

A hierarchical framework for the analysis of scale*

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Abstract

Landscapes are complex ecological systems that operate over broad spatiotemporal scales. Hierarchy theory conceptualizes such systems as composed of relatively isolated levels, each operating at a distinct time and space scale. This paper explores some basic properties of scaled systems with a view toward taking advantage of the scaled structure in predicting system dynamics. Three basic properties are explored:

(1) hierarchical structuring, (2) disequilibrium, and (3) metastability. These three properties lead to three conclusions about complex ecological systems. First, predictions about landscape dynamics can often be based on constraints that directly result from scaled structure. Biotic potential and environmental limits form a constraint envelope, analogous to a niche hypervolume, within which the landscape system must operate. Second, within the constraint envelope, thermodynamic and other limiting factors may produce attractors toward which individual landscapes will tend to move. Third, because of changes in biotic potential and environmental conditions, both the constraint envelope and the local attractors change through time. Changes in the constraint structure may involve critical thresholds that result in radical changes in the state of the system. An attempt is made to define measurements to predict whether a specific landscape is approaching a critical threshold.

Introduction

There is increasing awareness that landscapes and other ecological systems are scaled in space and time. Scaled structure has been noted in marine (Steele 1978), freshwater (Carpenter and Kitchell 1987), and terrestrial ecosystems (Delcourt *et al.* 1983). Recent reviews emphasize the awareness of

scale among both ecosystem (O'Neill, in press) and community (Wiens, in press) ecologists. Unfortunately, much of the literature focuses on the problems that result from scaled structure rather than providing a cohesive framework for taking advantage of scaled structure in the study of these complex systems.

Hierarchy theory is a theory of scaled systems. A

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series of monographs demonstrates the applicability of the theory to community (Allen and Starr 1982), ecosystem (O'Neill *et al.* 1986) and evolutionary (Eldredge 1985; Salthe 1985) ecology. This paper attempts to apply insights from hierarchy theory to the analysis of scaled ecological systems. The goal is to provide a comprehensive framework and to begin to apply the theory to predicting the general properties of scaled landscapes.

The basic premise of the paper is that all biological systems, ranging from a single cell to the total biosphere, are complex nonlinear systems that share three important properties. Biological systems are (1) hierarchically structured, (2) far from equilibrium, and (3) metastable. We use these three properties as departure points for explaining recent theoretical developments with particular reference to scale problems.

Hierarchical structure

The first property, hierarchical structuring, is a fundamental insight of biologists that can be traced back to the first observations that organisms are composed of cells. Allen and Starr (1982) and O'Neill *et al.* (1986) have argued that this intuitive structure is equally applicable to communities and ecosystems. Hierarchical structuring simply means that, at a given level of resolution, a biological system is composed of interacting components (i.e., lower-level entities) and is itself a component of a larger system (i.e., higher level entity).

The single most important consequence of hierarchical structuring is embodied in the concept of constraint. This concept emphasizes that the behavior of an ecological system is limited (1) by the potential behaviors of its components and (2) by the environmental constraints imposed by higher levels.

Some limitations on the dynamics of an ecological system come from lower levels and are imposed by the *biotic potential* of the components. These limitations are named 'initiating conditions' by Salthe (1985) and are analogous to rate-limiting steps in chemical dynamics. For example, a flock of birds, considered as a unit, cannot fly faster than

the slowest bird. A forested landscape cannot fix atmospheric nitrogen if the requisite organisms are not present.

Other limitations are imposed from higher levels as **abiotic** and biotic *environmental limits*. For example, constraints on population dynamics may be imposed by the community and ecosystem. Animal population growth may be limited by the available food supply, and plant growth may be limited by nutrient remineralization.

We can take advantage of the scaled structure of ecological systems to define a constraint envelope of physical, chemical, and biotic conditions within which the system must operate. The envelope represents the net result of both lower-level biotic potential and higher-level environmental limits.

Porter and Gates (1969) developed constraint envelopes, called climate diagrams, for individual organisms. They reasoned that an animal must maintain thermal balance with the environment. If the organism continuously gains or loses body temperature, biological function eventually becomes impossible. Animals possess a range of physical (e.g., fur, fat, feathers), metabolic, and behavioral mechanisms that allow them to regulate heat exchange. One can define the range of wind speed, air temperature, and absorbed radiation over which the mechanisms operate effectively. This range of conditions represents the constraint envelope within which the organism must remain.

Figure 1 shows a hypothetical constraint envelope of the type presented by Porter and Gates (1969). The boundaries are formed by the heat lost at night or gained during the day (environmental limits) over a range of metabolic conditions from complete rest to full activity (biotic potential). Basic principles of heat exchange prevent the organism from remaining outside this envelope for more than a brief time.

A different type of constraint envelope can be developed from the work of O'Neill and DeAngelis (1981) on the structural properties of woodland vegetation. Figure 2 shows the relationship between stand height and basal area for a number of woodland sites. The correlation between these parameters is well known to foresters. However, an understanding of constraints may help explain the

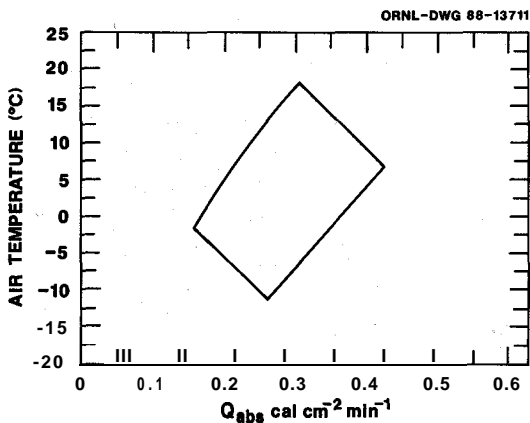


Fig. 1. Constraint envelope for a hypothetical mammal. Following Porter and Gates (1969), the envelope shows conditions of heat exchange and metabolic rates that define the feasible climate for this organism. Boundary conditions (left and right) are formed by the amount of heat absorbed in full sun or lost at night, under metabolic states (top and bottom) ranging from rest to maximum activity.

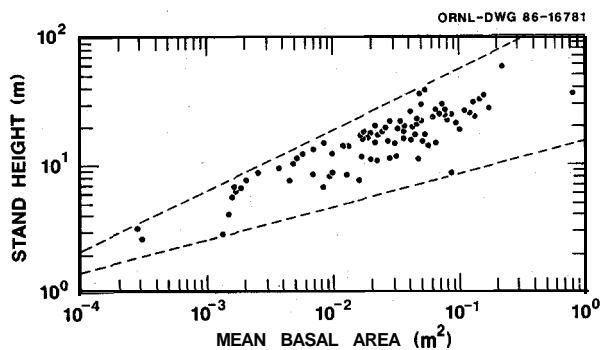


Fig. 2. Constraint envelope defining the structural properties of a woodland. Maximum height is related to the buckling height of a wood column, and minimum height is probably determined by the height of understory vegetation. (Redrawn from O'Neill and DeAngelis 1981.)

mechanisms behind the correlation. The stands all lie between an upper constraint related to the buckling strength of a column of wood (biotic potential) and a lower constraint probably representing the height of the understory vegetation (environmental limit).

At the level of the organism or population, the concept of a constraint envelope is isomorphic with a niche hypervolume (Hutchinson 1958; 1965). In this context, Edmondson (1944) developed a constraint envelope for rotifers with pH and bicar-

bonate concentration as critical limitations. Hutchinson (1970) presented a constraint envelope for *Myriophyllum* species based on pH and calcium concentration. Therefore, in one sense, the constraint envelope is simply a new name for the well-exercised concept of limiting factors. However, hierarchical structuring permits the concept to be extended because all levels of an ecological system have constraints imposed by biotic potential (*i.e.*, lower levels) and environmental limits (*i.e.*, higher levels).

The important point to note is that the constraint envelope has considerable predictive power. Exactly where an organism, population, or landscape is operating within the envelope, *i.e.*, the deterministic behavior of an individual system, may be difficult or impossible to predict. Often it is the constraints, coming from the scaled structure of the system, that yield deterministic predictions. We can state with considerable assurance that a system is within the constraint envelope but we may not be able to state the exact location of any specific system.

Weinberg (1975; Weinberg and Weinberg 1979) presents a classification of complex systems that may clarify the situation. Following earlier discussions by Weaver (1948) and Mandelbrot (cited in Stent 1978), Weinberg discusses three types of systems. Small-number systems contain few components, and each can be described by an individual equation. These systems yield to traditional scientific analysis. Large-number systems contain so many identical components, interacting randomly, that their statistical properties appear to be deterministic, *e.g.*, the temperature of a container of gas. Medium-number systems contain an intermediate number of components that interact in non-random fashion. These systems cannot be analyzed by traditional methodology and often appear to be stochastic. Unfortunately, landscapes are clearly medium-number systems.

As a result, it may often be easier to specify the constraint envelope than to determine precisely where within the envelope a medium-number system can be found. For example, Urban and O'Neill (in press) developed a model for bird demographics on complex landscapes. Clutch size (females

fledged per female per year) is an important determinant of population size. At high and low clutch sizes, the population can be predicted with a fair degree of precision because the population is tightly constrained. At intermediate reproductive capacity, the population size is determined by complex interactions involving competition, dispersal, patch size, and distance between patches. Thus, within the constraint envelope, one is caught squarely in a medium-number system, and one's ability to predict is severely constrained. The complexity of interactions on the landscape introduces stochasticity that may form an upper bound to predictability (Pielou 1972).

The dilemma is nicely illustrated by attempts to model the dynamics of aquatic ecosystems. Mechanistic models (e.g., Park *et al.* 1975) detail the interactions among phytoplankton, zooplankton, and fish populations. The models are useful for many purposes and do an excellent job of simulating typical lake dynamics. However, the models do not always predict the behavior of a specific lake. Even if the model could predict what an average lake would do, it often cannot predict what a particular lake will do.

The inability to deal with the lake as a medium-number system is in marked contrast to our ability to predict lake dynamics based on constraints. Vollenweider (1975; 1976) and Schindler (1977; 1978) showed that lake production was constrained and predicted by the input of a limiting nutrient, phosphorus. By considering the constraints within which the lake operates, they arrived at a useful prediction.

The constraint envelope specifies the set of conditions within which the ecological system can operate. At the community level of organization, competition and related mechanisms tend to spread out the species within the constraint envelope. As soon as one population establishes an adaptive pattern, other organisms can take advantage of this pattern and the envelope tends to fill. As a result, it may be easier to specify the constraint envelope for the community than to predict the exact position of a single species.

Our analysis of the first property of scaled biological systems, hierarchical structuring, leads to

the conclusion that predictions may come most easily by emphasizing constraints that result from the scaled structure of the system. The contribution of hierarchy theory to this problem is sparse because the theory does not predict which factors will be limiting. Determination of specific constraints remains the critical problem in any field situation. The theory simply predicts that one will find a scaled structure in a landscape and that limiting factors are likely to be found in biotic potential and environmental limits.

Nonequilibrium dynamics

The scaled structure of the landscape results in constraints that set limits to dynamics. But the concept of constraint has an additional dimension. Some constraints form attractors, within the envelope, toward which the ecological system will move through time. To illustrate this class of constraints, we turn our attention to the second property: ecological systems are far from equilibrium (DeAngelis and Waterhouse 1987).

Ecological systems can be viewed as complex biogeochemical systems processing materials and energy (Schindler *et al.* 1980). As such, ecological dynamics are subject to the laws of thermodynamics. This is not to say that all aspects of landscape behavior are determined by thermodynamic principles. The chemical environment and the genetic potential of biota are often needed to explain system dynamics. Nevertheless, thermodynamics defines an important class of constraints. We have seen above (Fig. 1) that thermal balance may help define the constraint envelope. Now we will consider whether nonequilibrium thermodynamics can also define a set of attractors within the envelope.

The application of thermodynamics to landscape systems is complex. Classical thermodynamic theory deals with equilibrium states in which all chemical or thermal gradients are destroyed, chemical reactions have a net rate of zero, and the system displays no macroscopic dynamics. Biological processing of energy and material implies that ecosystems are nonequilibrium thermodynamic systems.

Classic thermodynamics predicts that the entrop-

py, S , of an isolated system, can only increase or remain constant over time. The variation in entropy is constrained to be nonnegative, and the state which maximizes entropy is an attractor toward which the system will move. The attractor is the point of maximum entropy and is identical to thermodynamic equilibrium.

Nonisolated systems, like landscapes, that exchange energy or materials with their surroundings can be kept from thermodynamic equilibrium by free energy dissipated in irreversible processes. In a neighborhood near equilibrium, the thermodynamic forces can be regarded as linear functions of the process rate. In such situations, the nonequilibrium state corresponding to minimal entropy production, P , is an attractor (Prigogine 1967).

In ecological systems, far from thermodynamic equilibrium, the rates of irreversible processes are nonlinear functions of their driving forces, and the principle of minimum entropy production no longer holds. The systems can display self-organizing behavior resulting in coherence and order at a macroscopic scale. Such self-organizing systems depend on continued dissipation of free energy and are referred to as dissipative structures.

The asymptotic behavior of such systems is determined by the variation in entropy production, *i.e.*, the second-order variation in entropy. The time derivative of internal entropy production, S_i , is called excess entropy production, and it can be partitioned into two terms:

$$d^2S_i/dt^2 = dP/dt = d_xP/dt + d_jP/dt, \quad (1)$$

where d_xP/dt is the excess entropy production due to variation in the thermodynamic forces, and d_jP/dt is the excess entropy production due to variation in fluxes. If linearity in local entropy production can be assumed, d_xP/dt always decreases or remains constant (Glansdorff and Prigogine 1971). Thus, stationary states corresponding to local minima in excess entropy production are attractors.

Although broadly applicable, the theory does rely on the assumption that irreversible processes are linear at least on a microscopic scale. Zotin *et al.* (1978) have proposed a theory that does not make this assumption and was specifically designed for biological systems. The theory focuses on a

quantity, the specific dissipation function, D , that is proportional to entropy production:

$$D = (T/V) (dS_i/dt) = (T/V)P, \quad (2)$$

where T and V are the temperature and volume of the system. In systems far from equilibrium with irreversible processes occurring at a high rate, not all of the free energy dissipated by internal processes in fact leaves the system (Zotin *et al.* 1978). Open systems far from equilibrium will tend toward a state of minimum external energy dissipation:

$$dD_e/dt = 0. \quad (3)$$

This brief review indicates that thermodynamic constraints may determine an attractor, minimum external energy dissipation, within the constraint envelope. However, it remains to be demonstrated that thermodynamic attractors are relevant to ecological systems. Because microbial cultures are convenient systems for thermodynamic measurements, much of the experimental evidence is based on microbial microcosms.

Evidence for a thermodynamic attractor with local linearity is mixed. Stoward (1962) showed that total heat production (measured by microcalorimetry) from a batch culture of *Aerobacter aerogenes* was constant throughout the exponential growth phase and into the stationary phase. However, the rate of heat production per unit cell declined over time, resulting in a minimum value during the stationary phase. Stoward provisionally interpreted these results as consistent with the principle of minimum entropy production. However, Forrest and Walker (1962) observed a constant rate of heat production per unit biomass in a culture of *Streptococcus faecalis* throughout the exponential growth phase. They interpreted this result as inconsistent with evolution toward a state of minimal entropy production.

Both Stoward (1962) and Forrest and Walker (1962; 1964) considered exponential growth to be a transient thermodynamic phase during which the system was approaching a stationary thermodynamic state. Bermudez and Wagensberg (1985; 1986) show that the exponential growth phase is itself a type of stationary state. Their calculations of entropy balance indicated that the assumption of

linear nonequilibrium thermodynamics was appropriate for part of the exponential growth. Their work strongly suggests that a thermodynamic stationary state need not be a stationary state in terms of biomass or other variables.

Other studies have considered microbial microcosms in the nonlinear domain. Schaarschmidt *et al.* (1975) measured the bound dissipation function, D_u , as the difference between the heat production due to metabolic activity and the heat production actually leaving the system. In a subsequent paper, Schaarschmidt *et al.* (1977) argued that a semi-logarithmic relationship should exist between heat production and biomass, a prediction which was confirmed by several studies. These microcosm studies indicate that thermodynamic attractors exist, at least for simple ecological systems. The analysis of thermodynamic constraints would lead one to believe that other attractors, defined on nutrient availability, water use efficiency, or other limiting factors, might also exist.

Because of differences in biotic potential and local environmental limits, landscapes within the same constraint envelope may have different attractor points. The theory does not specify a single point to which a landscape would be attracted. It is also important to note that it is not immediately apparent how to estimate external entropy dissipation in landscapes. The theory does, however, predict that a scaled landscape system can be expected to remain within a constraint envelope and that there may exist local attractor points, defined on thermodynamic and other principles.

Metastability

Over long time scales, climate and other environmental limits change. Biotic potential may also change due to local invasion and extinction. Thus, both the constraint envelope and the attractors may be altered. These changes introduce dynamics that lead to the third property: Ecological systems are metastable.

Stability means that ecological systems remain relatively unchanged and return to the same attractor if subjected to minor disturbances. However,

changes in biotic potential and environmental limits may alter the constraints, and the system may cross a critical threshold and undergo a radical change. The property of metastability means that an ecological system can maintain itself over a limited range of conditions but may eventually undergo significant alterations if constraints continue to change.

Hierarchy theory (O'Neill *et al.* 1986) predicts that ecological systems can be described by state variables operating at distinct time scales. It is in this scaled temporal behavior that we find clues to understanding metastability.

Consider the dynamical system

$$\frac{dx}{dt} = f(x, p), \quad (4)$$

where x is a vector of state variables, and p is a vector of parameters. For an important class of such systems, a function $V(x, p)$ exists such that $-\partial V/\partial p = f(x, p)$. Such systems are called potential systems, and V is called a potential function. For a system of one state variable and one parameter, the potential function can be represented as a surface (Fig. 3) with the state of the system on the x -axis, the parameter value on the z -axis, and the value-of V on the y -axis. As a heuristic device, imagine a marble rolling on Fig. 3 until it finds a local minimum. Analogously, a potential system spontaneously changes state until the potential function is at a local minimum of attractor.

Now consider a system in which the parameters are allowed to change on a time scale which is slow relative to the dynamics of the state variables. The set of minima, where $\partial V/\partial p = 0$, corresponds to a connected set of local attractors that is called the manifold of the system. The manifold appears as a solid line in Fig. 3. Several authors (Naveh and Lieberman 1984; Forman and Godron 1986) have argued that landscape systems follow this type of dynamic.

A theorem due to Tikhonov (1950, presented in English by Plant and Kim 1975) describes the dynamics of a system in terms of fast and slow components. The dynamics of a system can be measured by the time required, T_r , to return to the attractor following a small perturbation. The time scale on which parameter shifts occur will be represented as T_p . If T_r and T_p are sufficiently different, then the

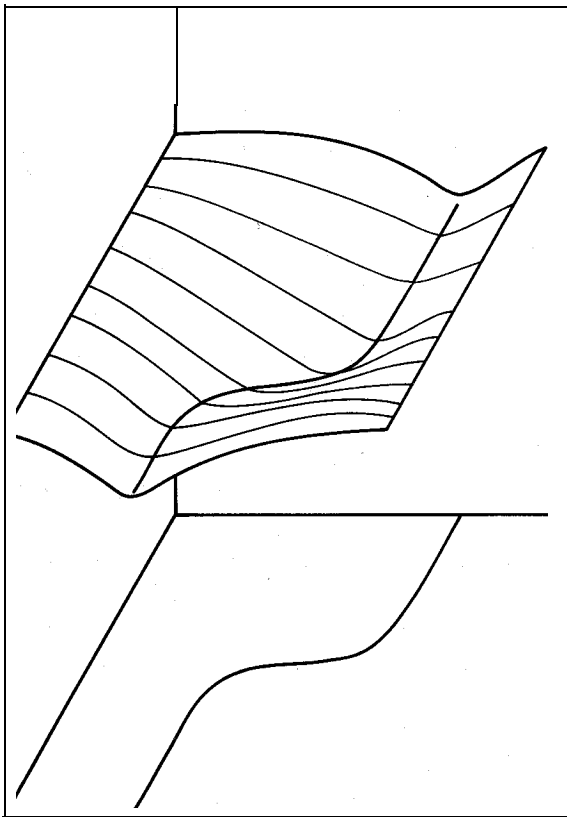


Fig. 3. A hypothetical potential function (y-axis) plotted as a function of the state of the system (x-axis) and a single parameter (z-axis). The solid line projected onto the x-z plane represents the manifold of the potential system.

long-term dynamics of the system can be described by the slow dynamics alone and the fast dynamics can be ignored. Such a system may pass through transient phases, during which both fast and slow components are important. Asymptotically, however, the effect of the fast components will diminish and the long-term, undisturbed behavior will be dominated by the slow dynamics. On short time scales, the fast dynamics will move the system toward a local point on the manifold. Over longer time scales, the slow dynamics will change the position of the local attractor, and the system will describe a state space trajectory that reflects the pursuit of a moving target.

The Tikhonov theorem allows one to simplify analysis of ecological systems and to take advantage of their scaled structure. But Tikhonov does

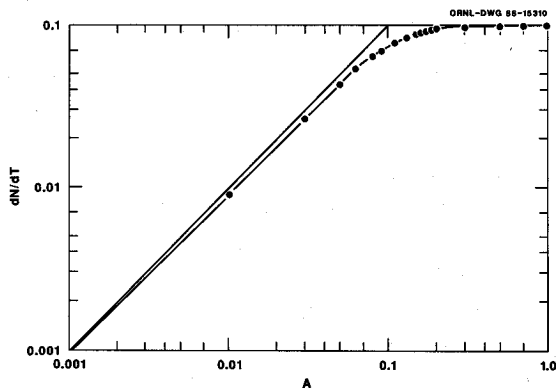


Fig. 4. Results of a simple population simulation. The rate of change of the population is plotted as a function of A, the rate of change in the carrying capacity. The straight diagonal line represents the population dynamics predicted by strict application of the Tikhonov theorem.

not say how far apart the time components have to be. The situation can be clarified by a simulation experiment. Consider a population with growth determined by an intrinsic rate of increase, r (biotic potential), and a carrying capacity, K (environmental limit). This type of growth can be described by (Pielou 1977)

$$X(t) = (K - X_0 e^{-rt}) / (1 - X_0 e^{-rt}/K). \quad (5)$$

From any initial condition, X_0 , the population grows toward K as an attractor. Now consider that the carrying capacity of our hypothetical system is slowly changing:

$$K(t) = K(t-1) + A K(t-1), \quad (6)$$

that is, K is incremented by the factor A at each time step in the simulation. According to Tikhonov, if the rate of change in K is slow relative to r , the long-term dynamics of the system will be determined by the dynamics of K .

Results of the simulation with $(N(0) = K(0) = 10$ and $r = 0.1$) are shown in Fig. 4. On the abscissa is A , the change in K at each time step. On the ordinate is the rate of change in N , averaged over 100 time intervals of the simulation. The straight diagonal line represents the expected rate of change in the population if the dynamics were exactly described by the rate of change in K .

For changes in K , $0.001 < A < 0.05$, the dynamics are dominated by A (Fig. 4) and the popula-

Table 1. A comparison of turnover rates ($t - 1$) for simplified food chains. Values are consumer turnover divided by food supply (foliage or detritus) turnover.

	Terrestrial foodchains	
	Foliage-based	Detritus-based
Old field (1)	108.26	
(2)	47.52	
(3)	231.18	
Tropical forest (4)	40.19	
(13)		3.88
(13)		5.29
(13)		8.09
Deciduous forest (5)	3.54	47.43
(6)		27.76
(13)	4.56	
(13)		2.24
Broadleaf evergreen (13)		9.33
Coniferous forest (13)	297.03	7.57
Aquatic foodchains		
	Plankton-based	Detritus-based
Marine (7)	0.83	
Cedar bog (8)	1.91	
Lake (8)	1.48	
Pond (9)	0.33	
Stream (10)		4.52
(11)	0.06	
(12)	5.12	
(14)		12.71

1. Golley 1960
2. Menhinick 1967
3. Pearson 1964
4. McGinnis *et al.* 1969
5. Satchell 1971
6. Witkamp and Frank 1970
7. Bolin 1970

8. Lindeman 1942
9. Whittaker 1961
10. Teal 1957
11. Tilly 1968
12. Odum 1957
13. Reichle *et al.* 1973
14. Fisher and Likens 1973

tion tracks K . For $0.2 < A < 1.0$, the slow dynamic becomes $r = 0.1$, and the population changes at an average rate of 0.1, no matter what the change in K . A reasonable interpretation is that a separation between fast and slow dynamics on the order of 2.0 is sufficient. It is only for $0.05 < A < 0.2$, that the system dynamic deviates in any important way from the predictions of the Tikhonov theorem. If fast and slow components of an ecological system differ by a factor of 2.0, we can reasonably assume that long-term dynamics will be dominated by the slow dynamics.

The question then becomes whether separations

of 2.0 or greater are common in ecological systems. Table 1 is a preliminary literature review designed to compare consumer dynamics with their food supplies. For 21 systems, including both terrestrial and aquatic ecosystems, the table gives the ratio of the turnover rate ($t - 1$) of consumers to the turnover rate ($t - 1$) of the food supply. In the case of the food supply, the turnover rate represents the foliage (not the entire tree biomass) or litter/detritus (not the entire soil organic matter).

If the ratio is greater than 2.0, we can assume that consumer dynamics are unimportant in the long term. The consumer will be relatively stable to a

manifold described by the dynamics of the food supply. If the ratio is less than 0.5, we can assume that the reverse situation holds: the food supply is relatively stable to a manifold determined by the consumer. It should be noted that predators and other components of the system are not considered in this analysis.

For terrestrial ecosystems, the consumer populations (arthropods and small mammals) have much faster dynamics than their food supply. The same is true for aquatic detrital consumers (invertebrates, largely arthropods).

The situation is more complex for planktivorous systems. Based on these data, the turnover rate of zooplankton is not consistently different by a factor of 2.0 from the turnover rate of phytoplankton. In two cases (0.33 and 0.06), the phytoplankton appear to be faster by a factor of 2.0, while in two cases (1.91 and 5.12), the phytoplankton appear to be slower. In two other cases (0.83 and 1.48), the dynamics do not differ by a factor of 2.0. Therefore, it is not clear whether consistent constraint operates between phytoplankton and zooplankton.

With the exception of the pelagic systems, food supply and consumers have dynamics that differ by more than a factor of 2.0. On this basis, it appears reasonable to talk about ecological systems in the context of the Tikhonov theorem. Dynamics of these simple systems should show a manifold determined by the slow dynamics with the fast dynamics being Lyapunov stable to this manifold.

We said, however, that biological systems are metastable. This means that we expect the landscape to respond stably only over a limited range of conditions. The parameters that determine the slow dynamics can change and alter the manifold in important ways. When the parameter reaches a critical threshold, the manifold may exhibit a topological discontinuity, called a bifurcation. Consider the system illustrated in Fig. 5. Assume that the value of p (z-axis) is initially at the back of the figure. As the parameter changes, the system moves along the valley, toward the front of the figure, until it reaches the dividing point or bifurcation. Further changes in the parameter cause a radical change in the state of the system, often involving multiple stable states, such as the two possible states shown in Fig. 5.

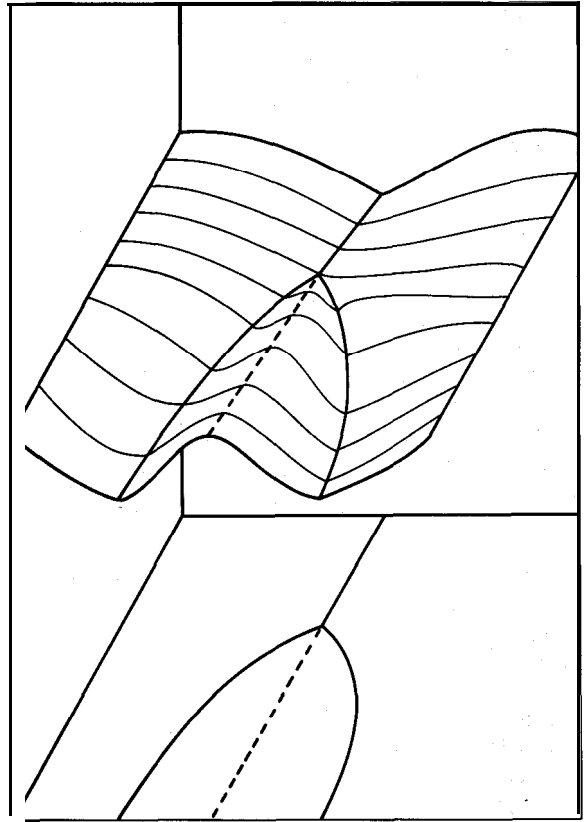


Fig. 5. A hypothetical potential function illustrating a bifurcation. The axes are the same as those defined for Fig. 3. As a parameter (z-axis) is slowly changed from the back of the figure toward the front, the system moves to a critical or bifurcation point. Further change in the parameter causes the state of the system to move to one of the two altered states. The dotted line represents a set of unstable attractors.

Bifurcations may underlie unexpected or surprising phenomena observed in landscapes. Jones (1975) argues that outbreaks of pests, such as the spruce **budworm**, are due to such dynamics. There is also evidence that this class of behavior occurs in climate change. Crowley and North (1988) demonstrate a fold catastrophe in a simple model of ice cap dynamics. Small changes in the solar constant lead to an abrupt transition to an ice-free earth. Crowley and North argue that such bifurcation phenomena may be responsible for climatic changes such as transitions between glacial and interglacial periods.

There is also evidence for bifurcation phenomena

in simple ecological systems, exemplified by microbial microcosms. Rozich and Gaudy (1985) and Worden and Donaldson (1987) report an inability to predict microbial transient response with the use of simple models that do not allow for bifurcations. An adequate model for the dynamics of a flow-through microbial culture might be

$$\begin{aligned} dB/dt &= MB - RB \\ dS/dt &= -MB/Y + R(S_0 - S), \end{aligned} \quad (7)$$

where B is the microbial biomass, M is the biomass-specific growth rate, S is the substrate concentration in the culture vessel, S_0 is the influent substrate concentration, Y is a yield efficiency factor, and R is the dilution rate. The growth rate, M, can be expressed as a function of the available substrate concentration. If the substrate is inhibitory at high concentrations, the Haldane relationship may be used to represent the growth rate:

$$M = M_m S / (K_s + S + S^2 / K_i), \quad (8)$$

where M_m is the maximum attainable growth rate, K_s is a half-saturation constant (i.e., the concentration at which growth is one half of maximum), and K_i is a constant describing the inhibition.

The dynamic equations with Haldane growth function can have as many as three steady states (two stable + one unstable). If there is substantial growth on the surfaces of the culture vessel, the washout of suspended organisms does not eliminate the microbes, and two nontrivial steady states are possible (Chi et al. 1974), one of high conversion efficiency (suspended) and one of low efficiency (wall growth). At intermediate flow rates, both states are stable, and which one is achieved depends upon initial conditions (Andrews 1968; Yano and Koga 1969; Borighem and Vereecken 1981; Gaudy et al. 1988). Pawlowsky et al. (1973) demonstrated that transitions between steady states can be achieved by perturbing either substrate concentration or microbial biomass. These studies demonstrate that metastability is a reality in simple ecological systems.

An important question is whether bifurcation phenomena can be predicted. Can some characteristic of the dynamics of the system on short time scales be used to anticipate impending bifurca-

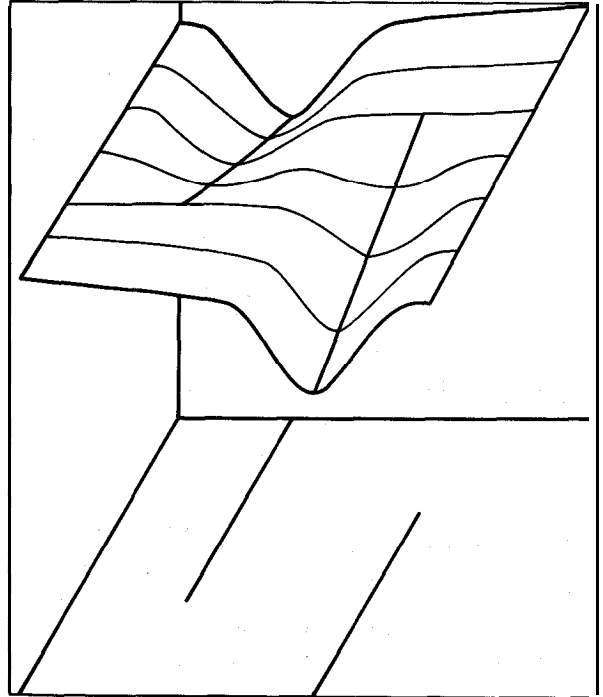


Fig. 6. A hypothetical potential function. The axes are the same as those defined for Fig. 3. In this situation, radical changes-between domains of attraction can only result from large-scale perturbations.

tions? If measurable characteristics can be identified, they could play a major role in monitoring anthropogenic changes on landscapes.

To address questions of anthropogenic effects, we must consider two possible ways for a landscape to undergo radical change. If a major disturbance occurs, the landscape can be driven into a radically new state. Consider the system illustrated in Fig. 6. The potential function has two 'valleys' or domains of attraction. A major disturbance would be required to drive the landscape from one domain of attraction to the other. If the disturbance is stochastic and unpredictable, there is no way to predict when the change will occur. Haken (1983) designates changes due to large disturbances as first-order phase transitions and introduces the concept of T_e , the equilibrium time characterizing the expected interval over which a system might be perturbed into all of its possible domains of attraction. First-order phase transitions can occur without any change in the parameters, p.

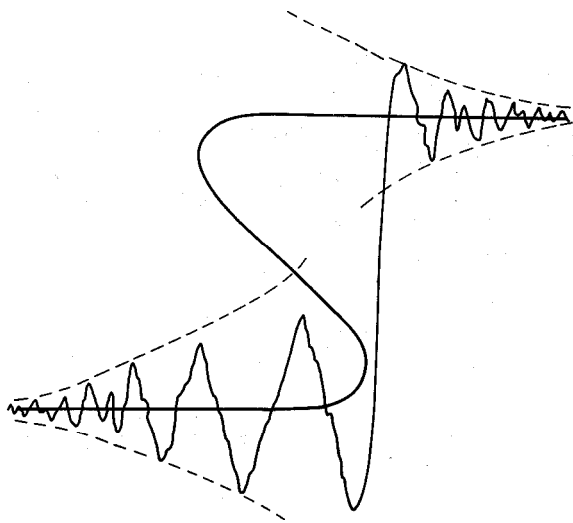


Fig. 7. Dynamics of a hypothetical system near a bifurcation point. As a parameter (x-axis) is slowly changed, random perturbations will cause increased fluctuations in the state of the system (y-axis) until the system moves through the bifurcation point and moves to a new domain of attraction.

On the other hand, the landscape may approach a bifurcation (i.e., a critical threshold) and undergo a radical change of state without a major disturbance, simply by changing the value of p (Fig. 5). Haken (1983) designates such changes as second order phase transitions. As the parameter approaches the critical threshold, two things happen. First, if the system is perturbed away from the manifold, the rate at which the state variables return to the manifold is slower. Second, the sides of the potential function become less steep as the bifurcation point is approached. If the system is subject to stochastic disturbances, the amplitude of the resulting fluctuations will increase (Fig. 7). Crowley and North (1988) demonstrated that a global energy balance model subjected to stochastic forcings showed greater variability as the solar constant was reduced toward a bifurcation point. Thus, decreased resilience or increased variability may be useful indicators of future qualitative changes in the long-term behavior.

This suggests three possible empirical methods for detecting approaching instability. (1) Increases in the relaxation time from small perturbations could be directly measured (O'Neill 1988; Schoner

and Kelso 1988). (2) An increase in the variance of observed fluctuations about the attractor could be measured (Schoner and Kelso 1988; Crowley and North 1988). (3) Schoner and Kelso (1988) point out that increased variability could also be detected as increased line width of the spectral density function in a time series analysis of the state variables.

In summary, the existence of scaled structure in a complex landscape permits the investigator to decompose dynamics into fast and slow components. The landscape will be metastable to the manifold defined by the slow dynamics. As the landscape moves toward a critical threshold, variability and local relaxation time may serve as **measurable** warning signs.

Conclusions

Hierarchy theory predicts that complex ecological systems, such as landscapes, will be composed of relatively isolated levels. Each level will operate at a relatively distinct time and space scale. We can take advantage of this scaled structure in analyzing complex landscape problems.

Significant predictive power comes from an analysis of constraints that result from the scaled structure. Biotic potential (lower-level limitations) and environmental limits (higher-level constraints) form a constraint envelope within which the landscape must operate. Within the constraint envelope, other factors, such as thermodynamics and nutrient/water use efficiency, may define local attractors. This constraint structure, resulting from scaling in space and time, represents one of our best predictive tools for complex landscape systems.

The constraint structure changes through time, and the landscape may move through critical thresholds and undergo radical changes. The theory predicts that landscapes approaching such a radical change will take longer to recover from minor perturbations and will become more variable in both time and space. These predictions are testable in microcosms and may provide critical input to designing monitoring systems to predict how **landscape** and even global systems will respond to anthropogenic changes.

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