dB(4,2)}{dt}
\end{bmatrix} =
\begin{bmatrix}
3.00 & -0.50 \\
2.00 & -4.00
\end{bmatrix}
\begin{bmatrix}
H(4,2)
\end{bmatrix} +
\begin{bmatrix}
3.00 \\
0.50
\end{bmatrix}
\begin{bmatrix}
H(3,1)
\end{bmatrix}
\]

\[
\begin{bmatrix}
\frac{dH(4,3)}{dt} \\
\frac{dB(4,3)}{dt}
\end{bmatrix} =
\begin{bmatrix}
3.00 & -0.50 \\
3.00 & -4.50
\end{bmatrix}
\begin{bmatrix}
H(4,3)
\end{bmatrix} +
\begin{bmatrix}
3.50 \\
0.50
\end{bmatrix}
\begin{bmatrix}
H(3,1)
\end{bmatrix}
\]

\[
\begin{bmatrix}
\frac{dH(4,4)}{dt} \\
\frac{dB(4,4)}{dt}
\end{bmatrix} =
\begin{bmatrix}
3.00 & -0.50 \\
4.00 & -5.00
\end{bmatrix}
\begin{bmatrix}
H(4,4)
\end{bmatrix} +
\begin{bmatrix}
4.00 \\
0.50
\end{bmatrix}
\begin{bmatrix}
H(3,1)
\end{bmatrix}
\]

Table 8. Transformational behavior for C(4,1-4). The equation for C(4,1) here is the same as C(4,1)'s equation in Table 4.
Figure 12. Three-dimensional representation of composite equilibrium loci. The loci marked by circles in Figure 11 are reproduced here along with the similarly marked steady state from Figure 8a. The three dimensions of this diagram represent habitat, biota, and level. Thus, the single point at level one represents the steady state marked by the circle in Figure 8a (recall that level one has only a single constituent, so no composite equilibrium locus appears at that level). The locus at level two matches the locus marked with the circle in Figure 11a. The corresponding loci at levels three and four likewise match the loci marked with circles in Figures 11b and 11c.
Figure 12.
denoted by the circles in Figure 8.

Just as a change in transformational behavior results in a change in steady state for the same environmental conditions in the case of a single constituent, so it is true that a change in transformational behavior results in a change in positioning and/or form of the composite equilibrium locus for the same environmental conditions in the case of a family of constituents constrained by the same higher-level constituent.

For example, Figure 13 shows how a particular composite equilibrium locus shifts its position between t=0 and the limit as t approaches infinity. Table 9 shows the transformational behavior of the constituent set \([\text{C}(2,1), \text{C}(2,2), \text{C}(2,3), \text{C}(2,4)]\) in canonical form, where the coefficients are linear functions of time. Both loci shown in Figure 13 are parameterized by \(H(1,1) = 5\) and \(B(1,1) = 5\). The light solid line shows the composite equilibrium locus for this set of constituents and this environmental state at t=0. The dark solid curve shows the locus as t approaches infinity. The dashed curves show the trajectories of steady states for each of the four constituents.

The construction of composite equilibrium loci is an example of how the steady-state behavior of a system may be
Figure 13. Time-dependent composite equilibrium locus. Implied steady-state points for the four level-two constituents were generated from the transformational behavior shown in Table 9. At $t = 0$, the implied composite equilibrium locus for level two at $H(1,1) = 5$ and $B(1,1) = 5$ is shown by the light solid line in the figure. With change in time, the implied composite equilibrium locus changes as dictated by the time-dependent equations of the transformational behavior. As $t$ approaches infinity, the composite equilibrium locus converges on the dark solid curve in the figure as a limit. The dashed curves in the figure show the steady-state trajectories of the individual level-two constituents.
$B(2,K)$

$K = I$

$t = 0, t = 0$

$H(1,1) = 5, B(1,1) = 5$

Figure 13.
\[
\begin{align*}
\begin{bmatrix}
\frac{dH(2,1)}{dt} \\
\frac{dB(2,1)}{dt}
\end{bmatrix} &= 
\begin{bmatrix}
1.00-2.00t & -0.25-0.25t \\
2.00+1.00t & -3.00-2.00t
\end{bmatrix}
\begin{bmatrix}
H(2,1) \\
B(2,1)
\end{bmatrix} + \\
\begin{bmatrix}
0.75+0.50t & 0.50+1.00t \\
1.50+1.25t & 1.25+1.50t
\end{bmatrix}
\begin{bmatrix}
H(1,1) \\
B(1,1)
\end{bmatrix} \\
\begin{bmatrix}
\frac{dH(2,2)}{dt} \\
\frac{dB(2,2)}{dt}
\end{bmatrix} &= 
\begin{bmatrix}
2.00-2.00t & -0.25-0.25t \\
2.00+2.00t & -3.00-4.00t
\end{bmatrix}
\begin{bmatrix}
H(2,2) \\
B(2,2)
\end{bmatrix} + \\
\begin{bmatrix}
0.75+1.50t & 1.50+1.00t \\
1.50+1.25t & 1.25+1.50t
\end{bmatrix}
\begin{bmatrix}
H(1,1) \\
B(1,1)
\end{bmatrix} \\
\begin{bmatrix}
\frac{dH(2,3)}{dt} \\
\frac{dB(2,3)}{dt}
\end{bmatrix} &= 
\begin{bmatrix}
-3.00-2.00t & -0.25-0.25t \\
2.00+3.00t & -3.00-6.00t
\end{bmatrix}
\begin{bmatrix}
H(2,3) \\
B(2,3)
\end{bmatrix} + \\
\begin{bmatrix}
0.75+1.50t & 1.50+1.00t \\
1.50+1.25t & 1.25+1.50t
\end{bmatrix}
\begin{bmatrix}
H(1,1) \\
B(1,1)
\end{bmatrix} \\
\begin{bmatrix}
\frac{dH(2,4)}{dt} \\
\frac{dB(2,4)}{dt}
\end{bmatrix} &= 
\begin{bmatrix}
-4.00-2.00t & -0.25-0.25t \\
2.00+4.00t & -3.00-8.00t
\end{bmatrix}
\begin{bmatrix}
H(2,4) \\
B(2,4)
\end{bmatrix} + \\
\begin{bmatrix}
0.75+2.00t & 2.00+1.00t \\
1.50+1.25t & 1.25+1.50t
\end{bmatrix}
\begin{bmatrix}
H(1,1) \\
B(1,1)
\end{bmatrix}
\end{align*}
\]

Table 9. Time-dependent transformational behavior for C(2,1-4). The equations of Table 6 obtain when t = 0.
simplified. The important step from simple isoclines to a representation such as the composite equilibrium locus comes in considering the steady states of commonly-constrained constituents not as \( n \) individual points but as a single entity. In the example system studied so far, the idea of a locus being used to summarize a number of individual steady states is a natural and efficient one. However, the idea of collapsing the dimensionality of \( n \) steady states into a single steady-state entity does not require the use of locus. A number of constructs could be employed to summarize individual points as a single entity.

For example, instead of constructing a locus which unifies the points by connecting them, a hypersphere could be constructed which contains all the points. It is also possible to conceptually unify the points by considering them as a single set, although this conceptualization does not transmit well graphically. Among the factors to consider in deciding upon the appropriate construct for summarizing a number of individual steady states is efficiency of description. Although any of the constructs mentioned above may be described as single entities either conceptually or graphically, the precise definition of the entity requires a different number of specifications in each case. For example, in describing the individual points as a set, a full definition of the set requires enumeration of
every point therein, in which case very little economy is to be found in the method. Specifically, to describe a set of values of n constituents each containing m state variables would require nm terms using the "set" approach of description.

Alternatively, the "locus" method can always describe the points with at least the same economy of terms, and in fact is almost always more efficient in this regard. In the worst case, it is always possible to describe a locus incorporating n points in two dimensions by a polynomial of degree n-1. Thus, precisely defining a locus in a space described by two state variables of n commonly-constrained constituents requires at most n terms. Of course, it may be possible to describe a locus in fewer terms if some of the polynomial coefficients are zero. This, in fact, is the case for the composite equilibrium loci of Figure 11a, which are exactly linear. In this case, two of the coefficients in the third-degree polynomial sufficient to connect the four constituent steady states are zero. In other cases, the locus may not be exactly linear but so nearly so that a linear approximation will be adequate for most purposes. For example, fitting linear regressions to the composite equilibrium loci of Figures 11b and 11c yield $R^2$ values of greater than .995 in every case.
In this example, then, the composite equilibrium loci for the constituents one through four at any level two through four can be expressed for all practical purposes as points in two dimensions, one for the slopes and the other for the intercepts of the loci. The loci for all three levels (two through four) can be expressed by adding "level" as a third dimension. This is done in Figure 14a, where the general equilibrium loci for constituents one through four at levels two through four under four different environments are summarized. Such a representation affords considerable economy compared to the "set" approach, which would require locating 12 points in 24 dimensions. In fact, the present example may be reduced still further by the locus method, since a careful examination of Figure 14a will reveal that the slopes of the loci depicted are virtually identical within each level. Since nearly all of the variability in the loci of a given level can be accounted for by differences in intercept, the loci may be depicted reasonably well in two dimensions, as shown in Figure 14b.

Thus, while the "locus" method is in a sense more artificial than the "set" method, in that it includes non-steady-state points as well as steady-state points in its description, it is also more efficient in economy of description.
Figure 14. Graphical representation of composite equilibrium locus coefficients. Figure 13 depicted the loci as curves plotted against level as a third dimension. Since these curves are all very nearly linear, they may be described just as well by the two coefficients of a linear equation, meaning that each locus may be plotted as a single point in the three dimensions of slope, intercept, and level.

Figure 14a. Three-dimensional representation of locus coefficients. Four loci are depicted here, representing the composite equilibrium loci corresponding to [H(0,1),B(0,1)] values of (1,3), (1,5), (5,3), and (3,5). For each set of environmental conditions, one approximately linear locus obtains at each level. This locus can thus be represented by the values of its slope, intercept, and level, as shown here.

Figure 14b. Two-dimensional representation of locus coefficients. Since the slope of all loci at a given level in this example are approximately equal, the within-level locus variability may be attributed almost entirely to variability in intercept value. Here, intercept value is plotted against level for the four loci described in Figure 14a, suppressing the "slope" axis.
Figure 14.
The "hypersphere" method may or may not be as efficient as the locus method, depending on the system in question. Steady states for a set of \( n \) commonly-constrained constituents each with \( m \) state variables can be described in \( n-1 \) terms by the hypersphere method. As with the locus method, the hypersphere method tends toward more economical description than does the set method, but also like the locus method incorporates points which do not correspond to any constituent steady state.

Other methods with their own various strengths and weaknesses may be described as well. Some statistical methods can reduce the overlap between composite equilibrium entities, but at a cost of omitting some true steady states. An example here would be construction of a hyperellipse with axes based on 95% confidence intervals. Or, if the goal is merely to minimize the dimensionality of the composite equilibrium entity, principal component analysis provides a means for accounting for the maximum amount of data variability in a given number of dimensions, given its constraints of using only linear transformations of data and requiring orthogonality of axes (Pimentel 1979).

Generally speaking, the choice of composite equilibrium entity must depend largely on the objectives of the analysis and the organization of the target system.
Introduction of Time Scale Heterogeneity

The sample system examined so far has been described in terms of its transformational behavior, which in its canonical form consists of a set of differential equations. The notion of instantaneous rate of change is a restrictive assumption which is not required for the validity of the principles so far described. One of the most important contributions of hierarchy theory has been an increased understanding of the role of nonhomogeneous time scales in system functioning (Allen and Starr 1982, Pattee 1969 and 1973, Simon 1962 and 1973, Bastin 1969). The central idea here is that different subsystems may behave with different characteristic frequencies. An extreme example is one given by Allen and Starr:

"The lower holon (subsystem) does not exist long enough, have memory long enough, or exert an influence wide enough to have behaviorally significant communication with the higher holon. An example here is the probable irrelevance of any behavior of our galaxy to the processes of life on this planet. The Milky Way does provide an inertial frame which is a constraint in a certain general sense, but there is unlikely to be any galactic constraint that has relevance to the livingness of life. Any or even no galaxy would probably do just as well, and there is no
As a result of possessing different behavioral frequencies, "slow" subsystems may act as constraints on "fast" subsystems, while the "fast" subsystems always appear to be near steady state from the perspective of the "slow" subsystems. This concept may be mathematically formalized by viewing the system from complementary perspectives: from the point of view of the fast subsystems, the slow subsystems become formally constant and act as part of the fast subsystems' environment, while from the point of view of the slow subsystems, their own behavior is dynamic and is constrained by an environment at the next level up.

This approach is akin to that used by Walker et al. (1981) and Ludwig et al. (1978). Ludwig et al., in discussing a simple model of forest/insect interactions, partitioned the system into categories of fast variables (insects) and slow variables (forest). The equations representing the insect dynamics were then solved, holding the forest state variables at given levels; i.e. the difference in time resolution was exaggerated to the point that the slow variables were taken to act as though they did not change at all. Since the equations of Ludwig et al. allowed for the possibility of cusp behavior (steady states
that are not globally stable), the dynamics of the slow variables were then analyzed in terms of different fixed values of the fast variables.

Walker et al. (1981) used the idea of differing time scales to examine the stability of semi-arid savanna grazing systems. The equations of Walker et al. also allow for steady states which are not globally stable, so considerable emphasis is given in their paper to questions of resilience and domains of attraction. Their paper is also noteworthy in its use of families of isoclines.

The simplifying effects of this type of analysis are demonstrated by analyzing a pair of linear, asymptotically stable systems. The first of these is described by the two equations in Table 10. The transformational behavior corresponding to the first equation in Table 10 represents a single level-one constituent in which a habitat subsystem interacts with two biotic subsystems \([B1(1,1) \text{ and } B2(1,1)]\), and all three are constrained by a level-zero constituent consisting of a habitat subsystem and a biota subsystem. Figure 15a shows sample isoclines for the system. Pictured are non-reduced isoclines for \(B1(1,1)\) and \(B2(1,1)\), two-dimensional subsystem isoclines for \(B1(1,1)\) and \(B2(1,1)\), and two-dimensional system isoclines, all in the \([B1(1,1), B2(1,1)]\) phase plane.
\[
\begin{bmatrix}
\frac{dH(1,1)}{dt} \\
\frac{dB_1(1,1)}{dt} \\
\frac{dB_2(1,1)}{dt}
\end{bmatrix} =
\begin{bmatrix}
-1 & -1 & -1 \\
1 & -2 & -1 \\
1 & 1 & -2
\end{bmatrix}
\begin{bmatrix}
H(1,1) \\
B_1(1,1) \\
B_2(1,1)
\end{bmatrix} +
\begin{bmatrix}
3 & 4 \\
2 & 3 \\
1 & 1
\end{bmatrix}
\begin{bmatrix}
H(0,1) \\
B(0,1)
\end{bmatrix}
\]

\[
\begin{bmatrix}
\frac{dB_1(2,1)}{dt} \\
\frac{dB_2(2,1)}{dt}
\end{bmatrix} =
\begin{bmatrix}
-2 & -1 \\
1 & -2
\end{bmatrix}
\begin{bmatrix}
B_1(2,1) \\
B_2(2,1)
\end{bmatrix} +
\begin{bmatrix}
1 & 2 & 3 \\
1 & 1 & 1
\end{bmatrix}
\begin{bmatrix}
H(1,1) \\
H(0,1) \\
B(0,1)
\end{bmatrix}
\]

Table 10. Transformational behavior of simple system illustrating effects of time scale. Upper equation treats all three subsystems of the level-one constituent as though they operate on the same time scale. Lower equation treats the biotic subsystems as though they react to a constant level-one habitat (i.e. habitat behaves more slowly than biota).
Figure 15. Behavior and organization of simple system exhibiting time-resolution heterogeneity. This figure represents the behavior and organization of the two systems corresponding to the transformational behaviors shown in Table 10.

Figure 15a. \([B_1(1,1), B_2(1,1)]\) phase plane corresponding to upper set of equations in Table 10. This phase plane represents the steady-state behavior of the biotic subsystems of \(C(1,1)\) under one set of environmental (level zero) conditions: \(H(0,1) = 1\) and \(B(0,1) = 1\). Shown are 1) non-reduced, 2) two-dimensional system, and 3) two-dimensional subsystem isoclines for both biotic subsystems. Under the environmental conditions assumed, \(H(1,1)\) takes on a steady-state value of two, so this value parameterizes the two-dimensional subsystem isoclines of both biotic subsystems.

Figure 15b. \([B_1(2,1), B_2(2,1)]\) phase plane corresponding to lower set of equations in Table 10. Since there are only two variables involved in this level, the non-reduced and two-dimensional subsystem isoclines are now formally identical. Another difference between this figure and Figure 15a is that in this system \(H(1,1)\) parameterizes the two-dimensional subsystem isoclines. Also, the two-dimensional system isoclines are now parameterized by two environmental variables, instead of just one.

Figure 15c. Digraph for system described in upper half of Table 10. The digraph corresponding to the equations in the upper half of Table 10 is composed of only two levels (zero and one), with a single three-variable constituent at level one. Arcs between non-distinct vertices are ignored. This digraph is \(K(2/3)\).

Figure 15d. Digraph for system described in lower half of Table 10. This system is identical to the first, except that the two biotic subsystems have been shifted downward to a new level (two), where they form their own constituent. \(H(1,1)\) is now the sole variable at level one. Arcs between non-distinct vertices are ignored.
Figure 15.
However, suppose that the biotic subsystems at level one behave with relatively high frequencies, but that the level-one habitat subsystem behaves with a relatively low frequency, in fact so low that from the perspective of the biotic subsystems the habitat appears constant. In terms of the system's digraph, this shift in perspective causes the deletion of the arcs running from the fast biotic subsystems to the slow habitat subsystem, as shown in Figures 15c and 15d. The result of these deletions is to split the target constituent \( C(1,1) \) into two constituents \( (H(1,1) \) and \( [B1(2,1), B2(2,1)] \)), one of which constitutes a new level just below the level of the original target constituent. If a hierarchy is originally of the nested variety, splitting off a new constituent and level in this manner automatically causes the hierarchy to become non-nested.

Performing such an operation on the system of Figure 15 in effect amounts to switching from the transformational behavior in the first equation of Table 10 to that found in the second equation. Sample isoclines for this transformational behavior are shown in Figure 15b. These isoclines indicate the simplifying effects of such a shift in perspective. Since there are only two dimensions in the new target system \([B1(2,1) \) and \( B2(2,1)]\), the non-reduced and two-dimensional subsystem isoclines are now formally identical, with \( H(1,1) \) becoming a parameter of the
two-dimensional subsystem isoclines. Some complication does occur, however, in terms of the number of families of two-dimensional system isoclines, which increases from two to three to incorporate the new environmental variable $H(1,1)$.

There is no mathematical restriction, of course, on how many state variables within a given constituent may be taken as constants. The first equation of Table 11 shows the transformational behavior of a hypothetical constituent comprised of four state variables: one habitat subsystem $[H(1,1)]$ and three biotic subsystems $[B1(1,1), B2(1,1), \text{and } B3(1,1)]$. Sample isoclines for this system are shown in Figure 16a.

Suppose now that subsystems $B1(1,1)$ and $B2(1,1)$ behave with high frequency relative to $B3(1,1)$ and $H(1,1)$. The transformational behavior of the system would now appear as shown in the lower half of Table 11. Sample isoclines for this system are shown in Figure 16b. As with the system of Table 10/Figure 15, the non-reduced and two-dimensional subsystem isoclines on the "fast" phase plane become formally identical, but the number of families of two-dimensional system isoclines increases by the number of new environmental variables (2).
Table 11. Transformational behavior of more complex system incorporating effects of time scale. This table is similar to Table 10, except that a "slow" biotic subsystem is added. In the upper equation, the four subsystems of the level-one constituent are treated as though they behave according to the same time scale. In the lower equation, the habitat subsystem and one biotic subsystem are treated as though they behaved very slowly relative to the other two (fast) biotic subsystems.
Figure 16. Behavior and organization of a more complex system exhibiting time-resolution heterogeneity. The system(s) pictured here have transformational behaviors corresponding to the equations of Table 11. This example differs from that of Figure 15 in that there are three biotic subsystems in this case; one "slow" biotic subsystem and two "fast" ones.

Figure 16a. \([B2(1,1), B3(1,1)]\) phase plane, corresponding to the equations in upper half of Table 11. When the system's transformational behavior is viewed according to the upper half of Table 11, \(B2(1,1)\) and \(B3(1,1)\) are merely two variables in a four-variable constituent that also includes \(B1(1,1)\) and \(H(1,1)\). Shown here are 1) non-reduced, 2) two-dimensional subsystem, and 3) two-dimensional system isoclines for \(B2(1,1)\) and \(B3(1,1)\) under environmental conditions of \(H(0,1) = 1\) and \(B(0,1) = 1\).

Figure 16b. \([B2(2,1), B3(2,1)]\) phase plane, corresponding to the equations in lower half of Table 11. Here, \(B2(2,1)\) and \(B3(2,1)\) form a new lowest level (two) in the hierarchy. The non-reduced and two-dimensional subsystem isoclines are now formally identical. Also, there are two additional families of two-dimensional system isoclines, corresponding to the number of new environmental variables constraining \(C(2,1)\).

Figure 16c. Digraph for system described in upper half of Table 11. This digraph consists, like its counterpart in Figure 15, of two levels (zero and one), with a single constituent occupying the lower level. Arcs between non-distinct vertices are ignored. This digraph is \(K(2/4)\).

Figure 16d. Digraph for system described in lower half of Table 11. Here, \(B2(1,1)\) and \(B3(1,1)\) have been moved down to form a new level (two) of the hierarchy, where they become \(B2(2,1)\) and \(B3(2,1)\). From the viewpoint of the level-two system, the possible existence of arcs between the level-one variables is irrelevant, so these arcs have been omitted from the figure. Arcs between non-distinct vertices are ignored.
Figure 16.
The source digraphs for the systems of Table 11 are shown in Figures 16c and 16d. The system of Figures 16b and 16d are in a sense analogous to the example of Ludwig et al. (1978) in that both involve a slow biotic component \([B(1,1) \text{ and trees}]\) and a fast biotic component \([C(2,1) \text{ and insects}]\). In both cases, the slow biotic component appears as a static fixture of the environment from the perspective of the fast biotic component.

The dynamics of a system of the type illustrated in Figures 16b and 16d makes the multiple steady state nature of such systems especially apparent. For as \(B(1,1)\) and \(H(1,1)\) converge on the steady states determined by the levels of \(H(0,1)\) and \(B(0,1)\), each new value of \(C(1,1)\) appears as a new "constant" environment to \(C(2,1)\). Thus \(C(2,1)\) will, at any given instant, be tracking a steady state on an isocline parameterized by some value of \(C(1,1)\) which from the viewpoint of \(C(2,1)\) is quite constant but which from the viewpoint of \(C(1,1)\) is in transition toward its own steady state.

From the point of view of \(C(1,1)\), in fact, it is \(C(2,1)\) which will appear constant, not because it moves slowly (it does not), but precisely because it moves so rapidly that it will always appear to \(C(1,1)\) to be at steady state. Furthermore, \(C(0,1)\) will behave relative to \(C(1,1)\) in a
manner analogous to that in which C(1,1) behaved relative to C(2,1), namely it will behave as a constraining constant. Writing from the point of view of a "middle level" constituent [such as C(1,1)], Simon (1969) writes,

"Motions of the system determined by the low-frequency modes will be so slow that we will not be able to observe them - they will be replaced by constants.

"Motions of the system determined by the high frequency modes will control, for the reasons already given, the internal interactions of the components of the lower level subsystems in the hierarchy, but will not be involved in the interactions among those subsystems. Moreover, these motions will be so rapid that the corresponding subsystems will appear always to be in equilibrium and most of their internal degrees of freedom will vanish. In their relations with each other, the several subsystems will behave like rigid bodies, so to speak.

"The middle band of frequencies, which remains after we have eliminated the very high and very low frequencies, will determine the observable dynamics of the system under study - the dynamics of interaction of the major subsystems."

This type of model can be especially helpful in
understanding ecosystems in which gradual change in one subsystem serves as a constraint on the development of another. An example of such a system follows.

Application of the Model to Selected Community Studies

Choice of Studies

In attempting to apply the proposed model of ecological hierarchy, it would be most desirable to obtain data which would enable illustration of all facets of the model. Also, primary data would be preferable to secondary, in that greater controls on type of data and method of collection are possible with the former. However, the proposed model deals with entities which are so large and deals with them so extensively that the cost of data collection becomes a major concern. Furthermore, in illustrating the use of the model it would be preferable to divert attention from details of the data collection process, so that the focus could instead be upon the utility of the model. For these reasons the proposed model shall be applied not to an original data set, but instead to several well-known studies in the ecological literature.

To illustrate the use of composite equilibrium descriptions of non-lineal ecological hierarchies, it is
necessary to utilize data collected not only at a variety of levels of organization, but also for several geographic subsystems at each level. A classic example of such a data set is found in Whittaker's (1956) study of the Great Smoky Mountains in eastern Tennessee. Unfortunately, this data set does not illustrate the principles of time-resolution heterogeneity quite as well. To fully illustrate the use of the proposed model, then, it will also be necessary to examine some data sets involving variables with marked differences in behavioral frequencies. Well-known examples of this type of system may be found in the various studies which explore the successional dynamics of both overstory vegetation and avian fauna in forest ecosystems. The illustration may then proceed using the tree populations as slow variables and the bird populations as fast variables. The studies to be utilized from this group are those of Hagar (1960), Karr (1968), Kendeigh (1948), Kricher (1973), and Odum (1950).

A Hierarchical View of a Large-Scale Plant Community

Whittaker (1956) viewed the vegetation of the Great Smoky Mountains in terms of two forest systems, an Eastern Forest System and a Boreal Forest System, of which only the former will be dealt with here. The Eastern Forest System is composed of eleven forest types (it also includes one
non-forest type which will not be discussed in this treatment): cove forest, hemlock forest, beech forest, red oak-hickory forest, oak-chestnut forest, oak-chestnut heath, red oak-chestnut forest, white oak-chestnut forest, Virginia pine forest, pitch pine heath, and table mountain pine heath. Furthermore, Whittaker's data set typically covers more than one forest site within each forest type. Thus, Whittaker's conception of the Great Smoky Mountains' Eastern Forest System vegetation can be illustrated as a spatially-nested hierarchy, as shown in Figure 17.

Whittaker's study of the Great Smoky Mountains was one of the first examples of gradient analysis performed in the United States. More specifically, it was an early example of "direct" gradient analysis (Whittaker 1967), in which elevation and a dessication index were used as complex gradients to ordinate the data. The domains of the various forest types in elevation/dessication space are shown in Figure 18. By ordering sites along these gradients and noting the sites' respective species compositions, Whittaker was also able to classify the various species in terms of moisture affinity. The classifications used were "mesic" for the most hydrophilic species, then "sub-mesic," "sub-xeric," and finally "xeric" for the most hydrophobic species. For the purposes of the present investigation, the last three classes will be lumped into a single "xeric"
Figure 17. Hierarchical representation of Great Smoky Mountain study areas. The study areas of Whittaker's (1956) analysis can be conceived of as a spatially-nested, three-level hierarchy. As a spatially-nested hierarchy, the uppermost level must consist of a single constituent, the constituent in this case being the Eastern Forest System. This constituent consists of eleven level-two constituents, the various forest types. The forest types are in turn composed of a number (one to seven) of forest sites at the third level of the hierarchy.
Figure 17.
Figure 18. Domains of forest types plotted on dessication and elevation axes (after Whittaker, 1956). Whittaker was able to map the domains of the eleven forest types (and a twelfth non-forest vegetation type) of the Eastern Forest System in terms of occurrence along complex dessication and elevation gradients. Note that this figure does not correspond to a map of the forest types in physical space. Units along the dessication axis are undefined.
Figure 18.
Whittaker's (1956) Appendix C lists composite stand counts of tree species by elevation and forest type. Each count for a particular elevation and forest type will be referred to here as a "site." In order to use composite equilibrium loci to represent this data, it must be assumed that the system was close to its steady state at the time of Whittaker's study. While such an assumption may be problematical, it is encouraging to note that the same assumption was made by Whittaker (1956, 1975) himself.

Another step involved in attempting to summarize the vast amount of information contained in this study is the selection of some integrative measure of system performance. Any of the popular diversity measures would suffice in this regard. In part because of its popularity in the studies to be discussed later regarding time-resolution heterogeneity, Shannon's information statistic (Shannon and Weaver 1949) shall be used.

In order to facilitate display of system performances on phase planes, it will of course also be necessary to measure at least two such performances. The organization of Whittaker's data in terms of mesic and xeric species might suggest that mesic and xeric diversity constitute two appropriate performances for measurement. However, a better
picture is obtained when mesic diversity is plotted against the increment to total diversity supplied by xeric diversity, namely total diversity minus mesic diversity. This variable is strongly and positively related to xeric diversity itself, but the relationship is a purely statistical one. Figure 19 shows the relationship between the two variables based on the results of a Monte Carlo simulation. The correlation coefficient for this plot is .86, with the 95% confidence interval extending down only to a value of .65.

Taking mesic and xeric diversity measurements for all sites yields a single point in phase space for the Great Smoky Mountains Eastern Forest System, as shown by the open circle in Figure 20. Viewed from the perspective of the proposed model, this represents a particular state of the system at the highest level. According to Whittaker's own conception, the system is a spatially-nested hierarchy. If the system can also be viewed as a hierarchy in terms of control, then the state of the system at the Eastern Forest System level would determine the state of the subsystems incorporated by the Eastern Forest System, namely the eleven forest types.

Mesic and xeric diversity values may be obtained for each of the various forest types, as well. These are
Figure 19. Total diversity minus mesic diversity plotted against xeric diversity. A Monte Carlo simulation of diversity values was conducted as follows: A community of sixteen species was assumed. The number of individuals in each species was assumed to number between two and eight. The population sizes were distributed as shown below.

<table>
<thead>
<tr>
<th>Population size</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. species in size class</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

Thus, species #1 had two individuals, species #2 and #3 had three individuals, species #4, #5, and #6 had four individuals, etc. Given this distribution, twenty random permutations were made of the species list. The first eight species occurring on the list after each permutation were assumed to be mesic, and the second eight xeric. From this information, xeric and mesic diversity indices were calculated. Total diversity was constant across all permutations at 3.9247. A linear regression of total diversity minus mesic diversity (Hz) against xeric diversity (Hx) gave the following equation: Hz = .9563Hx - 1.8105 (R² = .74).
Figure 19.
Figure 20. Composite phase plane of Eastern Forest System forest types. Total diversity and mesic diversity were calculated for each the Eastern Forest System as a whole (open circle), as well as for each of the eleven forest types. Mesic diversity is plotted on the y-axis, and total diversity - mesic diversity is plotted on the x-axis. A weighted parabola was regressed on the points plotted on axes rotated by 19.556 degrees. The parabola was weighted according to the number of sites in each forest type. The angle of rotation equals the angle of the axis orthogonal to the line which bisects the angle formed by the intersection of linear regressions through the sets [HF,BF] and [CF,OF,RC,OH,RH,WC,TM,PP,VP]. The equation of the parabola (in the rotated dimensions) is

\[ y = -4.8181 + 10.1137x - 3.4518x^2 \ (R^2 = .71). \]

In the original dimensions, this equation translates to

\[ y = 3.159 - 2.818x \pm (.003x^2 + 7.727x - 2.481)^{.5} . \]

Symbols:
BF = beech forest
CF = cove forest
HF = hemlock forest
OF = oak-chestnut forest
OH = oak-chestnut heath
PP = pitch pine heath
RC = red oak-chestnut forest
RH = red oak-hickory forest
TM = table mountain pine heath
VP = virginia pine forest
WC = white oak-chestnut forest
Figure 20.
plotted as the solid circles in Figure 20. A parabola based on rotated axes has been regressed through these points to represent the composite equilibrium locus for these constituents when the constraining constituent (the Eastern Forest System) is at the state identified by the open circle. If this system may indeed be viewed from the perspective of the proposed model, then this locus would have a different form and position for any performance of the Eastern Forest System other than that shown.

Again, if the spatially-nested patterns of this system can be thought of as patterns of control as well, then each forest type (solid circle) in Figure 20 represents a constraining constituent for each of its incorporated sites. Thus, mesic and xeric diversity values may be calculated for each site. These values yield the phase plane shown in Figure 21. Here, commonly-constrained constituents (sites of a given forest type) are linked by composite equilibrium loci. Under the assumption that each incorporating system controls its incorporated subsystems, the shapes and positions of the composite equilibrium loci shown in Figure 21 correspond to the unique values of the forest types shown in Figure 20. In other words, had the performance of any forest type been different than that identified with the relevant solid circle in Figure 20, the corresponding composite equilibrium locus in Figure 21 would have taken on
Figure 21. Composite phase plane of Eastern Forest System sites, by forest type. Forest site diversity values are plotted in the same manner as forest type diversities in Figure 20. No particular importance is ascribed to the shapes of the curves linking the points on the various composite equilibrium loci. Of greater significance is the fact that different loci tend to occur in fairly distinct regions of phase space. If these curves can be taken to represent steady-state entities, then each curve would have a different position and/or form under a different state of its constraining constituent (the relevant forest type).
Figure 21.
a different form and location.

The multiple steady state nature of the system (when viewed from the perspective of the proposed model) is illustrated by Figure 22. Figure 22a shows the Great Smoky Mountains Eastern Forest System as a single point (solid circle) on a hypothetical composite equilibrium locus of forest systems constrained by the state of something like Bailey's (1976) Appalachian Oak Forest Section. The state of the Appalachian Oak Forest Section corresponding to this locus is labeled "state 1." However, if the performance of the Appalachian Oak Forest Section had been different ("state 2"), the entire locus would have shifted, as shown in the figure. Likewise, the steady state of the Great Smoky Mountains Eastern Forest System would also have been different (open circle, Figure 22a).

Figure 22b shows the system at the forest type level. The rotated parabola here corresponds to the parabola in Figure 20. As stated previously, the position and form of this composite equilibrium locus is determined by the state ("state 1") of the constraining constituent, the Great Smoky Mountains Eastern Forest System. The state of the oak-chestnut forest type is shown on this locus by the solid circle. Since it is one of the constituent subsystems constrained by the state of the Great Smoky Mountains
Figure 22. Hierarchical view of Great Smoky Mountains vegetation across three levels. In this figure, solid curves and solid circles indicate curves/points for which data is presented. Dashed curves and open circles indicate purely hypothetical curves/points. The term "state #1" denotes the actual state of the system at the time of Whittaker's (1956) study. "State #2" refers to a different, hypothetical state for purposes of comparison.

Figure 22a. Forest system level. The solid circle represents the state of the Eastern Forest System, and corresponds to the open circle in Figure 20. The Eastern Forest System is taken to be one of a set of systems commonly constrained by the incorporating Appalachian Oak Forest Section described by Bailey (1976). The hypothesized composite equilibrium locus is thus parameterized by the Appalachian Oak Forest Section in state #1. If that system had been in state #2, however, the entire locus (including the point representing the Eastern Forest System) would shift.

Figure 22b. Forest type level. The solid curve represents the composite equilibrium locus for the eleven forest types under state #1 of the Eastern Forest System. The solid circle represents the state of the oak-chestnut forest type. If the state of the Eastern Forest System had been different (e.g. state #2, as shown in Figure 22a), the entire locus would shift, along with the steady state for the oak-chestnut forest type (dashed curve and open circle, respectively).

Figure 22c. Site level. The solid curve represents the composite equilibrium locus for the sites constrained by the oak-chestnut forest type. The position and form of this locus is determined by the state (#1) of the oak-chestnut forest type. If that forest type had been in a different state (e.g. state #2, as shown in Figure 22b), the entire locus would shift (dashed curve).
Figure 22.
Eastern Forest System, if the performance of that System had been different ("state 2"), the oak-chestnut forest type would have exhibited a different steady-state performance also (open circle, Figure 22b).

Finally, Figure 22c shows the system at the site level. The solid parabola here corresponds to the composite equilibrium locus for the oak-chestnut forest type shown in Figure 21. One particular site is highlighted here by the solid circle on that locus. Like the loci discussed previously, the position and form of this locus is dependent upon the state ("state 1") of the constraining constituent, in this case the oak-chestnut forest type. Again, if the state of this constraining constituent were to change (to "state 2"), the entire locus would shift (dashed curve, Figure 22c). Likewise, the particular site represented by the solid circle would have a new steady state (open circle, Figure 22c).

This multiple steady state behavior is strictly analogous to that of the hypothetical system analyzed in Figures 6-12. The ecological significance of viewing a system in this manner is similarly straightforward. A subsystem's observed behavior is always subject to the effects of changes in its environment, that is, its incorporating system. Such changes will likewise affect
commonly-constrained subsystems, and consideration of these subsystems as a unit can help to make the system's behavior more understandable.

The Role of Time Scale in Vegetation/Avifauna Systems

The idea that forest vegetation acts in a control-like fashion in determining the composition of the associated bird community is implicit in most of the literature on the subject. In light of the proposed model, this shall be interpreted to mean that the involved systems behave in a manner analogous to the system of Figure 16, in which bird species (divided for purposes of phase plane analysis into carnivorous and herbivorous species) behave with relatively high frequencies, while their habitat (tree species and abiotic habitat factors) behaves with relatively low frequency.

In other words, the life spans of the involved bird species are so short and avian community development is so rapid relative to the life spans of the involved tree species and the long-term development of the canopy that from the point of view of the birds, the state of their biotic environment appears constant. Thus, given a constant abiotic environment and a particular performance of the canopy, the bird community will move toward a particular
steady-state configuration associated with that vegetation performance and overall habitat state.

As noted above, the bird communities for each study are divided into two sub-communities (carnivorous and herbivorous) for purposes of phase plane analysis. The problem of assigning each bird species to one of these two categories is a non-trivial one, considering that most bird species are truly omnivorous, and that diet for most species varies with location, season, and life-history stage. However, remembering that the purpose of this analysis is illustration of a model's usefulness rather than establishing a permanent classification of bird species' trophic statuses, it will hopefully not prove too problematic to establish a tentative classification based on the findings of some previous studies.

For the purposes of this classification, a consensus opinion was obtained on the trophic status of each bird species based on the studies of Marcot (1979), Willson (1974), and Martin et al. (1951). The entire set of species classifications is displayed in Appendix I. Nomenclature for bird species follows that of the American Ornithologists' Union (1982). Of the five studies to be examined in this analysis
(Hagar 1960, Karr 1968, Kendeigh 1948, Kricher 1973, Odum 1950), both tree and bird species data are available for all but one (Odum 1950), for which only bird data is available. However, the site used in Odum's study is only 50 km from the Great Smoky Mountains, and the two forest types represented are both found in Whittaker's (1956) study. If it can be assumed that the forests in Odum's site represent additional points on the composite equilibrium loci constrained by the states of the respective forest types in the Great Smoky Mountains, it becomes possible to link the above interpretation of the Great Smoky Mountains vegetation as a non-lineal hierarchy to the present attempt at interpreting vegetation/avifauna communities as examples of time-resolution heterogeneity. Again, it should be emphasized that this exercise is merely an attempt to illustrate the use of the proposed model, not to prove that the systems in question are organized precisely as pictured.

Odum's (1950) study recognizes two forest types in the area of Ravenel's Woods, in southwestern North Carolina: the oak-chestnut type and the hemlock type. The successional trajectory for the vegetation in the oak-chestnut type moves from a xeric shrubland stage to a mixed deciduous stage to an oak-chestnut climax. The hemlock sere begins with a mesic shrubland stage, moving to a hemlock-hardwood stage, and finally to a virgin hemlock climax.
In the interpretation being given, then, the bird community on an oak-chestnut site would first move toward a steady-state configuration associated with a xeric shrubland type of biotic environment. Eventually, however, the biotic environment would shift to a mixed deciduous state, and a new steady-state performance would be implied for the bird community. Finally, the biotic environment shifts to an oak-chestnut climax state, and the implied steady state for the bird community shifts again. Of course, if the abiotic environment does not remain constant, the complexity of the avian trajectory is further compounded, but for simplicity's sake this possibility will not be dealt with here.

The trajectories for the bird communities both in oak-chestnut and in hemlock sites are shown in Figure 23. It should be noted that these trajectories are not the only ones that could develop under the oak-chestnut and hemlock seres. Rather, they are specific to the states of the vegetation in each seral stage. In other words, the vegetation subsystems at two sites could be in the same seral stage and have significantly different performances in terms of composition or other factors. To the bird community, these differences would appear as differences in environment and would therefore elicit different performances from the bird community. This is emphasized in Figure 23 by labeling the states of the vegetation
The bird communities of the two seres in Ravenel's Woods are each depicted as following steady-state trajectories through phase space. On sites of the oak-chestnut type, for example, the initial xeric shrubland state of the vegetation is taken to provide a relatively constant environment for the avian community, leading to a steady state corresponding to the particular state of the relevant xeric shrubland community. As succession proceeds, the vegetation moves into a particular state within the mixed deciduous stage, dictating another steady state for the bird community. Finally, as the vegetation attains a particular state within the oak-chestnut climax, the bird community moves to a climax steady state. At any of the three successional stages, of course, the plant community could have been in a different state (without necessarily violating the identified sere). If that had been the case, the avian trajectory would have taken on a different form as well.
Figure 23.
corresponding to each steady state as "state 1," implying that there could have been another vegetational state corresponding to the same seral stage, and so a different avian response.

Figure 24 links the vegetation phase planes of Figure 22 to the avian trajectory of the oak-chestnut sere in Figure 23, thus incorporating the features of both hierarchical non-lineality and time-resolution heterogeneity. The first three panels of Figure 24 correspond to Figure 22, except that the vegetational trajectory of a hypothetical oak-chestnut site in Ravenel's Woods is included in Figure 24c. Note that under a different state (state 2) of the oak-chestnut forest type, not only would the steady-state performance of the Ravenel's Woods oak-chestnut site be different, but the successional trajectory would be different as well.

Figure 24d is basically the same as Figure 23, except that hypothetical isoclines are drawn through the steady-state points, showing that under different states of the Ravenel's Woods oak-chestnut site (even given the same seral stages), the avian trajectory would have tracked different steady-state performances. Note that each isocline is parameterized by a seral stage. It should also be noted that these are true isoclines, not composite
Figure 24. Hierarchical view of Eastern Forest System vegetation and avian subcommunities.

Figure 24a. Forest system level. Same as Figure 22a.

Figure 24b. Forest type level. Same as Figure 22b.

Figure 24c. Site level (vegetation). A given site within the oak-chestnut forest type will move toward the steady state determined by the state of its environment, the oak-chestnut forest type. If that forest type is in state #1, the site will move to a point along the solid curve in the figure. Along the way, it will pass through xeric shrubland and mixed deciduous stages before reaching a steady state in the oak-chestnut climax stage. If the oak-chestnut forest type were in a different state (e.g. #2), the plant community's trajectory would follow a trajectory toward a steady state on a different locus, although it would be expected to pass through the same seral stages. The composite equilibrium loci in this figure are the same as those in Figure 22c.

Figure 24d. Site level (birds). The bird community moves along a trajectory toward steady states along a series of isoclines corresponding to the seral stages of the plant community. Which steady state obtains on a given isocline depends on the state of the plant community within that seral stage. The trajectory in this figure is the same as that in Figure 23.
Figure 24.
equilibrium loci, since only one site is being considered.

Admittedly, the transition from the vegetation of the Great Smoky Mountains to the bird community of a site 50 km distant requires some problematic assumptions. Such assumptions are not necessary, however, in the four remaining studies of vegetation/avifauna communities, since both tree and bird species data are available for each. Hagar's (1960) study includes both types of data for two seral stages in Happy Camp Mountain Forest in Northwestern California. Karr's (1968) study contains bird species data for five seral stages and tree species data for the first four of these stages on sites in and around Trelease Woods in east-central Illinois. Tree species data for the climax stage is given by Boggess (1964). Kendeigh's (1948) study gives bird species data for four seral stages and tree species data for the first three of these stages at the University of Michigan Biological Station in northern lower Michigan. Finally, Kricher's (1973) study shows bird species data for three seral stages in Hutcheson Memorial Forest in central New Jersey. Tree species data for all three of these stages is given by Bard (1952).

In analyzing these studies, the presentation of the vegetation data will deviate somewhat from the presentation of Whittaker's (1956) data. The chief modification in this
regard has to do with the usefulness of the mesic/xeric classification of tree species on the sites in question. Unlike the situation in the Great Smoky Mountains, the moisture requirements of the species occurring on these sites place almost all of them toward the mesic end of the spectrum, making the mesic/xeric phase plane behavior of these systems uninteresting.

In lieu of a mesic/xeric breakdown, two other measures of the vegetation subsystem's performance will be utilized. MacArthur and MacArthur (1961) viewed plant species diversity and foliage height diversity as two determinants of bird community structure. In similar fashion, canopy (tree) species diversity and canopy height diversity will be chosen here as the two measures of vegetation performance. Canopy species diversity is simply total diversity of the tree subcommunity, broken down by species. Canopy height diversity was calculated by forming species height classes at ten-meter intervals, based on average heights listed in Sargent (1965). Height and density data are listed for all tree species by site in Appendix II. Nomenclature for tree species follows that of Little (1979).

Canopy species diversity, canopy height diversity, avian carnivore diversity, and avian herbivore diversity are displayed by site and seral stage in Table 12. Note that
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<th>SITE</th>
<th>SST</th>
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<th>CHD</th>
<th>ACD</th>
<th>AHD</th>
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<td>4.187</td>
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Table 12. Diversity data for birds and trees in different sites and seral stages.

Abbreviations:
SST = seral stage
CSD = canopy species diversity
CHD = canopy height diversity
ACD = avian carnivore diversity
AHD = avian herbivore diversity
for each study except that of Hagar (1960), the first seral stage is herbaceous, so both canopy species diversity and canopy height diversity are zero for Hutcheson Memorial Forest, Trelease Woods, and the University of Michigan Biological Station. Also, no vegetation data was available for the climax stage at the University of Michigan Biological Station.

The phase plane behavior of these systems is shown in Figure 25. Figure 25a depicts the successional trajectories of the vegetation subsystems (herbaceous initial stages are omitted). The lack of apparent pattern, other than an overall positive correlation between the two diversity measures, is illustrative of the dangers inherent in trying to predict phase plane behavior without detailed knowledge of system organization, initial conditions, and environmental performance. In this case, nothing is known of the environment of any of the four sites other than that each must have followed some pattern of performance during the development of the systems. It is important to remember, however, that the pattern followed by each environment was a particular one, and that had it been different, the trajectory of the corresponding vegetation subsystem would have been different also.

Following Bailey's (1976) classification, all four
Figure 25. Vegetation and avian phase planes for selected sites. Data from four sites in the United States: HCMF = Happy Camp Mountain Forest (Hagar 1960), HMF = Hutcheson Memorial Forest (Kricher 1973), TW = Trelease Woods (Karr 1968), UMBS = University of Michigan Biological Station (Kendeigh 1948).

Figure 25a. Canopy species diversity vs. canopy height diversity. Numbers on trajectory indicate seral stage number.

Figure 25b. Avian carnivore diversity vs. avian herbivore diversity.
Figure 25.
sites are extremely different in terms of their incorporating environmental systems (Table 13). In fact, these sites are not commonly constrained at all below the level of Bailey's Humid Temperate Domain, which covers most of the contiguous 48 states. Importantly, then, if Bailey's hierarchical classification can be viewed in terms of the proposed model, a change in environment at any level below the domain level would result in a change in implied steady state for only one of the four sites. On the other hand, a change in the performance of the humid temperate domain would change the implied steady states for all four sites.

Figure 25b displays the successional trajectories of the avian subcommunities on the four sites. As with the trajectories of Figure 25a, little pattern is apparent. The important point to note is that each trajectory here is a response to the particular trajectory of the corresponding vegetation subsystem shown in Figure 25a. Had the environment of the system been slightly different, the successional trajectory of the vegetation subsystem would have been altered, even though the overall nature of the seres might have been preserved. In Figure 25b, then, the trajectory would have moved toward steady states on the same seral stage isoclines (not shown), but these points would have been different than those shown in the figure.
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<td></td>
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<td>Mem. Forest</td>
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<td>Biol. Station</td>
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<td>Mtn. Forest</td>
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</tr>
</tbody>
</table>

Table 13. Classification of sites.
The message of this analysis, then, is that it is possible to use the proposed model as a sort of lens through which natural systems may be viewed. In using this lens, certain possible interpretations of system organization come into focus, and, of course, certain others may be blurred. As will be discussed in the next section, use of the model per se neither proves nor disproves that the resulting interpretation of system organization is valid. If it is valid, however, then certain implications for system performance result. Some of the more important of these have already been noted, for example the existence of multiple steady state behavior. Another is the manner in which change in a subsystem at one level is exploded into changes in the implied steady states of its constrained subsystems. Also implied is the ability of certain subsystems to exercise constraining influence by virtue of differences in scales of behavior, even though they may not spatially subsume their constrained subsystems. Further implications will be discussed in another section.
The philosophy of science is currently in a state of flux, with no particular view among the wide variety offered being able to command a consensus among philosophers. This may be due in part to the fact that each of the major views tends to have something important to offer the philosophy of science. Apparently, though, no single author has been able to address all of the major problems confronting the philosophy of science to the satisfaction of the bulk of the philosophic and scientific communities.

In suggesting a possible view of conceptual structures and the use of models, it might be best first to lay down a general framework, taking into consideration the major schools of thought. In forming such a framework, it should be acknowledged that many of the post-positivists (e.g. Hanson 1958, Feyerabend 1965, Kuhn 1970) have argued persuasively against the "objective" view of science supported by the logical positivists and their successors. In the post-positivist tradition, any viable philosophy of science must allow a role for the humanness of human
This is not to say that the picture of science painted by the positivists is not grand; it is clearly easy for many, at least many raised in twentieth century Western culture, to find beauty in the ideal of objective science. Nor is it suggested that the role of logic in science be eliminated; surely the advances in the field of logic made by the positivists and their followers can play an important part in a properly-defined science.

In opposing the artificial objectivity required by the positivists, however, the post-positivists have displayed an unfortunate tendency to move toward the opposite extreme. Complete relativism is not a reasonable picture of how scientists actually behave, nor would it be a constructive position for them to take. The idea that people may view reality in any way they please, or that they may view it in any of a finite number of contradictory but equally "good" ways, or worst of all that reality does not even exist would be extremely perplexing for both science and society.

A philosophy far more appealing would be one which admits that there certainly is a reality, and furthermore that this reality bears some relation at least to our purely sensory perceptions of it. Given this, there remains the
question of the precise nature of the relationship. It is exceedingly difficult to get a handle on this question, due at least in part to the limitations of language. In other words, the problem at hand is of an exceptionally fundamental nature, whereas it could be argued that language is less fundamental, and thus a somewhat inappropriate tool for analyzing the problem. Perhaps all that can be asserted here is that the relationship of sense perception to reality is, or may be thought of as being, more or less rule-like. This is not to say that the same phenomenon may not be viewed differently by two different observers or even by the same observer at two different times. It denies, however, that reality is capricious, that the observer/object relationship consists of a random mechanism whereby the same object may arbitrarily elicit any of a number of possible sense perceptions.

Given that there is a reality, then, and that our sensory perceptions of it are determined in a somewhat orderly manner, some issues more obviously in the domain of science may be addressed. For example, given that our observations in science are not merely sensory perceptions, but rather theory-laden interpretations of sensory perceptions, is it possible to say that one interpretation, or theory, is "better" than another, and if so in what sense? Even if it could be concluded that theories come in
varying degrees of "goodness," it would remain to be seen whether or not a human observer could rank them correctly. Finally, even if a human could be concluded to have the capacity to distinguish a good theory from a bad one, it would not follow that a single observer or even a collection of observers would necessarily tend, even in the long run, to progress toward better and better theories.

In deciding whether or not one theory might be better than another, one is forced to establish criteria of goodness. One criterion might be that a better theory is one which is more like the sense perceptions it seeks to interpret, but this would imply that the best theory is no theory at all, leaving only the pure sense perceptions.

Another criterion might be that a better theory is one which is more like reality. This, of course, presumes that reality may be directly perceived and understood. However, if it is assumed that the rule-like relationship between sensory perception and reality is in fact of unknowable quality, then it would be difficult to argue that a human observer could ever tell which of two theories was better by this criterion.

To preserve both the utility of having theory and the ability to distinguish between theories of different merit,
a third position is called for. Perhaps the simplest such position would consist of an assertion that a standard does indeed exist by which theory may be judged, and that this standard is accessible to a human observer. Such a position could be further refined by asserting that there is something about being human that enables a person to non-arbitrarily prefer one view of nature over another, that this "something" is not of his or her own creation entirely, and that it is not (in a basic sense) different for every person.

Such a view bears some resemblance to the philosophy of structuralism (Chomsky 1957, Levi-Strauss 1963, Piaget 1970). Just as one may hypothesize there to be a deep structure of language, culture, and/or behavior implanted in the condition of humanness, so might one hypothesize that there is a basic human standard of theory evaluation. Like similar structuralist arguments, this in the final analysis is only an assertion; it is non-falsifiable and non-demonstrable. Also like other structuralist ideas, this one is meant to imply that the basic ability to distinguish between theories of differing merit can develop differently in different societies and/or individuals, thus inferring that any two societies (or individuals) might not weigh two given theories alike.
There are, of course, other arguments which could be made in order to admit the possibility of a human observer justifiably choosing between theories. Toulmin (1973) makes a case for a method of non-arbitrary theory evaluation modeled after Western judicial systems. He asserts that judges' decisions, while personal, are still rational. Scientists, it is argued, function in the same manner. In any case, having postulated one of these arguments, and deducing therefrom that individual scientists can justifiably claim to be striving toward better and better theories, one may rightly inquire to what extent science as a whole succeeds in doing so.

On this point Toulmin's (1973) evolutionary model of scientific change seems particularly useful. In population biology, evolutionary theory implies that if a population is large enough, then given a constant relative environment, an unlinked genetically-transmitted trait which is adaptive in that environment will eventually come to dominate alternative (less adaptive) traits. If this notion were applied to science itself, one might jump to the conclusion that, given enough scientists and enough time, a better theory will always come to be accepted in preference to a poorer one.

However, it must be remembered that science exists in
an environment, just as does the hypothetical population. For science, the environment is a society with its associated culture. Given that different societies (or even individuals) can develop different ideas of what constitutes a "good" theory, this model only assures that the theory which comes to predominate in a large society will be good given a constant cultural context within which science takes place, and even then it will only necessarily appear good to that society. Thus, in any other society, or even to a non-conforming individual within the same society, it might not appear as though science were progressing.

Furthermore, the number constituting "enough" scientists or "enough" time is indeterminately large, so that even within the mainstream of society where the science is taking place, it is not necessary for science to be progressing at any given point in time. The analogy in population biology would be "genetic drift" pushing evolution in a direction other than that which would be expected in the long run. It is also interesting to note that via the same mechanism, a less fit genotype (or in the case of science, a poorer theory) can become "fixed," that is, it may completely eliminate all alternative genotypes (or theories). Then only a new mutation or immigration from another population (society) can reintroduce a more fit genotype (theory).
Summarizing the discussion so far, a possible view of perceptual experience and the development of scientific theories could be developed around the following ideas: 1) the existence of a reality independent of human observation, 2) an orderly relationship between reality and sensory perception, 3) the ability of an observer to evaluate the merits of alternative theories (interpretations of sensory perception) according to a non-arbitrary standard which is developed in the context of a cultural environment, and 4) a concept of scientific progress analogous to biological evolution at the population level.

Having outlined the main ideas of this view, it might be appropriate to elaborate in greater detail on the development of the theory evaluation process and how theories are interrelated in the mind of the individual scientist.

A Hierarchical View of Personal Conceptual Structures

Part of each human being's development is the gradual formulation of a personal conceptual structure. The elements of this structure shall be defined here as the set of all statements of belief (propositions, axioms, theories) held by an individual, either explicitly or implicitly. Since even implicitly held statements are included, it is
likely that such structures include immense numbers of statements.

It should be remarked at the outset that use of the term "belief" in the above definition should not imply any inconsistency with the position that the relation of perceptual experience to reality is of unknown form. Rather, in light of this position, "belief" may be translated "belief in the truth of an assertion so far as humans are capable of knowing the truth about anything involving perceptual experience."

It shall be conjectured here that the set of statements constituting an individual's conceptual structure can be ranked, theoretically at least, in order of generality. For example, a particular personal conceptual structure might contain the following three statements: 1) The universe is governed by natural laws. 2) The law of gravity applies to all material bodies. 3) If an apple detaches from a tree, it will fall toward the ground. That these three statements are listed in order of decreasing generality may be seen by observing that for any pair of these statements, the lower-numbered statement in some manner addresses all the phenomena addressed by the higher-numbered statement, while the higher-numbered statement does not address the same range of phenomena addressed by the lower-numbered
Thus, statements at the highest levels in a personal conceptual structure so ordered would represent something like "world-view," while those at the lowest levels would represent the most particular hypotheses. A pair of statements at a given level or pair of levels may or may not be consistent. This follows from the definition of personal conceptual structure, in which all implicitly or explicitly held statements of belief, even if contradictory, are included. A conceptual structure will be said to be consistent, then, if all possible pairs of statements at any level or pair of levels are internally consistent.

A graphical representation of this view of personal conceptual structures is shown in Figure 26. In this figure, each statement addresses three possible statements at the next lower level, where each statement is represented by a vertex in the graph. It is assumed that the conceptual structure depicted is consistent. Open circles indicate statements which have been implicitly or explicitly accepted in this particular conceptual framework, cross-hatched circles indicate consistent positions which could be accepted in the future, and solid circles indicate those statements which have been defined to be inconsistent with those held, or which cannot be subsumed by accepted
Figure 26. Hierarchical organization of personal conceptual structures. Each vertex in this graph represents a particular statement in a personal conceptual structure. Open circles indicate statements which have been accepted (implicitly or explicitly), cross-hatched circles indicate currently unadopted statements consistent with those already held, and solid circles indicate those statements which would contradict those already adopted. The higher rows in this graph are taken to correspond to the more general statements in the structure, i.e. those that address a greater range of experience. The number of vertices per row decreases with generality, as might be expected in most conceptual structures. It might be assumed that no low-level statement could be adopted which is not subsumed by some high-level statement. If all edges in this graph were replaced by downward-pointing arcs, this assumption would mean that no statement could be adopted unless its vertex could be reached from the top level by a path traversing only vertices labeled with open circles. Note that more than one low-level statement may be consistent with a given high-level statement. Also, the same low-level statement may be consistent with more than one high-level statement.
Figure 26.
higher-level statements. This figure is meant to impart only a general idea of the view being presented; the particulars of the figure (e.g. number of levels, number of statements, pattern of connectivity, etc.) are by no means general.

The view of scientific development presented in the preceding section has application in the conceptual structures both of individuals and of whole scientific communities. An individual is thus suggested to possess a standard of theory evaluation, developed through the process of his or her own growth and maturation, by which theories are judged. This standard of theory evaluation is applied throughout life as the individual's cumulative experience increases, with the inevitable result that his or her conceptual structure will undergo continuous revision.

In examining the nature of this revision process, it is helpful to draw upon the work of Polanyi (1962), particularly upon his development of the importance of personal commitment in science. In Polanyi's view, the theories held by a scientist tend not to be impersonal hypotheses entertained in some detached manner, but rather sincere beliefs to which the scientist is personally committed.
So far, the precise nature of the hypothesized human standard of scientific evaluation has not been addressed. It should not be too problematic to assert, however, that any such standard would likely include a rationale for resolving conflicts between contradictory statements in a personal conceptual structure. As noted earlier, the proposed definition of conceptual structure does not preclude the existence of such contradictions within a given structure. On the contrary, since the conceptual structure is defined to include all explicitly or implicitly held statements of belief, it seems inevitable that contradictions should arise in all personal conceptual structures.

It might be further asserted that the likely effect of such contradictions becoming explicit is tension in the mind of the individual holding the conflicting beliefs. It will then hopefully not be too controversial to suggest that a reasonable means of resolving such conflicts between beliefs is for the individual to abandon the one(s) to which he or she is less committed.

Some examples might help to visualize this procedure. Suppose that John is out driving in his car one day, and he makes the following assertion: "I believe that I shall make it to the upcoming stoplight before it turns red." Suppose
further, however, that while he is still a good distance away, the stoplight turns yellow. John is then confronted with a fairly straightforward perceptual experience (the stoplight, still a good distance away, turning yellow) which, when combined with his reservoir of past experience concerning the rate at which stoplights change from yellow to red, creates conflict in his personal conceptual structure. Most probably, John will note that his commitment to his original assertion is weak in comparison to his faith in his present experience, and he will abandon his original assertion. Here, then, is an instance in which a single new perceptual experience, working in combination with previous experience, is clearly sufficient to cause the abandonment of a low-level theory.

However, not all theories are so easily falsifiable. It might be suggested in this regard that the possibility of a single perceptual experience causing abandonment of a currently-held belief decreases with each increase in level in the conceptual hierarchy. As an example, suppose that John also holds the fairly high-level belief that all matter obeys the law of gravity. Suppose, then, that one evening John attends a magic show. During the performance, John sees the magician levitate his assistant, with no apparent physical means of support. The magician even passes hoops around his levitated assistant, further enforcing John's
impression that the law of gravity is being violated. Will John abandon his belief in the law of gravity? More likely, he will conclude that his eyes "played a trick" on him, or that the assistant was supported by some device which escaped his attention. In other words, John will abandon his belief that he actually "saw" the anomalous incident in deference to his deeply-held belief that all matter obeys the law of gravity. Polanyi (1962) makes similar reference to the human tendency to "discredit the irresistible testimony of our eyes by classing something as an optical illusion."

In fact, it may not be assuming too much to suggest that for the most part, higher-level beliefs are held more deeply and so are more difficult to dislodge from a conceptual structure than are lower-level beliefs. Not only does the greater personal commitment involved in high-level beliefs work against their dismissal, but conservation of high-level beliefs at the expense of low-level beliefs also affords greater economy. This follows from the definitions of "high" and "low" levels, wherein a higher-level belief is declared to address a greater portion of an individual's experience of the world. Thus, abandonment of a high-level belief would cause an individual to restructure his or her view of a greater domain of experience than would abandonment of a low-level belief.
As mentioned earlier, the upper levels of a personal conceptual structure correspond to what is generally termed "world view" in the philosophy of science. The statements occupying these levels are the most all-encompassing in the conceptual hierarchy, addressing the entire spectrum of lower-level statements. World view thus colors the full range of perceptual experience, and determines the possible theoretical interpretations of that experience.

Pepper (1942) presents one particular analysis of world views, or, in his terminology, "world hypotheses." His definition of a world hypothesis is "a hypothesis of unlimited scope." In other words, a true world hypothesis is one which is able to explain or "deal with" adequately the totality of human experience.

Pepper's work is significant in that it not only asserts the existence of more than one adequate world hypothesis, but thoroughly details four of them. These are, in Pepper's terms, formism, mechanism, contextualism, and organicism. Pepper's development involves the use of "root metaphors" to get at what he considers to be the pure forms of these world hypotheses, and he admits that probably no philosopher has ever subscribed to any of these views precisely as outlined. Still, to facilitate communication regarding these views it is possible to associate with each
of them certain philosophic traditions that come closest to embodying Pepper's description.

Formism can be associated with Platonic idealism, in which category Pepper lumps most of the scholastic tradition. Pepper derives his formulation of this world hypothesis using the concept of "similarity" as a root metaphor.

Mechanism is a materialist, empiricist view of the universe, and may be associated with the philosophies of Descartes, LaPlace, Locke, Berkely, and Hume. The root metaphor of mechanism is the machine.

The contextualist world-view corresponds to the philosophy of pragmatism, and finds proponents in Peirce, James, and Dewey. Its root metaphor is the historic event.

Organicism is Pepper's formulation of the dialectical world view of philosophers such as Hegel. The root metaphor of organicism is integration.

The purpose of listing these curt descriptions of Pepper's four world hypotheses is obviously not to exhaust their implications for understanding perceptual experience, but rather to point out that the existence of a plurality of
compelling world views is not just an abstract potentiality. Importantly, world views similar to the four described by Pepper are influential not only in terms of their impact on the course of history, but in actively shaping the beliefs of present-day societies as well.

While Pepper contends that these four world views are the only historical ones that withstand the tests of adequacy, this contention is certainly debatable. Part of Pepper's rationale for this assertion stems from his insistence on the mutual exclusivity of competing world views. From a strictly logical viewpoint, though, there is no apparent reason why the universe of high-level conceptual generalizations should necessarily be partitionable into a small number of mutually exclusive sets, which would be the case were Pepper's assertion correct. Thus, it could be argued that the diversity of world views is even greater than Pepper suggests.

The Role of Models in Personal Conceptual Structures

A common view of the relation of model to theory holds that a model is in some sense a particular form or partial expression of a theory. Some, e.g. Levins (1966), would invert this suggestion, asserting that a theory is simply a cluster of models.
Another school of thought is the one which views models as "metaphors," a term which will be defined shortly. In the language of the present discussion, this would mean that of all the statements in a conceptual hierarchy, all those that are metaphorical are models. In such a view, models can occur at any level in the conceptual hierarchy, as opposed to the concept of models as inherently low-level explanations.

The view of model as scientific metaphor was first formulated by Black (1962), who utilized Richards' (1936) "interactive" concept of metaphor. Hesse (1965) and Poythress (1983) have further developed the argument. In Poythress' terms, a metaphor "juxtaposes two domains of thought, and by so doing sets in motion a complex interaction of those domains that opens up a new way of looking at the world."

Such an approach to metaphor is in opposition to, for example, the "substitution" view of metaphor (Black 1962). In the substitution view, a metaphorical expression is taken to be used in place of some equivalent literal expression. The substitution view tends to be accompanied by a concept of metaphor as decoration; i.e. adding nothing of substance to a statement, only style.
Black (1962) gives an example of how the statement "The chairman plowed through the discussion" might be viewed from the substitution perspective: "A speaker who uses the sentence in question is taken to want to say something about a chairman and his behavior in some meeting. Instead of saying, plainly or directly, that the chairman dealt summarily with objections, or ruthlessly suppressed irrelevance, or something of the sort, the speaker chose to use a word ('plowed') which, strictly speaking, means something else. But an intelligent hearer can easily guess what the speaker had in mind."

In the interactive approach, however, the metaphor has no equivalent literal expression. Rather, two subjects are viewed as acting together in the eyes of an observer to produce meaning. For example, in the metaphorical statement "Man is a wolf," the two subjects consist of the principal subject, Man, and the subsidiary subject, Wolf (Black 1962). Viewing model as metaphor, then, makes the principal subject the thing or process in the world that is being modeled, and the subsidiary subject the thing used to do the modeling (Poythress 1983). Regretably, there is some ambiguity here regarding whether the model is defined as the subsidiary subject itself or the dynamic interaction resulting from juxtaposing the two subjects. Fortunately, though, context often clarifies which meaning is intended.
Following the interactive approach, the operation of the metaphoric process may be described as follows: First, the metaphor applies to the principal subject a system of "associated implications" characteristic of the subsidiary subject. In so doing, the metaphor selects, emphasizes, suppresses, and organizes features of the principal subject by implying statements about it that normally apply to the subsidiary subject (Black 1962). The principal subject is not, however, a purely passive object of the metaphoric process. Rather, it is an active participant in the process, in that it has its own set of associated implications that interplay with those of the subsidiary subject. In this view, a metaphor may be thought of as a lens through which the principal subject is viewed (Black 1962). What the observer then sees is the product of a complex system involving himself, the subsidiary subject, and the principal subject.

This description pictures metaphor in a scientific, observational setting. Of course, the use of metaphor is not unique to science. The distinctiveness, in this view, of scientific metaphor (model) is that it is relatively controlled. The "control" of a metaphor, according to Poythress (1983), concerns the ability of the scientist to focus on those aspects of the metaphor which are most relevant. Control, then, comes in degrees, yielding a
continuum between highly controlled metaphors (strict models) and uncontrolled metaphors (poetry).

Such a view results in increased freedom for the scientist in terms of the use of models. For example, in a world view such as Pepper's (1942) formulation of contextualism, a concept of model as "special theory" would virtually prohibit the use of mathematical models, for it is extremely difficult to see how a mathematical model could ever be a special form of any truly contextualistic theory. However, in a view of model as metaphor, even a pure contextualist may have occasion to say, "X may be metaphorically represented by this set of equations."

On the other hand, this approach also results in increased responsibility for the scientist in terms of the control of the model. That is, the scientist must be careful not to dismiss out of hand potentially relevant phenomena which the metaphor does not symbolize well, or on the other hand being careful not to deduce consequences based on those aspects of the metaphor which are irrelevant to the domain being modeled (Poythress 1983).

Importantly, even though mathematical models may be appropriate as metaphors in a number of conceptual structures, it does not follow that their meanings as
metaphors will be the same in each of the different conceptual structures. In other words, a mathematical model viewed as a metaphor in a contextualistic conceptual structure would very likely have a different meaning than the same model viewed as a metaphor in a mechanistic conceptual structure.

Given the above framework, the following sections examine the uses and implications of the types of steady-state models developed so far in terms of four different (though partial) conceptual structures: 1) the "Resilient Nature" perspective of Holling (1978), 2) the "gradient analysis" approach to plant ecology, 3) a particular theory in the field of natural resource economics, and 4) the biological conceptual framework of Warren et al. (1979).

A View of Nature Based on Stability and Resilience

The past decade has witnessed the rise in the ecological literature of a partial conceptual structure which purports to be a "very different view of the world" (Holling 1973). It is a view of nature that emphasizes the properties of stability and resilience, and has spawned a companion theory of natural resource management known as "adaptive" management (Holling 1978).
Like the two partial conceptual structures that will be examined in the next two sections, this one (referred to hereafter as "the stability and resilience view") is generally compatible with a mechanistic world view (Pepper 1942). Ironically, its proponents advance it as an alternative to the traditions of analysis in ecology that "have been largely inherited from developments in classical physics" (Holling 1973). The influence of classical physics, in this argument, has been to place undue emphasis upon equilibrium states, a view which is alleged to be essentially static, providing little insight into the transient behavior of systems.

However, if there is a root metaphor for this view, it is one which could hardly be more mechanistic: a relatively simple (30 coefficients), two-variable computer model which generates multiple domains of attraction in the phase plane (Holling and Ewing 1971). In fairness, though, it should be added that proponents of this view would likely reject the interpretation of this model as a metaphor, since they tend to adhere strongly to the belief that the merit of their view is its direct correspondence to reality.

As far as rebelling against classical physics is concerned, the only facet of the stability and resilience perspective that deviates from the LaPlacian ideal is the
belief that "the behavior of ecological systems is profoundly affected by random events." When such events are included in ecological models they are taken to represent an added "level of realism" (Holling 1973). This, of course, is out of step with the classical form of mechanism only, and would in no way be out of place in a mechanistic world view enlightened by modern physics.

Thus, if the stability and resilience view of nature may be safely placed within the mainstream of mechanism, it remains to be seen in what sense this perspective constitutes a "very different view of the world." The difference of this view, it turns out, is a difference relative to the view which holds that natural systems can truly be represented by constant-coefficient mathematical systems exhibiting either globally-stable equilibrium points or globally-stable limit cycles.

The mechanistic alternative provided by the stability and resilience view is that natural systems can truly be represented by mathematical systems exhibiting multiple equilibrium points for each set of coefficient values. Such mathematical systems constitute the basis for the stability and resilience view. The definition of stability adopted in this view usually approximates the standard definition of asymptotic stability. Resilience, however, is defined in a
number of distinct, though related, fashions. A few of the proposed definitions, or measurements, of resilience are listed below:

"...a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables" (Holling 1973).

"...the overall area of the domain of attraction" (Holling 1973).

"...the height of the lowest point (on the rim) of the basin of attraction" (Holling 1973, phrase in parentheses added).

"...probabilities of extinction" (Holling 1973).

"...a property that allows a system to absorb and utilize (or even benefit from) change" (Holling 1978).

"...the ability to adapt to change by exploiting instabilities, rather than the ability to absorb disturbance by returning to a steady state after being disturbed" (Walker et al. 1981).
The type of mathematical model that gave rise to this view can be profitably contrasted with multiple steady state models by analyzing their associated digraphs. In the formulation of isocline theory presented earlier, the existence of multiple system isoclines was shown to be dependent on the existence of what was termed the "effective environment" in the system digraph. In the graph-theoretic interpretation of isocline theory, the variables of the effective environment were defined as those which could be reached from the system by a semipath of length one but by no path. An example of a system and its associated effective environment is shown in Figure 27a.

In contrast, the prototypic model of the stability and resilience school has no effective environment (Holling and Ewing 1971). The coefficients of this mathematical system are constant. An example of such a system is shown in Figure 27b. For this system, steady-state behavior cannot vary with changes in the state of the environment, for there is no environment.

The example of Figure 27 is drawn in a way that might suggest to some that the basic model of the stability and resilience school is simply a special case selected from the set of possible system/environment complexes, namely the "null" case in which the system has no environment.
Figure 27. Graph-theoretic view of the system/environment distinction.

Figure 27a. System together with its effective environment. Environmental vertices are labeled with open circles. System state variables are labeled with solid circles.

Figure 27b. System with no effective environment. This figure is the subgraph of Figure 27a obtained by deleting the environmental vertices and all arcs emanating from them.
Figure 27.
However, such a conclusion would largely be a matter of perspective. Had the digraphs of Figure 28 been chosen as examples of the two system types instead of the digraphs of Figure 27, a very different conclusion might have been inferred, namely that "effective environment" is merely an artifact of making a more complex system simple by ignoring certain relationships. From this perspective, systems with associated effective environments are viewed as special cases selected from the set of more fully-connected systems.

The possibility of this difference in perspective arises from the fact that the digraphs of Figures 27 and 28 represent purely mathematical systems. As these systems are not claimed to constitute models of any natural systems in particular, it is impossible to ascertain which is more general; i.e. whether the non-environmental view ignores significant variables, or whether the system/environment view ignores significant relationships between variables.

The difference between the two views can also be used to illustrate how an observer's own conceptual structure determines how he or she interprets perceptual experience. For example, to an observer holding the system/environment model as a metaphor of natural systems, the observation of a natural system asymptotically approaching state A during one time period and state B during another time period might
Figure 28. Another view of the system/environment distinction.

Figure 28a. System together with its effective environment. Environmental vertices are labeled with open circles. System state variables are labeled with solid circles.

Figure 28b. System with no effective environment. Figure 28a is the subgraph of this figure obtained by deleting all arcs leading to the outermost vertices on the top row.
Figure 28.
likely be "seen" as the consequence of a change in the system's environment.

On the other hand, to an observer holding the non-environmental model as a metaphor of natural systems, the same observation might likely be "seen" as the consequence of a perturbation forcing the system across the boundary between two domains of attraction. Resolution of this dilemma will not be found in naive efforts to establish the ontological veracity of one view or the other. Rather, evaluation of the two views will depend largely on the incorporating conceptual structure of the evaluating individual or scientific community, and the role the views are asked to play within that structure.

The above discussion deals with the non-environmental, constant-coefficient type of models that formed the initial framework for the stability and resilience view. However, continued development of this school of thought has gone far toward relaxing the restrictions of these models. For example, it is now acknowledged that the boundaries between ecosystem stability regions move as an outcome of natural selection, and that models should mimic "behavior over time and for a variety of conditions" (Holling 1978). In this more sophisticated form, the stability and resilience perspective does not pose any necessary conflict with the
system/environment type of model, but, depending on the conceptual structure in which it is incorporated, may complement it.

The stability and resilience view is particularly significant in that it is one of the few theoretical developments in ecology which has been articulated hand-in-hand with a theory of ecosystem management ("adaptive management," Holling 1978). Just as the stability and resilience perspective is something less than a total world view, however, so the adaptive management perspective is something less than a complete theory of ecosystem management.

The tenets of adaptive management generally appear to be consistent with the tenets of the stability and resilience view, although it is not always clear that the former necessarily follow from the latter. Still, the proponents of the two theories seem to view the relation between them as one of logical implication (i.e. stability and resilience implying adaptive management): "A management based on resilience ... would emphasize the need to keep options open, the need to view events in a regional rather than a local context, and the need to emphasize heterogeneity" (Holling 1973).
Likewise, seven principles of adaptive management are said to "emerge" from the following four "basic properties" of ecological and human systems (Holling 1978): 1) organized connection between parts, 2) spatial heterogeneity, 3) resilience, and 4) dynamic variability. The seven principles which are said to emerge from these are as follow (Holling 1978):

"1) Environmental dimensions should be introduced at the very beginning of the development or policy design process and should be integrated as equal partners with the economic and social dimensions.

"2) Thereafter, in the design phase, there should be periods of intense, focused innovation involving significant outside constituencies, followed by periods of stable consolidation.

"3) Part of the design should include benefits attached to increasing information on unknown or partially known social, economic, and environmental effects. Information can be given a value just as jobs, income, and profit can.

"4) Some of the experiments designed to produce information can be part of an integrated research plan, but others should be designed into the actual management
activities. Managers as well as scientists learn from change.

"5) An equally integral part of the design is the monitoring and remedial mechanisms. They should not simply be post hoc additions after implementation.

"6) In the design of those mechanisms there should be a careful analysis of the economic trade-offs between structures and policies that presume that the unexpected can be designed into insignificance and less capital intensive mechanisms that monitor and ameliorate the unexpected.

"7) Variability of ecological systems, including occasional major disruptions, provides a kind of self-monitoring system that maintains resilience. Policies that reduce variability in space or time, even in an effort to improve environmental 'quality,' should always be questioned."

Clearly, all seven of these statements are of a normative nature. It may be noted, for example, that each includes a statement of something that "should" be done. However, it is impossible to derive normative statements from a set of positive (non-normative) properties such as the four "basic properties" listed above, independent of a
companion theory of value or welfare or the equivalent. Ironically, this fact seems to be implicitly recognized by the proponents of the theory: "Comparison of alternative policies can occur only if someone places values on the results of each alternative" (Holling 1978).

For the same reason, the steady-state model proposed in the present research cannot be shown to imply the tenets of adaptive management. However, it is possible to discuss whether or not the proposed model is concordant with these tenets. It may also be possible to critique certain non-normative aspects of adaptive management from the perspective of the proposed model.

The basic message of adaptive management, that change is both inevitable and good, and that a central aim of environmental management should be to preserve future options, has contextualistic overtones that might appear surprising to some in light of the solidly mechanistic background in which the stability and resilience view is cast (Pepper 1942). Likewise, even though the mathematical framework of the proposed steady-state model is totally at home in a mechanistic conceptual framework, both the explicit allowance for variable coefficients and the incorporation of the system/environment distinction help to mitigate any tension with more contextualistic aims.
The multiple steady state nature of the proposed model meshes especially well with the idea that ecosystem managers ought to keep their options open. If ecosystems can be usefully modeled as existing in the context of an incorporating environment, and if that environment should change, then an unalterable management strategy tailored to one particular state of the environment could lead to extinction of valuable resources (Thompson 1981).

Likewise, the hierarchical nature of the proposed model appears to be concordant with adaptive management's need for a workable means of viewing the system to be managed: "An explicit effort to structure models as hierarchies can help to formalize the problem. That is, the problem can be structured as a hierarchy and defined by focusing on three or four levels of that hierarchy that differ in their speed or geographic scale or both" (Walker et al. 1981). The model's hierarchical characteristics also facilitate adaptive management's concern for a regional emphasis in ecosystem management.

Gradient Analysis of Plant Communities

"Gradient analysis" is a term used to denote both a technique in plant ecology and an associated point of view regarding certain aspects of biological organization. The
origin of gradient analysis can be found in the work of Ramensky (1924), although its acceptance as a fundamental concept in vegetation ecology is owed mainly to the work of Whittaker (1948, 1951, 1956) and the "Wisconsin School" (Curtis and McIntosh 1951, Brown and Curtis 1952).

The basic model of gradient analysis consists of a set of species distributions mapped in an n-dimensional Cartesian space. The mathematical nature of this model thus allows gradient analysis to fit easily into a mechanistic conceptual structure. As will be seen later, the proponents of gradient analysis also tend to reduce systems to their more elementary (and allegedly more "real") components. This, too, tailors gradient analysis for incorporation within a mechanistic conceptual structure. Pepper (1942) distinguishes the "consolidated" mechanism of modern physics from the simple determinism of "discrete," or Newtonian mechanics. In this dichotomy, gradient analysis' emphasis on the statistical nature of species distributions would make it more adapted to a consolidated form of mechanism.

Gradient analysis may conveniently be divided into "direct" and "indirect" approaches, of which only the former will be dealt with here. In direct gradient analysis, vegetation samples are arranged and studied according to known magnitudes of (or indices of position along) an
environmental gradient which is accepted as a basis of the study (Whittaker 1967). This gradient may correspond to a line in physical space. For example, a path extending from a low to a high elevation on a hillside might constitute an "elevation gradient" in this type of study.

A fundamental belief of gradient analysis' stronger proponents is that the population is the proper unit of study in plant ecology; i.e. that communities are more a contrivance of human observers than a natural level of biological organization. By way of analogy, the biological community taken in the context of its surrounding communities may be thought of as a single color in the context of the spectrum of light wave lengths (Brown and Curtis 1951; Whittaker 1967, 1975). The spectrum, like a broad expanse of vegetation, is (in this view) essentially continuous. Due to the nature of his or her own observational capacity, however, a human observer tends to single out certain stretches of the spectrum (or vegetation expanse) as discrete entities.

It is further claimed that this belief is supported by the patterns of species distributions which result when species densities are plotted along environmental/spatial gradients. In the prototypic applications of gradient analysis, species densities so plotted did not reveal
"package" distributions, but rather quasi-Gaussian curves, with each species curve exhibiting a unique mean and variance (Figure 29). Since such population-level distributional analysis did not reveal distinct community boundaries, it was concluded that "community" does not exist as a natural level of organization.

Whether or not this conclusion is true, use of hierarchy theory casts some doubt on the validity of the argument. In particular, the view of Allen and Starr (1982) emphasizes the illegitimacy of discounting the importance of a given level of organization (such as the community level) based on analysis of a lower level (such as the population level). Humans, as individual organisms, find themselves closer to the population level of organization than to the community level, and so might be expected to more easily recognize the former more easily.

It should also be noted that the technique of discounting higher levels based on apparent spatial continuity of lower levels can be used, assuming its validity, to dismiss the existence of almost any organizational level whatsoever. For example, while proponents of gradient analysis have no apparent objection to the reality of the population level of organization, a gradient analysis of populations focusing on individual
Figure 29. Three possible species distribution patterns (after Whittaker 1975). Each curve represents the distribution of a population along an environmental gradient.

Figure 29a. Sharply-demarcated species assemblages. In this pattern, certain species tend to occur together as "packages," with little overlap between assemblages.

Figure 29b. Overlapping species assemblages. In this pattern, certain species still tend to occur together as packages, but there is considerable overlap between assemblages.

Figure 29c. Individualistic distribution. In this pattern, species do not tend to occur together as packages, and there is considerable overlap between species distributions. This is the pattern which was found in the prototypic applications of gradient analysis.
Figure 29.
organisms would tend to "disprove" the existence of populations, since there are generally no discrete boundaries between populations as the term is usually defined.

Suppose, then, that instead of being purely observational artifacts, communities are just as much natural units as populations are. The problem then becomes one of how to interpret the results of those gradient analyses which tend to obscure community boundaries. A variety of possible solutions to this problem have been given elsewhere, and need not be reiterated here. Instead, an example of a hierarchically organized system will be given in which both classical gradient behavior and higher levels of organization are exhibited.

This example will be drawn from the system of Figure 6 in the section on model development. By definition, this system includes four levels of organization. Suppose that a particular gradient analysis were to focus on level four. Suppose further that the top row of Figure 6d were to constitute the spatial gradient used in the analysis. Moving from left to right along this gradient in physical space, the researcher would thus encounter constituents $C(4,1)$, $C(4,2)$, $C(4,5)$, $C(4,6)$, $C(4,17)$, $C(4,18)$, $C(4,21)$, and $C(4,22)$, respectively.
By the presuppositions of gradient analysis, the researcher would assume that the identified spatial gradient represents a "complex gradient" (Whittaker 1956) of environmental factors with which the observed pattern of performance is correlated. In this case, however, the immediate cause of the steady-state performances of each of these constituents is the state of the relevant constraining constituent. Note that there are four constraining constituents involved at level three: C(3,1) constrains C(4,1) and C(4,2), C(3,2) constrains C(4,5) and C(5,6), C(3,5) constrains C(4,17) and C(4,18), and C(3,6) constrains C(4,21) and C(4,22). Table 14 gives the canonical representations of C(4,5-8), C(4,17-20), and C(4,21-24). The canonical representations of C(4,1-4) are given in Table 8. All constituents have asymptotically stable steady states.

If the habitat and biotic performances of C(3,1), C(3,2), C(3,5), and C(3,6) were all fixed at values of (1,1), the biotic performances of the level-four constituents encountered along the hypothesized gradient could be plotted against a spatial position index as shown by the solid circles in Figure 30a. If, however, the performances of any of the constraining constituents were different, the performances of the corresponding level-four constituents along the hypothesized gradient would change as
\[
\begin{align*}
\frac{dH(4,5)/dt}{dB(4,5)/dt} &= \begin{bmatrix} 2.00 & -2.00 \\ -0.50 & 2.50 \end{bmatrix} + \begin{bmatrix} 2.50 \\ 1.00 \end{bmatrix} + \begin{bmatrix} 1.50 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,2) \\ B(3,2) \end{bmatrix} \\
\frac{dH(4,6)/dt}{dB(4,6)/dt} &= \begin{bmatrix} 3.00 & -1.00 \\ -1.50 & 1.50 \end{bmatrix} + \begin{bmatrix} 3.50 \\ 1.50 \end{bmatrix} + \begin{bmatrix} 1.00 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,2) \\ B(3,2) \end{bmatrix} \\
\frac{dH(4,7)/dt}{dB(4,7)/dt} &= \begin{bmatrix} 4.00 & -1.50 \\ -2.50 & 2.50 \end{bmatrix} + \begin{bmatrix} 4.50 \\ 2.00 \end{bmatrix} + \begin{bmatrix} 1.00 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,2) \\ B(3,2) \end{bmatrix} \\
\frac{dH(4,8)/dt}{dB(4,8)/dt} &= \begin{bmatrix} 5.00 & -2.00 \\ -3.50 & 3.50 \end{bmatrix} + \begin{bmatrix} 5.50 \\ 2.50 \end{bmatrix} + \begin{bmatrix} 3.00 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,2) \\ B(3,2) \end{bmatrix} \\
\frac{dH(4,17)/dt}{dB(4,17)/dt} &= \begin{bmatrix} 3.00 & -2.00 \\ -1.50 & 3.00 \end{bmatrix} + \begin{bmatrix} 3.00 \\ 1.00 \end{bmatrix} + \begin{bmatrix} 0.50 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,5) \\ B(3,5) \end{bmatrix} \\
\frac{dH(4,18)/dt}{dB(4,18)/dt} &= \begin{bmatrix} 3.00 & -2.50 \\ -3.00 & 4.00 \end{bmatrix} + \begin{bmatrix} 4.00 \\ 2.50 \end{bmatrix} + \begin{bmatrix} 1.50 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,5) \\ B(3,5) \end{bmatrix} \\
\frac{dH(4,19)/dt}{dB(4,19)/dt} &= \begin{bmatrix} 3.00 & -2.00 \\ -4.00 & 5.00 \end{bmatrix} + \begin{bmatrix} 5.00 \\ 3.00 \end{bmatrix} + \begin{bmatrix} 1.00 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,5) \\ B(3,5) \end{bmatrix} \\
\frac{dH(4,20)/dt}{dB(4,20)/dt} &= \begin{bmatrix} 3.00 & -2.00 \\ -5.50 & 6.00 \end{bmatrix} + \begin{bmatrix} 6.00 \\ 3.50 \end{bmatrix} + \begin{bmatrix} 0.50 \\ 2.00 \end{bmatrix} \begin{bmatrix} H(3,5) \\ B(3,5) \end{bmatrix} \\
\frac{dH(4,21)/dt}{dB(4,21)/dt} &= \begin{bmatrix} 1.50 & -1.50 \\ -2.00 & 1.50 \end{bmatrix} + \begin{bmatrix} 1.50 \\ 2.00 \end{bmatrix} + \begin{bmatrix} 1.50 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,6) \\ B(3,6) \end{bmatrix} \\
\frac{dH(4,22)/dt}{dB(4,22)/dt} &= \begin{bmatrix} 2.00 & -1.50 \\ -3.00 & 3.00 \end{bmatrix} + \begin{bmatrix} 2.50 \\ 1.50 \end{bmatrix} + \begin{bmatrix} 2.50 \\ 1.00 \end{bmatrix} \begin{bmatrix} H(3,6) \\ B(3,6) \end{bmatrix} \\
\frac{dH(4,23)/dt}{dB(4,23)/dt} &= \begin{bmatrix} 2.50 & -1.50 \\ -4.00 & 3.50 \end{bmatrix} + \begin{bmatrix} 3.50 \\ 3.00 \end{bmatrix} + \begin{bmatrix} 3.50 \\ 2.00 \end{bmatrix} \begin{bmatrix} H(3,6) \\ B(3,6) \end{bmatrix} \\
\frac{dH(4,24)/dt}{dB(4,24)/dt} &= \begin{bmatrix} 3.00 & -1.50 \\ -5.00 & 4.50 \end{bmatrix} + \begin{bmatrix} 4.50 \\ 3.50 \end{bmatrix} + \begin{bmatrix} 4.50 \\ 2.50 \end{bmatrix} \begin{bmatrix} H(3,6) \\ B(3,6) \end{bmatrix}
\end{align*}
\]

Table 14. Transformational behavior of C(4,5-8), C(4,17-20), and C(4,21-24).
Figure 30. Gradient plots of performance indices from top row of level-four constituents in Figure 6. The index on the y-axis represents some performance measure of the biotic subsystems. The gradient consists of a spatial index (x-axis), with constituent number shown in parentheses. The value of each of the four constraining constituents is fixed at (1,1), except that an alternate performance is also shown for B(4,1) and B(4,2) when the environment of those two subsystems [C(3,1)] is fixed at a value of (1,1.4).

Figure 30a. Simple plot of biotic performance against spatial gradient. Solid circles represent points obtained under uniform environment of (1,1). Open circles represent points obtained under C(3,1) = (1,1.4).

Figure 30b. Population breakdown of biotic performances. The same four populations (A, B, C, and D) are assumed to constitute the biotic community of each constituent. Each letter on the graph represents the density of that population at that point along the gradient. Circled letters indicate population performances under alternate C(3,1) value of (1,1.4).

Figure 30c. Smoothed performance gradients. In this figure, the letters of Figure 30b have been replaced by points and connected by smooth curves. A gradient for total population performance is also shown. Dashed curves indicate gradients obtained under alternate C(3,1) value of (1,1.4).
Figure 30.
well. The open circles in Figure 30a show the change in the overall pattern of steady-state performance that would result from a shift in C(3,1) performance from a value of (1,1) to a value of (1,1.4). Note that this shift in C(3,1)'s performance results in steady-state performance shifts only for the level-four constituents constrained by C(3,1), namely C(4,1), C(4,2), C(4,3), and C(4,4). However, since only two of these four constituents [C(4,1) and C(4,2)] occur along the relevant gradient, the steady-state shifts of only these two constituents appear in Figure 30a.

The performances plotted in Figure 30a represent some measure of overall biotic performance. The precise nature of this measure has so far gone undefined. For the purpose of this illustration only, it shall be assumed that the measurement represents total biomass. To facilitate further discussion, it shall also be assumed that four species (A, B, C, and D) occur along the hypothesized gradient, though all species need not occur in each constituent subsystem. Figure 30b shows some hypothesized levels of the four populations along the gradient. These levels were chosen to be consistent with the overall biotic performances given in Figure 30a (i.e. summing the species densities gives the total density).

To an observer viewing this data from the perspective
of gradient analysis, the next logical step would be to connect the points for each species by a smooth curve, as shown in Figure 30c. Note that the species performance values were chosen not only to be consistent with the overall biotic performances, but also to yield smooth Gaussian curves; in fact, Gaussian regressions performed on the species data yield $R^2$ values of at least .98 in each case. Thus, there would be no reason for the gradient practitioner to view these results as anything other than typical.

It must be remembered that the system in question exhibits very real levels of organization not only at the level of the gradient analysis (level four), but at three higher levels as well. Thus, this system represents a case in which the "typical" findings of gradient analysis in no way prohibit the existence of higher levels of organization.

The phase plane behavior of the system is shown in Figure 31a, and replicated in Figure 31b. The solid curves in Figure 31a show the composite equilibrium loci for the constituents constrained by $C(3,1)$, $C(3,2)$ $C(3,5)$, and $C(3,6)$, when these level three constituents are all held at values of (1,1). The solid circles represent those constituents occurring along the gradient, while the open circles represent commonly-constrained constituents not
Figure 31. Composite phase planes of gradient behavior. Performances of biota and habitat subsystems have been plotted for each constituent along the gradient, and related in two different manners.

Figure 31a. Composite equilibrium loci for commonly-constrained constituents. The performances of each of the eight constituents along the gradient are shown here as solid dots, labeled according to constituent number. The performances of other commonly-constrained constituents are plotted as open dots. Each of the four sets of commonly-constrained constituents is joined by a composite equilibrium locus (solid curves). The dashed curve shows the position of the locus for C(4,1-4) when the state of the environment [C(3,1)] changes from (1,1) to (1,1.4).

Figure 31b. Translation of gradient to phase space. Here, the constituent performances have simply been plotted and connected by a curve according to their positions along the spatial gradient. The dashed curve indicates the form the path would take if C(3,1) had taken on a value of (1,1.4).
Figure 31.
occuring along the gradient. The dashed curve represents the composite equilibrium locus corresponding to $C(4,1-4)$ when $C(3,1)$ has a value of $(1,1.4)$.

When viewed in this manner, the organization of the system is clarified, since the steady-state performance of each constituent can be viewed in terms of its relation to the performances of commonly-constrained constituents. Figure 31b shows the steady-state performances of only those level-four constituents lying along the gradient. Here, the underlying organization of the system is ignored, and the performances are simply linked by a smooth curve following the order in which they lie along the gradient. This is how the data would be viewed by one who discounted the existence of other levels of organization. In this example, very little understanding is gained by adopting such a perspective.

None of this is meant to demean the importance or validity of gradient analysis per se. Rather, the intent is merely to suggest that gradient analysis of population-level data cannot disprove the existence of higher levels of organization, and that ignoring patterns of control involving such higher levels can detract from a full understanding of the system, even at the population level.
Importantly, this suggestion is not made from a viewpoint totally alien to gradient analysis. There is nothing inherently incompatible between the hierarchical model used here as an illustration and the mathematical models of gradient analysis. Any incompatibility that might be perceived arises when gradient analysis is used to address areas of ecological organization that it only poorly illuminates.

Multiple-Use Natural Systems in an Economic Framework

The Metaphor of the Multiple-Product Firm

Economics and ecology are in many ways closely allied disciplines. The domain of each consists of exceedingly complex systems, characterized by both qualitative and quantitative types of change. Both are commonly thought of as "new" sciences, at least relative to physics and astronomy. In addition, both have experienced attempts to force their respective theories to fit the form of Newtonian physics. As a result, both tend to adapt their theories and models for incorporation into a generally mechanistic conceptual structure (Pepper 1942). Finally, each has relied increasingly on a "systems" approach to understanding its domain. Perhaps it is no coincidence that two of the founding fathers of modern general systems theory were an
A natural interface between economics and ecology may be found in the area of natural resource management. Natural resources, as important components of ecosystems, certainly fall within the domain of ecology. Due to the fact that humans are among the primary utilizers of natural resources, management of these resources just as certainly falls within the domain of economics. Unlike the stability and resilience perspective discussed earlier, economics has a well-developed theory of welfare, thus enabling the normative issues of natural resource management to be addressed.

Within the discipline of economics, then, there exists a set of theories and models which, taken together, form a partial conceptual structure addressing natural resource management. One well-known element of this set is a model whose principal subject is the multiple-use natural system (e.g. state and national forests, Bureau of Land Management holdings, and the like), and whose subsidiary subject is the multiple-product firm (Gregory 1955, Zivnuska 1961, Hagenstein 1962).

This metaphor shall be explored here in order to understand 1) its usefulness in helping to manage
multiple-use natural systems, and 2) whether steady-state analysis would be more useful. This shall be done by first noting in a general way how multiple-use natural systems might differ from the notion of a "typical" multiple-product firm. Then the theory of the multiple-product firm will be examined in greater detail, along with some specific problems that multiple-use natural systems present in this regard. Finally, a model will be presented and analyzed, illustrating certain points concerning the nature of multiple-use natural system organization and some implications of steady-state analysis.

Convery (1977) lists a number of characteristics which to some degree distinguish the management of multiple-use natural systems from the management of multiple-product firms. One of these is the length of production time involved in growing trees, which may be several centuries if the site involved has value as a wilderness area. Another is the public goods nature of some of the products of multiple-use natural systems. Such public goods include satisfaction yielded to individuals who benefit from simply knowing that the resources exist (vicarious consumption), benefits accruing to individuals as a result of having the option of personally enjoying the resources (option demand), and of course "non-consumptive" utilization of the resource (where such utilization takes place on a small enough scale
that participants' derived utility is not diminished by crowding from other participants).

Other products of multiple-use natural systems which cannot really be classified as public goods may still bear an important similarity to public goods in that many are non-market commodities. One of the most significant of these is recreation. Recreation is also distinguished on the basis that it is a final consumption good, and can in a sense be viewed as being consumed by the same individuals which "produce" it. That is, the "on-site" nature of recreation production/consumption confuses the two processes.

Another distinguishing characteristic of multiple-use natural systems given by Teegarden (1979) is the comparative fixity of the overall set of possible production services. In other words, a factory can generally re-tool to produce an extremely wide array of products (although this may be at no small expense), whereas the capacity of a given parcel of land to produce a variety of goods may be viewed as much more limited.

The role of the natural environment in multiple-use natural systems is an important one; as will be seen later it can overshadow disequilibrium economic considerations in
the long run.

Finally, a major difference between multiple-use natural systems and multiple-product firms in general is the public nature of multiple-use natural systems: not only do multiple-use natural systems yield public goods, but ownership of such systems is commonly public as well.

Before pursuing some of these distinguishing aspects in greater detail, it will be helpful to recall some of the basic theory of the multiple-product firm. First of all, it is necessary to find a good definition for "multiple-product firm." Depending on the degree of precision required, this need not be difficult. In general, a multiple-product firm is one which produces more than one distinct product (though attempting to distinguish "distinct" products from "similar" products creates room for debate even within this general definition). Beyond this, different authors vary in terms of specifics. Some seem to prefer to restrict use of the term to processes which either cannot yield fewer than two products, or which yield more than one with very little extra effort required. The classic example here is sheep raising, which produces both wool and mutton (Heady and Jensen 1954). A less restrictive definition would not limit the term to single processes yielding more than one product but would include sets of distinct processes which are
either located in the same plant or at least carried out under the same management (Henderson and Quandt 1958).

The basic theory of multiple-product economics can be found in a number of good texts (Carlson 1939, Henderson and Quandt 1958). For the simple, perfect competition case, the gist of the theory may be presented as shown in Figure 32. Multiple-product economics is often referred to as "joint product" economics. When referred to as such, the concept of a "joint production function" follows in a straightforward manner. A joint production function defines the relationship between the quantities of goods produced across some set of inputs. In Figure 32, the joint production function is shown in terms of a set of "iso-cost production possibility frontiers" (iso-cost PPF's). The iso-cost PPF defines the possible combinations of outputs (in this case for two goods), given that all bundles of inputs must have the same total cost. Thus, there exists a family of iso-cost PPF's, each associated with a given total cost level.

To optimize the production process illustrated in Figure 32, the firm would produce that bundle of goods where the absolute value of the derivative of the iso-cost PPF (dPRODUCT2/dPRODUCT1) was equal to the ratio of the product prices (P1/P2). Thus there would be an optimum point
Figure 32. Production possibility frontiers and expansion path. For a given total cost level, a curve is defined (the production possibility frontier) relating the tradeoff between production of products 1 and 2. The profit-maximizing firm will choose to produce at the point along the frontier where the absolute value of the curve's derivative is equal to the ratio of the product prices (price of product 1 divided by price of product 2). Linking these optima on the family of production possibility frontiers gives the firm's expansion path. The profit-maximizing firm will always produce along this path.
Figure 32.
associated with each iso-cost PPF (i.e. each total cost level). Linking these optima yields the bold dashed line in Figure 32, which is termed an "expansion path." Of course, the homothetic iso-cost PPF's in Figure 32 result in unambiguous relationships between total cost, production, and prices. However, it should be kept in mind that, in general, iso-cost PPF's may take on a variety of shapes, with the result that these relationships may be less clear.

For example, while there is only one optimum associated with a given curve in Figure 32, it is possible for a given curve to exhibit multiple optima. Also, the uniformly negative slope of the curves shown in Figure 32 represents the special case of "competitive" goods. If the iso-cost curves were positively sloped, the goods would be "complements," and if the slope were zero or infinity, the good whose quantity varied would be referred to as the "supplement" of the other. Of course, a given iso-cost PPF may exhibit two or all three types of behavior. (An iso-cost PPF which exhibited complementary behavior over some range would for obvious reasons be expected to show supplementary and competitive behavior over other regions.)

Naylor and Vernon (1969) expanded the basic analysis to deal with optimality conditions for markets with imperfect competition in factor purchases and/or product sales. Even
in their analysis, however, the existence of markets (through inclusion of terms such as marginal revenue and price) is implicit, a condition which may not be satisfied for many PRL outputs.

Given the foundation laid by the theory of multiple-product economics, it is possible to explore in greater detail some of the peculiarities of multiple-use natural systems relative to the typical multiple-product firm. To begin with, it is necessary to define the identities of the various producers, consumers, and products. The natural resources connected with the multiple-use natural system may be defined as the "primary" products of the production process, in which case society may be said to be the owner of the "firm," and thus a producer. The primary products are used as inputs by individuals and/or firms in conjunction with other inputs to produce "secondary" products, such as lumber, recreation, etc. At once problems of distribution come to mind: society is the producer of the primary products, which it "sells" to the secondary producers, which in turn are members of society itself.

A question of the definition of joint production also emerges. One view might be that joint production occurs at the primary product level, where society inputs both land
and management to the production process. The implications of such an argument are complex, however, since much of the management used in regulating production of primary products is the very use of already existing primary product inventories in the process of secondary production. In other words, logging could be considered an input to the timber-growing production process. This then implies that the lumber-producing process is inseparable from the timber-producing process.

Making the "joint product" nature of the process come in at the level of the secondary products is also somewhat difficult, since the individuals/firms engaging in secondary production are for the most part each producing only a single good (e.g. loggers produce lumber, ranchers produce cattle, etc.).

The distribution and production questions may be clarified by examining a particular problem: Suppose that timber and recreation opportunities are two of the products produced in a joint production process, where society is considered to be the entrepreneur. Society will then presumably receive rents charged to loggers for use of timber as an input to the lumber-producing process. However, society will receive either zero or minimal returns from producers/consumers of recreation unless the rent-free
benefits accruing to "recreators" can be considered to accrue to society as a whole, of which the recreators are a part. If the problem may be finessed in this manner, there would seem to be little to stand in the way of considering all costs and benefits of secondary production as accruing to society, thereby ignoring distributional considerations.

If this is the case, then total net benefits to society from primary and secondary production (TNB) may be totaled as follows:

\[ TNB = \text{rents charged to utilizers of primary products} (\text{a gain to the producers of primary products}) + \text{benefits to producers of secondary products} - \text{rents charged to utilizers of primary products} (\text{since a cost to secondary producers is considered a cost to society}) - \text{other costs to producers of secondary products} \]
\[ = \text{benefits to producers of secondary products} - \text{non-rent costs to producers of secondary products}. \]

From the theory of common-property resources (Gordon 1954) it may be argued that in steady state this difference should equal rents charged to producers of secondary products.
Thus, it may be legitimate to consider the secondary products as the true "joint products" of the multiple-use natural system's joint production process.

A Simple Model of a Multiple-Use Natural System

Suppose that a particular system consisting of two resource populations R1 and R2 (e.g. timber and forage), and two utilizer populations U1 and U2 (e.g. loggers and cattle ranchers) can be usefully modeled using simple differential equations. To begin with, suppose that the resource populations can be represented by combining Lotka-Volterra competition and predation equations (Lotka 1925, Volterra 1926).

The transformational behavior of each resource population (Ri, where i subscripts for either 1 or 2) can thus be represented as a linear combination of the following four terms: Ri, Ri^2, the product of Ri and its competitor (Ri*Rj), and the product of Ri and its predator (Ri*Ui). The product of each term and its coefficient in the linear combination represents the effect of growth, non-predatory mortality, competition, and predation, respectively.

The coefficient of Ri, the growth coefficient, differs from the innate capacity for increase because of deviations
in the state of the natural environment from the theoretical optimum (Krebs 1978). Thus, the growth coefficient will be described in this model as the product of two terms: a constant coefficient (Gi), and an environmental variable (N).

It will be assumed that changes in the magnitudes of the two utilizer populations are governed by economic factors. Increases (i.e. the positive component of the rate of change) in each utilizer subsystem will be taken to equal revenues to the utilizers. Constant prices will be assumed, so revenues will simply equal the product of price (Pi) and yield (Yi), where the latter is equal to the predatory losses of the resource population. The level of each utilizer subsystem will be taken to correspond to the level of utilization of the respective resource.

Market costs will constitute one source of loss to each utilizer component. Marginal costs will be taken to increase linearly with level of utilization, making total costs proportional to the level of utilization squared.

Each of the two utilizer populations in the system will also be subject to regulation in the form of a tax (T1 and T2) levied in proportion to level of resource use, as measured by the size of the relevant utilizer population.
Thus, the transformational behavior of each utilizer component (Ui) may be described by a linear combination of three terms: the product of the utilizer and its respective resource (Ui*Ri), Ui², and the product of the utilizer and its respective tax rate (Ui*Ti). The products of these terms and their respective coefficients in the linear combination represent revenues, costs, and taxes, respectively.

The canonical representation of the system appears, then, as follows:

\[
\begin{align*}
\frac{dR_1}{dt} &= G_1 N R_1 - M_1 R_1^2 - C_1 R_1 R_2 - Q_1 R_1 U_1 \\
\frac{dR_2}{dt} &= G_2 N R_2 - M_2 R_2^2 - C_2 R_2 R_1 - Q_2 R_2 U_2 \\
\frac{dU_1}{dt} &= P_1 Q_1 R_1 U_1 - K_1 U_1^2 - T_1 U_1 \\
\frac{dU_2}{dt} &= P_2 Q_2 R_2 U_2 - K_2 U_2^2 - T_2 U_2,
\end{align*}
\]

where the various coefficients take on the following meanings: G\textit{i}*N = growth coefficient, M\textit{i} = mortality coefficient, C\textit{i} = competition coefficient, Q\textit{i} = exploitation (yield) coefficient, and K\textit{i} = cost coefficient. P\textit{i} and P\textit{2} represent the price of the yield of product 1 (Y1, e.g. lumber), and the price of the yield of product 2 (Y2, e.g. beef), respectively. The stability characteristics of this model are discussed in Appendix III.
Solving the canonical representation results in one-dimensional system isoclines, two-dimensional system isoclines, and two-dimensional subsystem isoclines which are all linear. These calculations and all others referred to herein may be performed using the program listed in Appendix IV. Some of the two-dimensional subsystem isoclines are shown in functional notation below:

\[ R_1 = f_1(N,R_2,T_1) \]
\[ R_2 = f_2(N,R_1,T_2) \]
\[ R_1 = f_3(N,U_1,T_2) \]
\[ R_2 = f_4(N,U_2,T_1) \]
\[ U_1 = f_5(N,U_2,T_1) \]
\[ U_2 = f_6(N,U_1,T_2) \]
\[ U_1 = f_7(R_1,T_1) \]
\[ U_2 = f_8(R_2,T_2) \]

The two-dimensional system isoclines can be used to derive quadratic equations for \( Y_1 \) and \( Y_2 \) in terms of \( U_1 \) and \( U_2 \), respectively. For each possible pair of environmental variables, there corresponds a single linear equation for the two-dimensional system isocline family describing \( R_i \)'s steady state in terms of \( U_i \) and that pair of environmental variables. Multiplying both sides of this equation by \( Q_i U_i \) gives an equation for \( Y_i \) in the form shown
below:

\[ Y_i = A_i U_i^2 + (B_i E_1 + C_i E_2) U_i \]

where \( A, B, \) and \( C \) are coefficients, \( E_1 \) and \( E_2 \) represent any pair of environmental variables chosen from the set \([N, T_1, T_2]\), and \( i \) subscripts for either 1 or 2. The coefficients \( A, B, \) and \( C \) are specific to the pair \([E_1, E_2]\). Thus, there are three equations each for \( Y_1 \) and \( Y_2 \), since there are three possible pairs that can be chosen from the set \([N, T_1, T_2]\).

Furthermore, \( Y_2 \) can be solved for in terms of \( Y_1 \) and any pair of environmental parameters \([E_1, E_2]\), as follows: Taking the inverse of the above expression for \( Y_1 \), two roots of \( U_1 \) may be given as a function of \( Y_1 \) and the two environmental variables chosen. Since there also exists a two-dimensional system isocline giving \( U_2 \) as a linear combination of \( U_1 \) and the same two environmental variables, it is also possible to write \( U_2 \) as a function of \( Y_1 \) and the two environmental variables. Finally, since \( Y_2 \) can be written as a function (above) of \( U_2 \) and the two designated environmental variables, it can also be written as a function of \( Y_1 \) and the two environmental variables. This equation takes the following form:
\[ Y_2 = a Y_1 \pm (b E_1 + c E_2)(d E_1 + e E_2)^2 + f Y_1^{**0.5} \]
\[ + g E_1^2 + h E_1 E_2 + i E_2^2 , \]

where \( a, b, c, d, e, f, g, h, \) and \( i \) are constants specific to the environmental pair \([E_1, E_2]\). Again, there is one equation of this form for each of the three possible pairs that can be chosen from the set \([N, T_1, T_2]\).

The above equations all represent loci of steady states mapping state variables and/or system yields against one another as environmental conditions vary in steady state. Figure 33 shows samples of these loci in four-quadrant format. This figure is based on the following set of values for the coefficients of the canonical representation:

\[ G_1 = 2, \quad M_1 = 1, \quad C_1 = 1, \quad Q_1 = 1, \]
\[ G_2 = 3, \quad M_2 = 2, \quad C_2 = 1, \quad Q_2 = 2, \]
\[ P_1 = 1, \quad K_1 = 1, \]
\[ P_2 = 1, \quad K_2 = 1 . \]

In Figure 33, the second quadrant (numbering clockwise from the upper right) depicts three steady-state mappings of \( Y_1 \) against \( U_1 \). Two of these loci are redundant, namely those based on constant \([T_1, T_2]\) and constant \([N, T_1]\). The third locus (for constant \([N, T_2]\)) is distinct, and takes on the dome-shaped appearance familiar to fisheries scientists.
Figure 33. Four-quadrant diagram of steady-state yields and utilization levels. Three types of two-dimensional system isocline are given in each of four phase planes relating the two product yields (Y1 and Y2) and the two utilizer populations (U1 and U2). The lower right quadrant relates the steady-state production of Y1 to the steady-state level of U1. Since there are three environmental variables in this system, there are $3^{1/2} = 3$ ways in which to parameterize two-dimensional system isoclines. Environmental variable levels have been set at $N = 2$, $T_1 = 1$, and $T_2 = 1$. At these levels, two of the isoclines are redundant, namely those parameterized by $[2N,1T_1]$ and $[1T_1,1T_2]$. The lower left quadrant relates steady-state levels of U2 to U1. No redundancy occurs here among the three isoclines. The upper left quadrant relates steady-state levels of Y2 to U2. Here, the isoclines for $[2N,1T_2]$ and $[1T_1,1T_2]$ are redundant. Finally, the upper right quadrant shows the steady-state relationship of Y2 to Y1. No redundancy occurs here. On each phase plane, all isoclines intersect at a single point, which is the two-dimensional projection of the system steady state corresponding to environmental conditions of $N = 2$, $T_1 = 1$, and $T_2 = 1$. The dashed lines illustrate how the steady states on the different phase planes map into one another.
Figure 33.
as the "Schaefer (1954) yield curve." Along this locus, as $T_1$ is decreased in steady state and both $N$ and $T_2$ are held constant, $U_1$ increases while $Y_1$ increases to a peak and then decreases to zero as $R_1$ (not shown) is driven extinct. All three loci intersect at the same point in this quadrant, as by definition they must.

In the third quadrant of Figure 33, one representative of each type of two-dimensional system isocline in $(U_1,U_2)$-space is shown. As in the second quadrant, all three loci intersect at the same point.

The fourth quadrant is the analogue to the second for $Y_2$ and $U_2$. Here, the curves for constant $[T_1,T_2]$ and constant $[N,T_2]$ are redundant. The curve for constant $[N,T_1]$ is distinct, and takes on the appearance of a Schaefer yield curve.

Using the information from quadrants two through four it is possible to graphically locate the steady state in $(Y_2,Y_1)$-space corresponding to the steady states in the other four quadrants. This point is at the intersection of the three loci mapping $Y_2$ against $Y_1$ for the given values of the three possible pairs of environmental parameters. These three loci represent three types of production possibility frontiers.
Having earlier discussed the optimality conditions for the multi-product firm, and noting the availability of production possibility frontiers in (Y2,Y1)-space, it might be asked whether or not this system can be optimized in the same manner shown in Figure 32. The answer is that it cannot. First of all, the existence of three unique production possibility frontiers in the first quadrant of Figure 33 automatically rules out this possibility; setting the slope of "the" production possibility frontier equal to the negative price ratio has no meaning when there are in fact three curves, all with entirely different shapes.

A straightforward explanation of this paradox might begin in any of a number of ways. Perhaps the easiest of these is to note that the production possibility frontiers of Figure 32 were iso-cost PPF's. The PPF's of Figure 33's first quadrant are not iso-cost PPF's, but "iso-environment" PPF's, the derivatives of which have no necessary relationship to price ratio under optimum product mix or otherwise.

A second explanation involves factor ownership and the number of firms involved. In Figure 32, the system consists of a single firm which is able to vary its input mix to achieve any desired product mix along the production possibility frontier. In such a firm, it is permissible for
some production process(es) to forego increased profits if some other production process(es) can thereby be enabled to reap even greater profits. However, the system of Figure 33 does not assume a single multi-product firm, but rather two distinct production activities, each of which might employ any number of independent firms. By assuming that profit for each of the two activities is zero in equilibrium (as opposed to assuming that total profit is zero in equilibrium) it is implied that the firms involved in one activity are structurally independent not only from each other but from the firms involved in the other activity as well.

Finally, a full explanation of the differences between the two situations involves the distinction between short-run and steady-state analyses. To proceed with this explanation, however, first requires that the proper optimization of the model system be carried out. A zero rate of discount will be assumed throughout. Given the assumptions of the model, in the absence of non-zero tax rates the system produces no rents at steady state (long-run competitive equilibrium), since use of each resource increases (decreases) until total revenues equal total costs. All steady-state rents, then, accrue as the result of imposing non-zero tax rates on the utilizers.
Steady-state rent (SSR) can therefore be expressed by the following equation:

\[ SSR = T_1U_1^* + T_2U_2^* , \]

where \( U_1^* \) and \( U_2^* \) represent steady-state levels of \( U_1 \) and \( U_2 \), respectively.

Since \( U_1^* \) and \( U_2^* \) can both be expressed as linear combinations of \( N \), \( T_1 \), and \( T_2 \), steady-state rent can also be expressed as follows:

\[ SSR = aT_1^2 + (bN + cT_2)T_1 + dT_2^2 + (eN + fT_1)T_2 , \]

where \( a, b, c, d, e, \) and \( f \) are constants.

Setting partial derivatives with respect to \( T_1 \) and \( T_2 \) equal to zero and substituting gives optimal values for \( T_1 \) and \( T_2 \) each as linear functions of \( N \). Since all state variables may be expressed in steady state as linear combinations of the environmental parameters, this implies that the optimum values of the steady-state variables vary linearly with \( N \). Then, since \( Y_1 \) and \( Y_2 \) are each proportionate to the product of two such state variables, their optima will be proportionate to \( N^2 \). Finally, this implies that the optimal value of \( Y_2 \) will be proportionate
to the optimal value of $Y_1$. Due to the simple functional forms involved, all of these constants of proportionality are derivable algebraically.

Given the coefficient values chosen for this exercise, the optimal values for $T_1$ and $T_2$ are as follow:

\[
T_1 = 0.5N \\
T_2 = N
\]

Thus, if $N$ remained constant for a long enough period, a manager would set tax rates so that $T_1$ were one-half the value of $N$, and $T_2$ were equal to $N$. This in turn would structure the steady-state values of the state variables so that rent would be maximized.

The relation between optimal $Y_2$ and $Y_1$ forms a linear expansion path in $(Y_2, Y_1)$-space with slope $4/3$. Figure 34 shows two isoclines (for $[2N, 2T_2]$ and $[2N, 1T_1]$), and the expansion path. The solid circle at the intersection of the two isoclines and the expansion path represents the optimum steady-state output mix for the system given $N = 2$.

Now, to examine the difference between the result of this steady-state optimization and the situation obtaining in Figure 32, assume that the system is in steady state at
Figure 34. Steady-state expansion path. The three isoclines shown here (curved lines) correspond to the isoclines in the upper right quadrant of Figure 33. The solid circle represents the steady state which obtains under these environmental conditions. If maximization of steady-state rents is the criterion of management, the tax rates will always be set so that $T_1 = 0.5N$ and $T_2 = N$. Under these conditions, the steady-state expansion path for the system is linear in $(Y_2,Y_1)$-space. Since it is a steady-state path, it must pass through the solid circle in this figure. Note that this differs from the "false" expansion path which would be obtained under the same environmental conditions using the optimization criteria illustrated in Figure 32. The false expansion path consists of the locus of points defined by equating the absolute value of the iso-cost production possibility frontiers' derivatives with the product price ratio, which in this case is equal to one.
Figure 34.
the solid circle in Figure 34 (the steady-state optimum given \( N = 2 \)). To compare this outcome with that dictated by the price-ratio/iso-cost tangency criterion, it will be necessary to construct an iso-cost PPF. Since an iso-cost PPF represents those output mixes where total cost is equal to some constant, it is first necessary to determine this constant. The constant will equal the total cost incurred by both \( U_1 \) and \( U_2 \) when the system is at the steady state associated with the solid circle in Figure 34. This total cost level (TC) may be calculated using the following equation, which is based on the canonical representation:

$$
TC = C_1 U_1^2 + T_1 U_1 + C_2 U_2^2 + T_2 U_2.
$$

Note that the only state variables on the RHS of this equation are \( U_1 \) and \( U_2 \). This equation can be solved for two roots of \( U_2 \) which involve \( U_1 \) and \( TC \). Since \( Y_2 \) is a function of \( U_2 \), this enables \( Y_2 \) to be written in terms of \( U_1 \) for a constant value of \( TC \). And since \( Y_1 \) is a function of \( U_1 \), substituting the inverse of this function gives \( Y_2 \) in terms of \( Y_1 \), again for a constant value of \( TC \). This is the equation for the iso-cost PPF. The iso-cost PPF associated with the solid circle in Figure 34 is shown.

It is important to realize that all of this assumes the steady-state values of \( R_1 \) and \( R_2 \) associated with the solid
circle in Figure 34. In other words, this curve answers the question, "Given the steady-state values of R1, R2, and TC associated with the solid circle in Figure 34, what other values of Y1 and Y2 could be obtained from different mixes of U1 and U2?" The tangency of this curve to the negative price ratio gives the output mix at which total profit would be maximized, given the assumption of fixed R1, R2, and TC.

It can be shown that the expansion path (labeled "false expansion path" in Figure 34) resulting from this optimization will be linear and run through the origin, as with the true expansion path. However, the slopes of the two paths will not generally be equal. That this might be expected can be inferred from the different natures of the optimizations involved. The steady-state optimization maximizes total steady-state tax revenues. On the other hand, the price-ratio/iso-cost tangency optimum maximizes total profits (accruing to both U1 and U2), and will therefore in general not be a steady state. This follows because steady state for the model is by definition the point of zero profit for both U1 and U2 (thus total profit is zero as well). For the price-ratio/iso-cost tangency point to be both the point of maximum profit and zero profit would certainly be the most special of cases, implying that all output mixes but one result in net losses.
Although it has now been shown that the optimum based on maximum short-run total profit and maximum steady-state tax revenue are different, the "rightness" of the steady-state optimization (in terms of this model) has only been asserted, not proven. More importantly, the larger question of the appropriate optimization for multiple-use natural systems in general has not been addressed.

The fact (discussed earlier) that the maximum short-run total profit criterion is based on the model of the single multi-product firm is suggestive of the inappropriateness of this criterion. In the case of multiple-use natural systems, it would certainly be rare to find an example in which one firm was the sole user in every category of use. Thus, it could be argued that in general the price-ratio/iso-cost tangency criterion is an inappropriate method of optimization for the multiple-use natural system.

This conclusion, however, does not in itself vindicate the maximum steady-state tax revenue criterion, either for this particular model or for multiple-use natural systems in general. While it should be clear that the maximum tax revenue criterion is a preferable choice given the structure of multiple-use natural system user groups and the appropriateness of steady-state optimization in general, the
latter condition has not been demonstrated.

That steady-state analysis is appropriate in attempting to understand multiple-use natural systems (as opposed to, say, man-made industrial systems) is suggested by the role of the natural environment in such systems. In normal industrial situations there do exist system parameters which are subject to change (e.g., technology) but these are highly controllable by management. In contrast, the natural environment is largely out of the control of management. Furthermore, its influence on production is vast. As shown in Figure 33, the natural environment can conceivably dictate the levels of key inputs to secondary production processes to a large extent. This would tend to indicate that long-term planning for multiple-use natural system production would be better focused on long-term system/environment relationships than on short-run, purely economic relationships, in which case steady-state analysis can be an important tool in both understanding and management of such systems.

A Conceptual Framework for Biology

Warren et al. (1979) have proposed a set of generalizations and a set of procedural rules which constitute a conceptual framework for biology. A conceptual
framework is taken, in their terms, "to exist at the most encompassing level amenable to reasonably complete and adequate verbal articulation." In light of the fact that such a framework can be specific to a single discipline (e.g. biology), conceptual frameworks would occupy a level not far below that of world view in the conceptual hierarchy.

Unlike the partial conceptual structures examined so far, the conceptual framework of Warren et al. (1979) is more "at home" in a contextualist than in a mechanist world view. Strictly speaking, this conceptual framework is only relatively contextualistic; it does not imply nor fully conform to the pure contextualism described by Pepper (1942).

The first question that should be addressed, then, is how a mathematical model of the type presented in the present research might interface with such a (relatively) contextualist conceptual framework. More generally, it might be wondered what meaning any mathematical model might have in a contextualist conceptual structure.

As discussed earlier, viewing models as metaphorical statements rather than as special theories at least allows for the possible use of mathematical models in contextualist
conceptual frameworks. However, the precise nature of such a use is not immediately obvious. Certainly, the interpretation of a mathematical model as capturing the causal nature of biological processes would not be acceptable in a contextualist framework. Mechanistic frameworks, on the other hand, tend to promote a "causal-adjustment" theory of truth in which a view of equation-as-cause is at least a possibility (Pepper 1942). In such a framework, it should be pointed out, the entities that have been referred to so far as mathematical "models" might more accurately be labeled "theories," since the mechanist has the option of believing that the equations truly mirror the invariant causal mechanisms which he or she perceives to be governing the universe.

In a truly contextualist framework, however, there can be no "mathematical theory," only mathematical model. The set of equations or other mathematical construct is thus taken to be the subsidiary subject in an interactive metaphor. The question then becomes one of identifying the effect of juxtaposing a mathematical subsidiary subject and a natural principal subject within a contextualist scheme.

For one thing, the mathematical construct will be viewed as a transient phenomenon. In a model composed of a set of equations, the equation coefficients will not be
viewed as constants, but variables. As a true metaphor, the mathematical construct will impart certain "associated commonplaces" to the natural principal subject (Black 1962). Where the model consists of differential equations, one of the associated commonplaces which the model will draw to the attention of the user is the idea of change, the dramatic, dynamic active event which is the root metaphor of contextualism (Pepper 1942).

Where the model consists of a state-determined system of the type described by Ashby (1956, 1960), in which the time-derivative of each variable is a function of many other variables in the system, the interconnectedness of the model will also be meaningful to the contextualist.

Finally, the type of isocline model discussed in the present research is suggestive of the contextualist idea of "fusion." Fusion, to a contextualist, refers to the integration of a process into a culminated, whole event (Pepper 1942). In an isocline model, the differential equations of the canonical representation are integrated to obtain steady-state curves which represent the foci of the system's entire range of possible dynamic performances.

In addition to its relatively contextualistic orientation, the conceptual framework of Warren et al.
(1979) is significant in its development of the concept of "capacity" and its formulation of the system/environment distinction. These ideas emerge from the sets of generalizations and rules of the conceptual framework as listed by Warren et al. (1979):

"Generalization #1 (Organismic system operation, performance, and function): Any performance of any organismic system is an outcome of its operation, which consists of the interactive performances of its subsystems, and has functions or plays operational roles in the structure, organization, or replication of the organismic system and a more encompassing system.

"Generalization #2 (Organismic system potential capacity, realized capacity, and performance): The potential capacity of any organismic system predetermines all possible sequences of realized capacities, which in turn determine all possible performances, any occurring sequence of realized capacities depending on the environmental system through time, and any occurring performance depending on the immediately effective environment.

"Generalization #3 (Organismic system-environmental system relativity): Any performance of any organismic system requires space, time, energy, materials, and information,
which are provided in particular forms and limited amounts by its coextensive environmental system; potential and realized capacities determine the forms and amounts that will permit performance and thus determine the possible environmental systems within which the organismic system could persist.

"Generalization #4 (Organismic system incorporation): Any organismic system tends to incorporate in some degree not only its organismic subsystems but also their particular environmental systems.

"Rule #1: Only the performance of an organismic system or subsystem can be measured, its capacity and its operation being representable only indirectly and incompletely.

"Rule #2: Measurements of the performance of an organismic system or subsystem without relevant measurements on its coextensive, level-specific environmental system are of little explanatory value.

"Rule #3: Operational explanation of an organismic system should take into account the performances and operations of subsystems on successively lower levels of organization and cannot be based only on knowledge of subsystems on the lowest levels of organization.
"Rule #4: Explanatory generalizations pertaining directly to any one level of organization of an organismic system should contain at least one concept specific to that level and should subsume conceptual, methodological, or other sorts of indeterminacy that may exist with respect to lower levels of organization.

"Rule #5: Perception and explanation of organismic and environmental systems are always partial relative to the space and time dimensions and the components of the systems."

The model developed in the present research does not interface directly with all of these generalizations and rules, but there are important points of overlap. For example, the conceptual framework makes clear that a system's current performance is a product of its current realized capacity and the state of its effective environment; a concept which is highly concordant with the proposed model.

While the equations of a state-determined system can in no way be taken to reflect the complex capacity of a biological system, they do describe a type of capacity. Warren et al. (1979) implicitly define "capacity" as that which effective environment acts upon to produce
performances. Thus, the fact that different states of a (mathematical) state-determined system's effective environment elicit different system performances implies that the system has a capacity.

In fact, the state-determined system is a useful ground for illustrating the importance of capacity in the system/environment relationship. The simple system of Figure 8 illustrates the differences in steady-state system behavior that result from a single set of constant-coefficient equations when the effective environment is held at different constant levels.

Of course, the conceptual framework allows for changes in capacity, and this can be accommodated by the proposed model as well. The system of Figure 9, in which the coefficients of the canonical representation are functions of time, demonstrate some of the implications of a simple type of change in capacity. Among these is the fact that different system performances can result from differences in effective environment, capacity, or both.

Another point of clear concordance between this conceptual framework and the proposed model is the significance ascribed to "levels" in biological organization (see, for example, Rules 2, 3, and 4).
Given that the proposed model is compatible with this conceptual framework in terms of its essential features, the remaining task is to examine what the model adds to the perspective of ecosystems already outlined by the conceptual framework.

An important addition supplied by the proposed model is visualizability. The adopted view of model-as-metaphor is intrinsically tied to visualization (models are interpreted as lenses, primary subjects are seen in the light of subsidiary subjects, etc). Here, the visualization includes a variety of phenomena addressed by the conceptual framework. One of these is the existence of multiple steady state behavior. The isocline form of model representation makes clear the effects of different environmental conditions on steady-state system performance.

Another example of increased visualizability may be found in the model's treatment of system organization. Warren et al. (1979) regard organismic systems as nested hierarchies, with the system at any level forming a subsystem at the next higher level and in turn being comprised of a set of subsystems at the next lower level. In the proposed model, the idea of system performances being organized in this manner is made visualizable through the construction of composite equilibrium descriptions of system
performance. An important, though partial, view of system organization at a particular level is given by the composite equilibrium description of the constrained constituents at the next level down.

The chief mention of time in the conceptual framework is in generalization #4, where it is suggested that the organismic system exists in the context of a spatially and temporally coextensive environmental system. The role ascribed to time-resolution heterogeneity by the proposed model thus represents a particular viewpoint that is concordant with, but not necessarily implied by the conceptual framework. In this sense, it represents an additional tool for understanding biological systems.

Both the proposed model and the conceptual framework pose implications for management of ecosystems. However, like the stability and resilience perspective examined earlier, neither the model nor the conceptual framework make explicit reference to any particular value system. Thus, a full treatment of the possible implications of either must await the articulation of such a system.

Even in the absence of a fully articulated value system, though, it is possible to make some provisional judgements regarding the implications of the proposed model
and the conceptual framework for ecosystem management. One way to do this is to note that the conceptual structure under consideration rules out certain options for ecosystem management. For example, in the view being proposed, ecosystems are seen as essentially complex, and change is seen as a fundamental characteristic of both system capacity and environment. Thus, the possibility of managing ecosystems from any kind of "control" perspective, in which the system is manipulated along a single continuous curve to an optimum point, is for all practical purposes not an option.

A related alternative may still be admissible, however. Instead of relying on a fine-tuning type of mechanistic ecosystem control, it may still be advisable to retain the objective of finding the peak of a defined objective function, but only if pursued in a different manner. One possibility here is simply to turn the decision over to seasoned managers who will rely on their wealth of experience with the resource in question to manage the system for optimal performance. However, this option raises other issues, such as accountability of the manager for his or her actions. The tradeoffs resulting from raising these issues cannot be evaluated in the absence of an explicit value system.
An alternative to managing for a theoretically valid but practically incalculable optimum would be to manage for persistence of the resource. This approach bears a resemblance to some of the recommendations of Holling (1973) in his discussion of the stability and resilience view. However, an important question is left unaddressed, namely the precise identity of the entity whose persistence is to be the focus of the management effort. Holling, for instance, seems to imply that persistence of each species in an ecosystem should be the goal. However, in virtually any natural system of interest, the number of species present is immense. Furthermore, such systems are characterized by species entering and leaving the system with high frequency. Surely this is not a de facto indicator of management failure.

Rather than futilely striving to freeze the species composition of an ecosystem at some arbitrary point, it might be possible to focus on certain resource subsystems of special interest. This is no trivial matter either, however, in that the persistence of these subsystems will likely depend on the performances of any number of other subsystems as well as of the environment. Again, it is tempting to give the manager the task of determining which subsystems are in need of protection, but this raises the same issues of accountability mentioned above.
A more specific example of how the proposed view might have implications for ecosystem management lies in the area of patterns of constraint in ecosystem organization. If the proposed model proves useful in imparting an idea of the extent to which a particular ecosystem's organization follows a hierarchical pattern, certain considerations are brought into focus. For instance, spatial arrangements and other patterns of constraint should be examined to determine how changes in ecosystem performance at one level might effect subsystems at lower levels.

In similar fashion, managers should be warned against the pitfalls of attempting local "band-aid" solutions to problems that result from system dynamics on a larger scale. For example, Liss et al. (1982) have commented on the futility of trying to eliminate insect pests from a single orchard when re-colonization from surrounding orchards is both inevitable and immediate.

The converse of this observation is that patterns of constraint and connectivity can also be used as aids to persistence. For example, suppose that a certain set of sites form a subsystem at the next higher level in the sense that the sites taken together form the species pool for the individual sites. In this case, it might be expected that maintenance of different sites in varying states of
succession could provide whatever colonizing species might be required to re-stock a site where a major perturbation has caused a collapse of key resource species.

In conclusion, the utility of the proposed model can be seen to result from interaction of the model with the particular conceptual structure in which it is embedded. Of the four partial conceptual structures examined here, varying degrees of concordance have been evident. In those structures where the model has appeared less concordant, the areas of conflict can be used to draw attention to possible weaknesses both in the model itself and in the particular conceptual structure. In a structure where a great deal of concordance may be found, such as the conceptual framework of Warren et al. (1979), the model can be used as a specialized extension of the structure, enabling a closer look at a particular domain of experience.
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APPENDICES
Appendix I: Bird Species List

Legend:
TS = trophic status (C = carnivore, H = herbivore)
HCMF = Happy Camp Mountain Forest
HMF = Hutcheson Memorial Forest
RWH = Ravenel's Woods, hickory site type
RWO = Ravenel's Woods, oak-chestnut site type
TW = Trelease Woods
UMBS = University of Michigan Biological Station
X = species presence

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278
Mimus polyglottos Northern Mockingbird
Toxostoma rufum Brown Thrasher

FAMILY: MUSCICAPIDAE

GENUS Catharus
SPECIES fuscescens COMMON NAME Veery
SPECIES guttatus COMMON NAME Hermit Thrush
SPECIES mustelina COMMON NAME Wood Thrush
SPECIES caerulea COMMON NAME Blue-gray Gnatcatcher
SPECIES satrapa COMMON NAME Golden-crowned Kinglet
SPECIES sialis COMMON NAME Eastern Bluebird
SPECIES migratorius COMMON NAME American Robin

FAMILY: PARIDAE

GENUS Parus
SPECIES atricapillus COMMON NAME Black-capped Chickadee
SPECIES bicolor COMMON NAME Tufted Titmouse
SPECIES carolinensis COMMON NAME Carolina Chickadee
SPECIES rufescens COMMON NAME Chestnut-backed Chickadee

FAMILY: SITTIDAE

GENUS Sitta
SPECIES canadensis COMMON NAME Red-breasted Nuthatch
SPECIES carolinensis COMMON NAME White-breasted Nuthatch

FAMILY: STURNIDAE

GENUS Sturnus
SPECIES vulgaris COMMON NAME European Starling

FAMILY: TROGLODYTIDAE

GENUS Thryothorus
SPECIES ludovicianus COMMON NAME Carolina Wren
SPECIES aedon COMMON NAME House Wren
SPECIES troglodytes COMMON NAME Winter Wren

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<td>cerulea</td>
<td>Blue Elder</td>
<td>HCMF</td>
<td>1</td>
<td>12</td>
<td>1.9</td>
</tr>
<tr>
<td>Sorbus</td>
<td>americana</td>
<td>American Mountain-Ash</td>
<td>HMF</td>
<td>2</td>
<td>8</td>
<td>5.2</td>
</tr>
<tr>
<td>Taxus</td>
<td>brevifolia</td>
<td>Pacific Yew</td>
<td>HCMF</td>
<td>2</td>
<td>14</td>
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<tr>
<td>Tsuga</td>
<td>canadensis</td>
<td>Eastern Hemlock</td>
<td>URB</td>
<td>3</td>
<td>20</td>
<td>1.4</td>
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<tr>
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<td>rubra</td>
<td>Slippery Elm</td>
<td>HMF</td>
<td>2</td>
<td>20</td>
<td>7.8</td>
</tr>
<tr>
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<td>URB</td>
<td>3</td>
<td>20</td>
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<tr>
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<td>rubra</td>
<td>Slippery Elm</td>
<td>TW</td>
<td>4</td>
<td>20</td>
<td>20.3</td>
</tr>
<tr>
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<td>rubra</td>
<td>Slippery Elm</td>
<td>TW</td>
<td>5</td>
<td>20</td>
<td>2.6</td>
</tr>
<tr>
<td>Zanthoxylum</td>
<td>americanum</td>
<td>Common Prickly Ash</td>
<td>TW</td>
<td>5</td>
<td>8</td>
<td>3.8</td>
</tr>
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</table>
Appendix III: Model Stability

The canonical representation of the model of the multiple-use natural system proposed in the text appears as follows (see text for explanation of symbols):

\[
\begin{align*}
\frac{dR_1}{dt} &= G_1R_1 - M_1R_1^2 - C_1R_1R_2 - Q_1R_1U_1 \\
\frac{dR_2}{dt} &= G_2R_2 - M_2R_2^2 - C_2R_2R_1 - Q_2R_2U_2 \\
\frac{dU_1}{dt} &= P_1Q_1R_1U_1 - K_1U_1^2 - T_1U_1 \\
\frac{dU_2}{dt} &= P_2Q_2R_2U_2 - K_2U_2^2 - T_2U_2 
\end{align*}
\]

In any model where each equation of the canonical representation is a polynomial whose lowest-degree term is of degree greater than zero, zero will be a steady-state solution of the system. If the highest-degree term in each equation is of degree only one greater than the lowest term, then only two solutions exist: a zero solution and a non-zero solution. This is the case with the above model - each equation in the canonical representation is a second-order polynomial with no zero-degree terms.

Another way of looking at this is to note that this system's two-dimensional subsystem isoclines are linear, so only one intersection thereof is possible. Since zero is also an equilibrium, the stability characteristics of the system may be analyzed by examining these two equilibria.
The zero solution's stability may be analyzed as follows: The canonical representation of the model may be written in vector form as $dx/dt = Ax + g(x)$, where $g(x)$ is a polynomial in $x$ beginning with terms of degree two or greater:

$$
\begin{align*}
\frac{dR_1}{dt} &= [G_1N \ 0 \ 0 \ 0] \begin{bmatrix} R_1 \end{bmatrix} + [-M_1R_1^2 + C_1R_1R_2 - Q_1R_1U_1] \\
\frac{dR_2}{dt} &= 0 \ G_2N \ 0 \ 0 \begin{bmatrix} R_2 \end{bmatrix} + [-M_2R_2^2 - C_2R_2R_1 - Q_2R_2U_2] \\
\frac{dU_1}{dt} &= 0 \ 0 \ -T_1 \ 0 \begin{bmatrix} U_1 \end{bmatrix} - K_1U_1^2 + P_1Q_1R_1U_1 \\
\frac{dU_2}{dt} &= 0 \ 0 \ 0 \ -T_3 \begin{bmatrix} U_2 \end{bmatrix} - K_2U_2^2 + P_2Q_2R_2U_2
\end{align*}
$$

It is a general property of such systems that the stability conditions of the zero solution can be determined by examining the signs of the real parts of the "A" matrix's eigenvalues. The eigenvalues of the "A" matrix in this case correspond to the elements on the main diagonal, of which two are positive and two are negative. Since asymptotic stability requires that all eigenvalues have negative real parts, the zero solution of this model is unstable.

Having dispensed with the possibility of a stable zero solution, the non-zero solution's stability may now be analyzed. The model's canonical representation at the non-zero equilibrium may be "linearized" by forming a matrix consisting of the partial derivatives taken at equilibrium.
(equilibrium values of state variables are denoted by "*"):

\[
\begin{bmatrix}
(G1N-2M1R1*-C1R2*-Q1U1*) & (-C1R1*) & (-Q1R1*) & (0) \\
(-C2R2*) & (G2N-2M2R2*-C2R1*-Q2U2*) & (0) & (-Q2R2*) \\
(P1Q1U1*) & (0) & (P1Q1R1*-2K1U1*-T1) & (0) \\
(0) & (P2Q2U2*) & (0) & (P2Q2R2*-2K2U2*-T2)
\end{bmatrix}
\]

Fortunately, the diagonal elements of this matrix may be simplified. For example, the key to simplifying \(a(1,1)\) is found in the first equation of the canonical representation, shown below:

\[
dR1/dt = G1N1R1 - M1R1^2 - C1R1R2 - Q1R1U1 \\
= R1(G1N - M1R1 - C1R2 - Q1U1). 
\]

At equilibrium, both of the above equations must equal zero. Since the present examination concerns only the non-zero equilibrium, it cannot be the case that \(R1* = 0\). Therefore, in order for the second equation (above) to equal zero, the term in parentheses must equal zero. In the above matrix, then, \(a(1,1)\) may be re-written as follows:

\[
(G1N - M1R1* - C1R2* - Q1U1*) - M1R1* = -M1R1*. 
\]

The other diagonal terms may be likewise simplified, resulting the the following matrix:
It may be noted that if either $a(1,2)$ or $a(2,1)$ were positive, this system would be qualitatively stable, i.e. the system would be stable regardless of coefficient values (Quirk and Ruppert 1965, May 1974). Since this is not the case, eigenvalues must be calculated. Pivoting the above matrix (A) results in the following matrix (B):

$$
\begin{bmatrix}
-b(1,1) & 0 & 0 & 0 \\
-b(2,1) & b(2,2) & 0 & 0 \\
-b(3,1) & 0 & b(3,3) & 0 \\
0 & b(4,2) & 0 & b(4,4)
\end{bmatrix}
$$

where the $b(i,j)$'s take the following values:

$$
b(1,1) = a(1,1) - \frac{[a(3,1)a(1,3)/a(3,3)]}{[a(2,1)a(2,2)]} - \frac{[a(1,2)a(2,1)a(4,4)]}{[a(2,2)a(4,4)-a(2,4)a(4,2)]}$$

$$
b(2,1) = a(2,1)$$

$$
b(2,2) = a(2,2) - \frac{[a(2,4)a(4,2)/a(4,4)]}{a(4,4)}$$

$$
b(3,1) = a(3,1)$$

$$
b(3,3) = a(3,3)$$

$$
b(4,2) = a(4,2)$$
\[ b(4,4) = a(4,4) \ . \]

Since \( B \) is an upper diagonal matrix, its diagonal elements are also its eigenvalues. These are as follow:

\[ b(1,1) = -M_1R_1 - (P_1Q_1^2U_1^*R_1^*)/(K_1U_1^*) \]
\[ + (C_1R_1^*C_2R_2^*K_2U_2^*)/[(M_2R_2^*K_2U_2^*)+(Q_2R_2^*P_2Q_2U_2^*)] \]
\[ b(2,2) = -M_2R_2^* - (Q_2R_2^*P_2Q_2U_2^*)/(K_2U_2^*) \]
\[ B(3,3) = -K_1U_1^* \]
\[ B(4,4) = -K_2U_2^* \ . \]

Each of these is necessarily negative, except for \( b(1,1) \). Thus, in order for the non-zero solution to be stable, it is only necessary to insure that \( b(1,1) \) be less than zero. This is accomplished by satisfying the following condition:

\[ C_1C_2K_1K_2 < (K_1M_1 + P_1Q_2^2)(K_2M_2 + P_2Q_2^2). \]

It may be noted that the stability of the non-zero solution depends only on the values of certain coefficients in the canonical representation. Values of environmental variables are not a factor. The coefficient values chosen for application of this model in the text satisfy the above condition. Therefore, this model has only one non-zero solution for any set of environmental values, and that
solution is asymptotically stable.
Appendix IV: Basic Program for Multiple-Use Model

288

PRINT "THIS PROGRAM MODELS THE STEADY-STATE BEHAVIOR OF A SYSTEM OF"
PRINT "FOUR POPULATIONS: TWO RESOURCE POPULATIONS (R1 AND R2), AND"
PRINT "TWO UTILIZER POPULATIONS (U1 AND U2). THE TWO RESOURCE POPU-
ATIONS RECEIVE INPUTS FROM A NATURAL ENVIRONMENT (N). THE"
PRINT "UTILIZER POPULATIONS EACH EXPLOIT A SPECIFIC RESOURCE (U1 EXPLOITS R1 AND U2 EXPLOITS R2). IN TURN, THE UTILIZER POPULA-
TIONS ARE TAXED AT LEVELS (T1 AND T2, RESPECTIVELY) WHICH ARE"
PRINT "DETERMINED (ALONG WITH THE LEVEL OF N) BY THE PROGRAM USER."
PRINT "THE TRANSFORMATIONAL BEHAVIOR OF THE SYSTEM MAY BE REPRESENTED -"
PRINT "ED BY THE FOLLOWING SET OF DIFFERENTIAL EQUATIONS:"

PRINT "dR1/dt = G1 *N*R1 - M1 *R1i2 - C1 *R1*R2 - Q1 *R1*U1"
PRINT "dR2/dt = G2*N*R2 - M2*R2i2 - C2*R2*R1 - Q2*R2*U2"
PRINT "dU1/dt = P1*Q1*R1*U1 - K1*U1i2 - T1*U1"
PRINT "dU2/dt = P2*Q2*R2*U2 - K2*U2i2 - T2*U2"

WHERE THE VARIOUS COEFFICIENTS REPRESENT TERMS IN THE FOLLOWING"
PRINT "RATES: G - GROWTH, M - MORTALITY, C - COMPETITION, Q - EXPLOIT-
ATION, P - PRICE, K - COSTS, AND T - TAXES."

PRINT "TRANSFORMATIONAL BEHAVIOR"

PRINT "dR1/dt =";G1;"NRI -";MI;"R1i2 -";C1;"R1R2 -";Q1;"R1U1"
PRINT "dR2/dt =";G2;"NR2 -";M2;"R2i2 -";C2;"R1R2 -";Q2;"R2U2"
PRINT "dU1/dt =";P1;"*";Q1;"R1U1 -";K1;"011/42 - TIU1"
PRINT "dU2/dt =";P2;"*";122;"R2U2 -";K2;"02142 - T2U2"

D=(Ml*Kl+Pl*Q11/42)*(M2*K2+P2*Q21/42)-Kl*C1*K2*C2
R11=((M2*K2+P2*Q21/42)*G1*K1-C1*K1*K2*G2)/D
R21=((M1*K1+Pl*Q11/42)*G2*K2-C2*K2*K1*G1)/D
R12=(M2*K2+P2*Q21/42)*Q1/D
R22=(M1*K1+Pl*Q11/42)*Q2/D
R13=C1*K1*Q2/D
R23=C2*K2*Q1/D
U11=P1*Q1*R1i1/K1
U12=(P1*Q1*R1i2-1)/K1
U22=(P2*Q2*R2i2-1)/K2
U13=P1*Q1*R1i1/K1
U23=P2*Q2*R2i1/K2

ONE-DIMENSIONAL SYSTEM ISOCLINES

PRINT "ONE-DIMENSIONAL SYSTEM ISOCLINES"
PRINT "dR1/dt = DROUND(R11,4);N + DROUND(R12,4);T1 - DROUND(R13,4);T2"
PRINT "dR2/dt = DROUND(R21,4);N + DROUND(R22,4);T2 - DROUND(R23,4);T1"
PRINT "dU1/dt = DROUND(U11,4);N - DROUND(U12,4);T1 - DROUND(U13,4);T2"
PRINT "dU2/dt = DROUND(U21,4);N - DROUND(U22,4);T2 - DROUND(U23,4);T1"
289

700 PRINT CHR$(10)
710 PRINT Rn1=R21/R11
720 Rn2=(R12*R21+R23*R11)/R11
730 Rn3=(R13*R21+R22*R11)/R11
740 Rrt11=(R12*R21+R11*R23)/R12
750 Rrt12=R23/R12
760 Rrt13=(R12*R21+R23*R11)/R12
770 Rrt21=(R21*R13+R22*R11)/R13
780 Rrt22=R22/R13
790 Rrt23=(R21*R12-R23*R13)/R13
800 PRINT
810 Rn1=DROUND(Rn1,4)
820 Rn2=DROUND(Rn2,4)
830 Rn3=DROUND(Rn3,4)
840 Rrt11=DROUND(Rrt11,4)
850 Rrt12=DROUND(Rrt12,4)
860 Rrt13=DROUND(Rrt13,4)
870 Rrt21=DROUND(Rrt21,4)
880 Rrt22=DROUND(Rrt22,4)
890 Rrt23=DROUND(Rrt23,4)
900 PRINT
910 Rluln1=U11/R11
920 Rluln2=(U11*R12+U12*R11)/R11
930 Rluln3=(U11*R13-U13*R11)/R11
940 Rlult11=(U11*R12+U12*R11)/R12
950 Rlult12=U12/R12
960 Rlult13=(U12*R13-U13*R12)/R12
970 Rlult21=(U11*R13-U13*R11)/R13
980 Rlult22=U13/R13
990 Rlult23=(U12*R13-U13*R12)/R13
1000 PRINT
1010 Rluln1=DROUND(Rluln1,4)
1020 Rluln2=DROUND(Rluln2,4)
1030 Rluln3=DROUND(Rluln3,4)
1040 Rlult11=DROUND(Rlult11,4)
1050 Rlult12=DROUND(Rlult12,4)
1060 Rlult13=DROUND(Rlult13,4)
1070 Rlult21=DROUND(Rlult21,4)
1080 Rlult22=DROUND(Rlult22,4)
1090 Rlult23=DROUND(Rlult23,4)
1100 PRINT
1110 R2u2n1=U21/R21
1120 R2u2n2=(U21*R22+U22*R21)/R21
1130 R2u2n3=(U21*R23-U23*R21)/R21
1140 R2u2t11=(U21*R22+U22*R21)/R22
1150 R2u2t12=U22/R22
1160 R2u2t13=(U22*R23+U23*R22)/R23
1170 R2u2t21=(U21*R22+U22*R21)/R22
1180 R2u2t22=U22/R22
1190 R2u2t23=(U22*R23+U23*R22)/R23
1200 !R2u2t11=(U21*R22+U22*R21)/R22
1210 !R2u2t12=U22/R22
1220 !R2u2t13=(U22*R23+U23*R22)/R23
1230 !R2u2t21=(U21*R23-U23*R21)/R23
1240 !R2u2t22=U23/R23
1250 !R2u2t23=(U22*R23+U23*R22)/R23
1260 PRINT
1270 R2u2n1=DROUND(R2u2n1,4)
1280 R2u2n2=DROUND(R2u2n2,4)
1290 R2u2n3=DROUND(R2u2n3,4)
1300 R2u2t11=DROUND(R2u2t11,4)
1310 R2u2t12=DROUND(R2u2t12,4)
1320 R2u2t13=DROUND(R2u2t13,4)
1330 R2u2t21=DROUND(R2u2t21,4)
1340 R2u2t22=DROUND(R2u2t22,4)
1350 R2u2t23=DROUND(R2u2t23,4)
PRINT "SOME TWO-DIMENSIONAL SYSTEM ISOCILINES"

PRINT "R1 = R11 - R12 + R13"

PRINT "R2 = R21 - R22 + R23"

PRINT "U1 = U11 + U12 + U13"

PRINT "U2 = U21 + U22 + U23"

D1 = (M1*K1 + P1*Q12) / K1

D2 = (M2*K2 + P2*Q24) / K2

R11 = (G1*(M2*K2 + P2*Q24) - C1*K2) / D1

R21 = (G2*(M1*K1 + P1*Q12) - C2*K1) / D2

R12 = (C1*Q2) / D1

R22 = (C2*Q1) / D2

R13 = (Q1) / D1

R23 = (Q2) / D2

D1 = (M1*K1 + P1*Q12) * (M1*K1 + P1*Q12) - C1*C2*K2

D2 = (M2*K2 + P2*Q24) * (M2*K2 + P2*Q24) - C2*C1*K1

D1 = (M1*K1 + P1*Q12) * (M2*K2 + P2*Q24) - C1*C2*K2

D2 = (M2*K2 + P2*Q24) * (M1*K1 + P1*Q12) - C2*C1*K1

D1 = (M1*K1 + P1*Q12) * (M1*K1 + P1*Q12) - C1*C2*K2

D2 = (M2*K2 + P2*Q24) * (M2*K2 + P2*Q24) - C2*C1*K1

D1 = (M1*K1 + P1*Q12) * (M2*K2 + P2*Q24) - C1*C2*K2

D2 = (M2*K2 + P2*Q24) * (M1*K1 + P1*Q12) - C2*C1*K1

D1 = (M1*K1 + P1*Q12) * (M1*K1 + P1*Q12) - C1*C2*K2

D2 = (M2*K2 + P2*Q24) * (M2*K2 + P2*Q24) - C2*C1*K1

D1 = (M1*K1 + P1*Q12) * (M2*K2 + P2*Q24) - C1*C2*K2

D2 = (M2*K2 + P2*Q24) * (M1*K1 + P1*Q12) - C2*C1*K1
D2 = (2*M2 + P2*Q21/42)*(M2*M1 - C2*C1) + P2*C2*C1*Q21/42

Ulu21 = (P1*G1*Q1*(M1*M2 - C1*C2) - P1*Q1*C1*(C2*M1 - C2*C1))/D1

Ulu22 = P1*Q1*Q2*(M2*M1 - C2*C1) - P2*Q2*C2*(G1*M2 - C1*C2))/D2

Ulu23 = M1*(M1*M2 - C1*C2)/D1

U2u11 = P2*C2*Q2*(M2*M1 - C2*C1) - P2*(22*C2*(G1*m2 - C1*C2))/D2

U2u12 = P2*Q2*Q1*C2*M2/D2

U1u23 = M1*(M1*M2 - C1*C2)/D1

U2u22 = P2*Q2*Q1*C2*M2/D2

U2u23 = M2*(M2*M1 - C2*C1)/D2

R1ull = DROUND(R1ull, 4)

R2u21 = DROUND(R2u21, 4)

R1ull2 = DROUND(R1ull2, 4)

R2u22 = DROUND(R2u22, 4)

R1u13 = DROUND(R1u13, 4)

R2u23 = DROUND(R2u23, 4)

U1u21 = DROUND(U1u21, 4)

U2u11 = DROUND(U2u11, 4)

U2u12 = DROUND(U2u12, 4)

U2u23 = DROUND(U2u23, 4)

U1u23 = DROUND(U1u23, 4)

PRINT "SOME TWO-DIMENSIONAL SUBSYSTEM ISOCLINES"

PRINT CHR$(10)

PRINT "R1 = "; R112; "N - "; R122; "R2 + "; R132; "T1"

PRINT "R2 = "; R212; "N - "; R222; "R1 + "; R232; "T2"

PRINT "R1 = "; R1ull; "N + "; R1u12; "T1 - "; R1u13; "T2"

PRINT "R2 = "; R2ull; "N + "; R2u22; "T2 - "; R2u23; "T1"

PRINT CHR$(10)

PRINT "U1 = "; U1u21; "N + "; U1u22; "U2 - "; U1u23; "T1"

PRINT "U2 = "; U2u21; "N + "; U2u22; "U1 - "; U2u23; "T2"

PRINT "U1 = "; U1ull; "N - "; U1u12; "U2 + "; U1u13; "T1 - "; U1u22; "T2"

PRINT "U2 = "; U2ull; "N - "; U2u23; "U1 + "; U2u12; "T2 - "; U2u13; "T1"

PRINT CHR$(10)

PRINT "R1 = "; DROUND(R1ull, 4); "N - "; R122; "R2 + "; DROUND(R1ull2, 4); "T1"

PRINT "R2 = "; DROUND(R2u21, 4); "N - "; R2u22; "R1 + "; DROUND(R2u22, 4); "T2"

PRINT "U1 = "; DROUND(U1u21, 4); "N + "; U1u22; "U2 - "; DROUND(U1u22, 4); "T1"

PRINT "U2 = "; DROUND(U2u21, 4); "N + "; U2u22; "U1 - "; DROUND(U2u22, 4); "T2"

PRINT CHR$(10)

A1 = R1ull2/R1ull1
A2 = -R1ull3/R1ull1
A3 = 1/R1ull1
B1 = U1u21
B2 = U2u21
B3 = U3u1
C1 = -R2u23/R2u21
C2 = R2u23/R2u21
C3 = 1/R2u21
GOSUB Y2y1
GOTO Print_y2y1

Y2y1:  !

Yy1 = Q2*C3*(B3/2)/(Q1*A3)
Yy2 = Q2*B3*(2*C3*B1*A3-C1*A3-C3*B3*A1)/(2*Q1*A3/2)
Yy3 = Q2*B3*(2*C3*B2*A3-C2*A3-C3*B3*A2)/(2*Q1*A3/2)
Yy4 = Q1*A1
Yy5 = Q1*A2
Yy6 = Q1*A3
Yy7 = Q2*(C3*(B3/2)*(A1/2)/(2*(A3/2))-B3*A1*(2*C3*B1+C1)/(2*A3))
Yy8 = Q2*(C3*(B3/2)*A1/2)/(A3/2)
Yy9 = Q2*(C3*(B3/2)*B3/A2)/(A3/2)
Yy10 = Q2*(C3*(B3/2)*B3/A2)/(A3/2)-B3*A2*(2*C3*B2+C2)/(2*A3))
Yy11 = Yy9+Q2*B2*(C3*B2+C2)
Yy5=DROUND(Yy5,4)
Yy6=DROUND(Yy6,4)
Yy7=DROUND(Yy7,4)
Yy8=DROUND(Yy8,4)
Yy9=DROUND(Yy9,4)

Yla=Q1*A3
Ylb=Q1*A1
YlcsQ1*A2

Y2a=Q2*C3
Y2b=Q2*C1
Y2c=Q2*C2

RETURN

Print_y2y1:
PRINT "Y2 CAN BE WRITTEN IN TERMS OF Yj AND ANY PAIR OF ENVIRONMENTAL"
PRINT "PARAMETERS (P1,P2) IN THE FOLLOWING FORM:
PRINT CHR$(10)
PRINT "Y2 = aY1 +/- (bP1 + cP2)((dP1 + eP2)42 + fY1)1/4.5"
PRINT " + gP1k2 + hP1P2 + iP2k2"
PRINT CHR$(10)
PRINT "ALSO, Yj CAN BE WRITTEN AS A QUADRATIC FUNCTION OF Uj, P1, AND P2:"
PRINT CHR$(10)
PRINT "Yj = A1Uj + (B1P1 + C1P2)Uj"
PRINT "FOR P1 = T1, P2 = T2:"
PRINT "g =",Yy7,"h =",Yy8,"i =",Yy9
PRINT CHR$(10)

A1=-Rult11/Rult12
A2=-Rult13/Rult12
A3=-1/Rult12
B1=Uut11
B2=Uut13
B3=Uut12
C1=-R2ut11/R2ut12
C2=R2ut13/R2ut12
C3=1/R2ut12

GOSUB Y2y1

FOR P1 = N, P2 = T2:
PRINT "g =",Yy7,"h =",Yy8,"i =",Yy9
PRINT CHR$(10)

A1=-Rult21/Rult22
A2=Rult23/Rult22
A3=1/Rult22
B1=Uut21
B2=Uut23
B3=Uut22
C1=R2ut21/R2ut22
C2=R2ut23/R2ut22
C3=1/R2ut22

GOSUB Y2y1

FOR P1 = N, P2 = T1:
PRINT "g =",Yy7,"h =",Yy8,"i =",Yy9
PRINT "A1 =";Yla;"B1 =";Ylb;"C1 =";Ylc
PRINT "A2 =";Y2a;"B2 =";Y2b;"C2 =";Y2c
PRINT CHR$(10)
Maxt1=(2*U11*U22-(U13+U23)*U21)/(4*U12*U22-(U13+U23)1/4)
Maxt2=(2*U12*U21-(U13+U23)*U11)/(4*U12*U22-(U13+U23)1/4)
Maxt1=DROUND(Maxt1,4)
Maxt2=DROUND(Maxt2,4)
PRINT "MAXIMUM RENT OCCURS WHEN T1 =";Maxt1;"N, T2 =";Maxt2;"N"
Expath=Q2*(U21-U22*Maxt2-U23*Maxt1)*(R21+R22*Maxt2-R23*Maxt1)
Expath=Expath/(Q1*(U11-U12*Maxt1-U13*Maxt2)*(R11+R12*Maxt1-R13*Maxt2))
Expath=DROUND(Expath,4)
PRINT "EQUATION OF EXPANSION PATH IN (Y1,Y2): Y2 =";Expath;"Y1"
PRINT CHR$(10)
INPUT "DO YOU WISH TO FIND PARTICULAR EQUILIBRIA?",Answer$
IF Answer$="YES" THEN
INPUT "N= ?",N
INPUT "T1 = ?",T1
INPUT "T2 = ?",T2
RL=R11*N+R12*T1-R13*T2
R2=R21*N+R22*T2-R23*T1
U1=U11*RL-U12*T1
U2=U21*RL-U22*T2
Y1=Q1*RL
Y2=Q2*RL
PRINT CHR$(10)
PRINT "N =";N
PRINT "T1 =";T1
PRINT "T2 =";T2
RL=DROUND(R1,4)
R2=DROUND(R2,4)
U1=DROUND(U1,4)
U2=DROUND(U2,4)
Y1=DROUND(Y1,4)
Y2=DROUND(Y2,4)
PRINT CHR$(10)
INPUT "RUN AGAIN?",Answer$
IF Answer$="YES" THEN 3560
END IF
END