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STABILITY IN TIME-VARYING ECOSYSTEMS*

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Recently, many articles and books, both popular and scientific, have discussed perturbations and other disturbances of natural ecosystems. Many of these discussions are predicated on concepts of stability. However, explicit analyses of stability generally occur in contexts of specific mathematical models, and the specificity of these models may obscure the ecological significance of the definition of stability employed. As Holling (1974) has said: "Our traditions of analysis in theoretical and empirical ecology have been largely inherited from developments in classical physics and its applied variants. . . . It is similarly important, if a quantity fluctuates, to know its amplitude and period of fluctuation. But this orientation may simply reflect an analytic approach developed in one area because it was useful and then transferred to another where it may not be."

In the anecdotal literature, the concept of stability is often implicit and vague. Where defined explicitly, the concept is borrowed from, or equivalent to, the classical mechanics definition of a system that will tend to return to its equilibrium state, at rest, after being perturbed; we label this property *static stability*.¹ For example, the International Biological Program Grassland Biome "Glossary of Systems Ecology Terms" (Woodmansee 1974) defines a stable system as ". . . one that tends to return to initial conditions after being disturbed. It may overshoot and oscillate (like a simple pendulum that is set in motion), but the disturbances decline and die out." Equivalent definitions of stability occur in modern ecology texts such as Krebs (1972), Odum (1971), McNaughton and Wolf (1973), and Smith (1974). May (1973) presents an extensive account of the elegant mathematical analysis of ecosystem static stability. Static stability underlies the definitions of stability found in standard treatises on systems theory, e.g., Freeman (1964), Lee and Marcus (1967), Schwartz and Friedland (1965), and Zadeh and Desoer (1963).

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¹ We shall leave mathematical fine points aside and not distinguish between "stable," "asymptotically stable," and "globally asymptotically stable" as these terms are defined in systems theory.

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Static stability is used in recent ecological literature. In a study of isotope kinetics in a laboratory "microcosm," Patten and Witkamp (1967) define relative stability as

$$S = \left[\frac{x_j(\text{eq})}{\Delta x_j} \right] \left[\frac{\delta_j t}{\Delta_j t} \right],$$

where S is relative stability, $x_j(\text{eq})$ is the equilibrium amount of material in a compartment, Δx_j is the perturbation in the same units as the equilibrium amount, $\delta_j t$ is the duration of the perturbation, and $\Delta_j t$ is the time for a compartment to return to the original equilibrium.

In a study of the relative stability of mineral cycles in forest ecosystems, Jordan et al. (1972) use an equivalent definition and state: ". . . A stable system returns monotonically or with decreasing oscillations toward the steady state. An unstable system continues to depart from steady state, either monotonically or with increasing oscillations. An unstable but bounded system either assumes a new steady-state level or oscillates, but the amplitude of the oscillations remain constant. Mineral cycles in ecosystems which remain intact are all monotonically stable."

The concept of static stability is implicit in the classical notions of succession and climax. For example, in Cooper's (1913) classic study of the climax forests of Isle Royale National Park, he states that the boreal forest is ". . . the climax forest of that portion of the northeastern conifer region under consideration; in other words, that upon Isle Royale it is the final and permanent vegetation stage, toward the establishment of which all other plant societies are successive steps. . . . Both observational and experimental studies have shown that the balsam-birch-white spruce forest, in spite of appearances to the contrary, is, taken as a whole, in equilibrium; that no changes of a successional nature are taking place within it."

OBJECTIVES

The objectives of this paper are to suggest that the concept of stability just described may be inappropriate for the analysis of ecosystems, and to propose some notions of stability that are motivated by the ecological connotations of the phrase "stability" and by the history and dynamics of real ecosystems. Each notion is presented loosely in verbal terms and then translated into a plausible mathematical definition.

Those familiar with the mathematical study of stochastic processes will recognize that the definitions presented here are not new in concept. We merely state known mathematical notions, heretofore not applied in ecology, in ways that enhance understanding of the stability of real ecosystems. These notions, therefore, are pertinent to ecosystem management. In our discussion of these concepts, we show in a preliminary way how they might be applied in ecology.

The evaluation of alternative definitions of stability is more significant than a mere mathematical pastime. Frequent calls to arms based on claimed links between stability and species diversity are bugled to the scientific and lay

publics. The recent article by Holdren and Ehrlich (1974) is a good example. It is likely that public policy has been or (optimistically) shortly will be influenced by definitions of stability in vogue at the time.

1. TRAIL GUIDE

This paper is lengthy, but we hope that a trail guide will ease the reader's efforts to travel through our eight sections. Section 2 concerns the role of fire in the Boundary Waters Canoe Area in Minnesota. This context is a useful vehicle to introduce the discussion of stability of structural properties of ecosystems. We turn in Section 3 to formal definitions of stability in deterministic ecosystem models. The principal stability notions discussed there are *persistence* and *recurrence*. These notions are given formal definitions for stochastic ecosystem models in Section 4, and are applied to the Boundary Waters Canoe Area in Section 5. In Section 6, we turn to applications to models of predator-prey interaction. We find that the recurrence and persistence notions are again useful, and we advance new reasons to deny the empirical importance of the Lotka-Volterra equations. Section 7 discusses applications to functional properties of ecosystems as exemplified by the history of Berry Pond in Massachusetts. The principal conclusions drawn from our applications in Sections 5, 6, and 7 are summarized in Section 8.

2. FIRE IN THE BOUNDARY WATERS CANOE AREA

We examined reports of the histories of several real ecosystems and concluded that static stability is an inappropriate concept with which to analyze perturbations of these systems. A good example is provided by Heinselman's (1973) history of the forests of the Boundary Waters Canoe Area (BWCA) and the role of fire in these forests. Heinselman investigated forest history by examining pollen, charcoal, and other deposits in lake sediments, by examining historical records, and by directly observing evidence of fire and the current state of forested areas.

Pollen deposits from Lake of the Clouds in the BWCA (Craig 1972; Swain 1972) indicate that the last glaciation was followed by a tundra period, then by a boreal spruce forest which was replaced about 9,200 yr ago by a forest dominated by jack pine and red pine. Subsequently, paper birch and alder were added about 8,300 yr ago, then white pine entered about 7,000 yr ago, and afterward there was a return to spruce, jack pine, and white pine. Thus, on a geological time scale, the classical ecological concept of a climax forest—i.e., one that would dominate the landscape and reproduce itself through time if man would not interfere—does not fit the real history of the BWCA.

Classically, ecologists have avoided this problem by talking about climatic climaxes, or communities that dominate the landscape as long as the climate is constant. From this point of view one might argue that changes in forest composition are slow and that an equilibrium state might be obtained in periods of less than 1,000 yr. To refute this argument, we observe that it is likely that

the effects of initial conditions or catastrophes would influence an ecosystem for at least a few generations. Because the lifetimes of some of the tree species in northern hardwoods and coniferous forests are on the order of 400 yr, an equilibrium state in the BWCA seems inappropriate for intervals of centuries. Shorter periods involve local successional events for which it is also unreasonable to assume that the forest reaches an equilibrium. Thus the concept of an equilibrium state for an unmanipulated or "natural" forest is contradicted by history, and a definition of stability which involves a return to an equilibrium is not appropriate for the BWCA.

Terrestrial ecologists will recognize that this history is not unique. Such histories lead us to argue that static stability is a formalization having at best little ecological value. Evolutionary progression and adaptation provide another inducement to reject it.

Other writers also have rejected this concept of stability. Watt (1969) discusses histories of several phenomena which lead him to reject, implicitly, the notion of static stability. Margalef (1969) and Lewontin (1969) also attempt to confront the inadequacy of this notion.

How can one deal with the response of ecosystems to perturbations if one cannot talk about an equilibrium state? What does it mean to "preserve" a natural ecosystem, to investigate the effects of "perturbations," or to limit man's influences which might be "destructive" or "destabilizing"?

A good case in point is the occurrence of fire in the BWCA. It has been common in the twentieth century to believe that fire is an exogenous event imposed on a forest and that a forest would become an equilibrium climax community if fire were suppressed. Heinselman's (1973) paper contradicts this view. He states that fire in the BWCA has been a periodic disturbance, with an estimated period of 100 yr to burn 1 million acres. He cites evidence of fire occurring there 38,000 yr ago.

Not only has fire been a recurring event, but its frequency has varied. Fire apparently became less frequent 3,000–1,200 yr ago, with an accompanying increase in northern white cedar and a decrease in pine. Fires were more common from A.D. 1000 to A.D. 1400, then less common until about A.D. 1670.

The existence of species such as jack pine, which have evolved serotinous cones during the last 20 million yr, further supports the argument that fire has been a persistent factor for a long time.

Heinselman observes that the intentional suppression of fire in the present century has produced two trends. First, "dry matter accumulations, spruce budworm outbreaks, blowdowns and other interactions related to the time since fire increase the probability that old stands will burn." The large amounts of fuel available may lead to catastrophes such as destruction of the current vegetation patterns and thus the elimination of species which are adapted to the occurrence of moderate fires with a frequency on the order of once in 20 yr. The species in the old stands promote the severity of fire, when it occurs, by producing readily burnable litter. Too-frequent fires kill the regenerating plants (the saplings and seedlings) before they reach a reproductive stage; too-

infrequent fires may be so severe that they destroy the root system and all the mature seed trees and disrupt the soil.

The second current trend due to suppression of fire is the gradual replacement of currently dominant species (jack and red pine) by a fir-spruce-cedar-birch forest.

What does it mean to “stabilize” or “preserve” a forest when the natural undisturbed forest is changing through time, and when fire appears to be an intrinsic event?

3. NOTIONS OF STABILITY IN DETERMINISTIC MODELS

For expository convenience, our discussion of formal stability begins with deterministic ecosystem models. Time is an explicit parameter in the models we consider because time affects every ecosystem, if only to age its members.

For two reasons, we begin with models of ecosystems that are undisturbed by “external” influences. First, as previously discussed, a definition of stability has little pragmatic value if it invokes a return to equilibrium. Second, an undisturbed system that lacks a plausible kind of stability will not acquire stability when it experiences an external shock. It is conceivable, however, that a system, stable in some sense when undisturbed, might become unstable after experiencing a shock.

The preceding reasons urge the consideration of models that are “naturally” dynamic or time varying. Let $x(t)$ denote the “state” of an ecosystem at time t . The time scale is arbitrary, but it is convenient to let $t = 0$ denote the time at which we begin observing the system. “State” summarizes whatever characteristics of the system are of central interest, e.g., population size, the age and sex distributions of the biomass of several populations, etc. We shall let S denote the set of all conceivable states; throughout this section, let S be the set of all real numbers.² Let $x_0 = x(0)$ denote the initial state of the ecosystem, i.e., the state of the system when observations begin.

Persistence.—“Stability” has several connotations. An important one is moderation in the size of “natural” fluctuations in the graph of the state as a function of time. We shall use the labels “posterity” for $\{x(t), t \geq 0\}$ and “persistence” for a posterity that remains within a given distance of a specified point. Formally, we say that a posterity is Θ -persistent about the point x' if

$$|x' - x(t)| \leq \Theta \quad \text{for all } t \geq 0. \quad (1)$$

This definition depends on the chosen point x' as well as on the distance Θ .

Our concept of Θ -persistence, as well as its terminology, is related to definitions found elsewhere. In systems theory, for example, there is a nonstandard

² Throughout the paper, we shall ignore important mathematical points such as the extension from the reals with Euclidean distance to general metric spaces, the integrability or summability of functions, the measurability of functions or sets, the attainment of infima, and the existence of limits. Our definitions can be generalized to encompass these considerations.

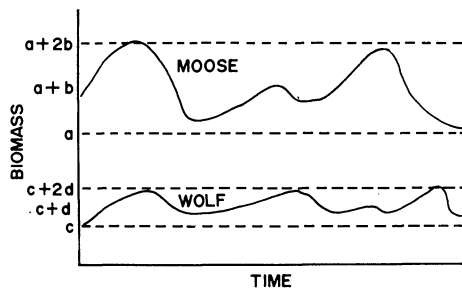


FIG. 1.—An example to illustrate Θ -persistence for idealized moose and wolf populations.

definition (cf. Schwartz and Friedland 1965) of an *equilibrium* state being *bounded* if there is a neighborhood, surrounding the state, that has the following property: if the initial state is any state in the neighborhood, then the posterity will always lie within a finite distance from the equilibrium state. Our definition of Θ -persistence, however, is not predicated on the existence of an equilibrium state. Terminologically, “persistence” arises early in Smith (1974). Definitions there include: “An ecosystem is *taxonomically persistent* if the species composing it remain the same for long periods . . . ; it is *numerically persistent* if the relative numbers of individuals in different species either remain constant, or return regularly to the same ratios, for long periods. . . .”

Example 1: If $x(t) = \sin t$, then the posterity is Θ -persistent about x' if and only if $\Theta \geq 1 + x'$.

Example 2: Figure 1 idealizes a posterity of moose biomass on Isle Royale in Lake Superior. The moose posterity is Θ -persistent about x' if and only if $\Theta \geq \max \{x' - a, a + 2b - x'\}$.

These examples illustrate that a posterity's persistence (or lack of it) depends on the location of the idealized state x' and on the *stringency* of the approximating neighborhood. For any comparison state x' , a posterity will be Θ -persistent about x' if Θ is selected sufficiently large (possibly ∞). Conversely, if the posterity is not a constant, then it will fail to be Θ -persistent about any x' if Θ is chosen sufficiently small.

If the posterity $\{x(t), t \geq 0\}$ is a record of population size or biomass, then it is convenient to apply the following altered definition of persistence: *the posterity is Θ -persistent about x' if*

$$|x(t) - x'| \leq \Theta \cdot \min \{x(\tau) : 0 \leq \tau < \infty\} \quad \text{for all } t \geq 0. \quad (2)$$

If the population size should drop to zero at some time, then (with this altered definition) the posterity would *not* be Θ -persistent for any $\Theta < \infty$.

The variant of Θ -persistence in (2) used a normalization of $1/\min_{\tau \geq 0} x(\tau)$. A different normalization may be useful when several different posterities, each representing population size (or biomass), are being compared. Then the normalization created by division by the mean population seems appropriate.

Specifically, instead of (1) or (2), a posterity is said to be Θ -persistent about x' if

$$|x(t) - x'| \leq \Theta \cdot \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x(\tau) d\tau \quad \text{for all } t \geq 0. \quad (3)$$

Recurrence.—Another important connotation of “stability” is the repetition of a previously occupied state. For example, consider a man who revisits a forest in the BWCA he saw in his childhood. He may be more concerned with verifying that the kinds of forests he saw as a child have recurred somewhere in the area than with verifying that the entire forest has remained unchanged during his absence.

The basic idea here is that the posterity is sure to revisit a state it has already occupied. For mathematical purposes, it is convenient to generalize the idea to the posterity getting arbitrarily close, at some future time, to a state it has already occupied. Specifically, we say that *state x' is recurrent* if for every $\delta > 0$ and $\tau > 0$ there is a $t \geq \tau$ such that $|x(t) - x'| \leq \delta$. This definition is equivalent to

$$\lim_{\tau \rightarrow \infty} \min_{t \geq \tau} |x(t) - x'| = 0. \quad (4)$$

If a state is not recurrent, then we call it *transient*. The interval $x' - \delta \leq u \leq x' + \delta$ is called the δ -neighborhood of x' . It follows from the definition of recurrence that, if a state x' is transient, then there is a $\delta > 0$ such that the posterity is never found in the δ -neighborhood of x' past some point in time. The set S of all states can be partitioned into two sets: the recurrent states S_R and the transient states S_T .³ We define a *posterity as recurrent* if all states in S are recurrent; i.e., if $S = S_R$. For instance, the posterities in examples 1 and 2 above are recurrent with $S = \{x: |x| \leq 1\}$ and $S = \{x: a \leq x \leq a + 2b\}$, respectively.

Example 3: A recurrent process may lack persistence, and a persistent process may be transient. For example, the posterity $x(t) = t \sin t$ with $S = (-\infty, \infty)$ is recurrent although it is not Θ -persistent about any x' for any $\Theta < \infty$. On the other hand, this posterity is sure to reiterate every previously visited state.

Example 4: The posterity $x(t) = 1 - e^{-t}$ with $S = (0, 1)$ is Θ -persistent about $\frac{1}{2}$ for all $\Theta \geq \frac{1}{2}$, but every state in S is transient, i.e., $S = S_T$.

Our definition of posterity recurrence is endowed with an element of tautology. Every posterity for which S_R is nonempty is recurrent if $S = S_R$; it fails to be recurrent if S_R is augmented with even one element of S_T .

Our definitions of persistence and recurrence are predicated on posterities of infinite duration, i.e., the domain of the function $X(\cdot)$ is the half line $(0, \infty)$. However, many ecosystem models are defined only over finite time horizons. Persistence seems to be useful for finite-horizon models because often one is interested in the range of values taken by a posterity of limited length. Fortunately, our definitions (1), (2), and (3) are applicable to the persistence of finite-horizon models if “for all $t \geq 0$ ” is interpreted as “for all t in the finite

³ It follows from the definition of recurrence that S_R is a closed set.

interval of time for which the posterity is defined." The notion of recurrence seems irrelevant for finite-time-horizon models because every state that occurs even once must occur for a last time.

Perturbation.—The effect of a perturbation is to alter the posterity that would otherwise have characterized the ecosystem. Let x_0 denote the initial state of the unperturbed system whose posterity, we shall assume, has state space $S = S_R \cup S_T$. Let Θ_0 denote the smallest $\Theta > 0$ such that the posterity is Θ -persistent about x_0 . It is meaningful to inquire if the ecosystem altered by its perturbation is "less" recurrent or "less" persistent. That is, let S'_R denote the set of states that are recurrent in the perturbed posterity, and let $S'_T = S - S'_R$. Also, let Θ'_0 denote the smallest Θ such that the perturbed posterity is Θ -persistent about x_0 .

We say that the perturbed posterity is less recurrent if S'_R is a smaller set than S_R (or, equivalently, if S_T is larger than S'_T). Similarly, we say that the perturbed posterity is less persistent if $\Theta_0 < \Theta'_0$ (and more persistent if the reverse inequality prevails).

Example 5: A good example is provided by Grand Monadnock (Mount Monadnock) in New Hampshire (Chamberlain 1968). Until the nineteenth century, Monadnock's summit was forested. However, the posterity was altered by repeated man-made fires. Complete destruction of the organic cover permitted the residual loose matter near the summit to erode away. Ever since, the uppermost 500 ft have consisted of open rock ledges covered only by crustose lichens and, in crevices, low mat-forming plants. Reestablishment of the forest near the summit seems unlikely in Monadnock's perturbed posterity. In fact, some evidence suggests that the timberline has moved downhill since the nineteenth century. Lichen-covered rock and crevices with mat-forming plants are the only recurrent state now, but the set of recurrent states would have been much larger had fires not been set repeatedly. The perturbed process is less recurrent than the unperturbed process. Moreover, $\Theta_0 = 0$ in the perturbed process, i.e., zero is the minimal value of Θ for which the perturbed process is Θ -persistent about the initial state of lichen-covered rock. In the unperturbed process, $\Theta > 0$ about any initial state. This example illustrates that a low value of Θ_0 is not necessarily "good"; the perturbed posterity is trivially and unfortunately maximally stable in the sense of Θ -persistence.

4. NOTIONS OF STABILITY IN STOCHASTIC MODELS

Posterities often contain unpredictable fluctuations that arise from inherent variability, errors of observation, incomplete scientific understanding of causal phenomena, and unanticipated external "shocks" to an ecosystem, e.g., the weather. Therefore, in place of a deterministic posterity, we now consider the stochastic process $\{X(t), t \geq 0\}$ giving rise to a probability space having probability measure $P(\cdot)$. Let S denote the set of all states at which the process could possibly take values, i.e., the "sample space" of $X(t)$.

Absorption.—Absorption is a stochastic analogue of persistence for determin-

istic posterities. It leads to S being partitioned into mutually exclusive subsets, one of stochastically persistent states and another of temporary states. Every text on stochastic processes (e.g., Karlin 1969) discusses absorption in the context of Markov Chains. Here, however, we do not predicate the notion of absorption on a Markovian assumption. Formally, a subset Z of S is called an *absorbing set* if the process necessarily remains within Z if it ever enters Z (or if it starts there). Notationally, Z is an absorbing set if

$$P\{X(t) \in Z \mid X(\tau) = i\} = 1 \quad \text{for all } t \geq \tau \geq 0 \quad \text{and all } i \in Z.$$

Example 6: The usual anecdotal account of a pond's posterity illustrates the notion of absorption. The pond begins in an oligotrophic condition and evolves into a eutrophic state. Sediments build up on the bottom and, if environmental conditions are appropriate, a floating mat develops on the surface. Gradually the pond fills in and passes through a bog stage, which in turn is gradually invaded by terrestrial vegetation. Allowing for the occasional incidence of disease and fire, the filled-in pond will always be found in a state of tundra, shrub, or forest; such states comprise an absorbing set.

In every stochastic posterity, the set of all states S is itself trivially an absorbing set. Usually we may delete some elements from such a gross absorbing set and the reduced set will still be absorbing. We define an absorbing set Z to be a *minimal absorbing set* if deletion of further elements from Z destroys the absorption property, i.e., if $Z - K$ is not an absorbing set for all nonempty subsets K of Z . If $Z = \{i\}$ is an absorbing set consisting of a single element, then i is called an *absorbing state*. Static stability asserts that the initial state will absorb the process, with probability = 1, after experiencing a perturbation.

If Z and Z' are absorbing sets whose intersection is nonempty, then their intersection $Z \cap Z'$ is necessarily also an absorbing set. Therefore, two different minimal absorbing sets are necessarily disjoint, i.e., their intersection is empty. Let A index the minimal absorbing sets so that $a \in A$ indicates that there is a minimal absorbing set Z_a . We define a state $s \in S$ to be *temporary* if it fails to lie in any minimal absorbing set, i.e., if

$$s \in S - \bigcup_{a \in A} Z_a.$$

In example 6, the hydrarch succession from pond to forest, all the states in which the pond holds surface water are temporary. Ordinarily, if a process begins in a temporary state, then it will eventually gravitate to one of the minimal absorbing sets. If q_a^s denotes the probability of ultimately entering Z_a when the initial state is s , then

$$q_a^s = P\{\lim_{t \rightarrow \infty} X(t) \in Z_a \mid S(0) = s\}, \quad a \in A, \quad s \in S.$$

Of course, if s is not a temporary state, then q_a^s is either 1 or 0 depending on whether $s \in Z_a$ or $s \notin Z_a$, respectively. For every $s \in S$, $\sum_{a \in A} q_a^s \leq 1$.

Recurrence.—Various stochastic analogues of the deterministic notion of recurrence are suggested by the theory of Markov processes. However, the

following definitions are not predicated on a Markovian assumption. They all concern the times between successive visits to a state or a subset of states. For any state s and subset K of S let $T_s(K, \tau)$ denote the time it takes the process to reach some state in K after departing from state s at time τ ; i.e.,

$$T_s(K, \tau) = \min \{t: t > 0 \text{ and } X(\tau + t) \in K\}, \quad X(\tau) = s.$$

In words, if the process begins in state s at time τ so that $X(\tau) = s$, then it takes $T_s(K, \tau)$ units of time until the process first occupies some state in K .

It follows from the definition of absorbing set that, if K is an absorbing set and $s \in K$, then K can surely be reached from s so that

$$P\{T_s(K, \tau) < \infty\} = 1.$$

On the other hand, if Z and Z' are disjoint absorbing sets with $s \in Z$ and $K \subseteq Z'$, then K can never be reached from s so that

$$P\{T_s(K, \tau) = \infty\} = 1.$$

For any state s and set K we define state s to be *K-recurrent* if the process is sure to reach set K starting from state s , i.e.,

$$P\{T_s(K, \tau) < \infty\} = 1, \quad \tau \geq 0.$$

We observe that state s can fail to be *K-recurrent* if and only if there is some chance of never reaching set K from state s , i.e., for some $\tau \geq 0$,

$$P\{T_s(K, \tau) < \infty\} < 1 \Leftrightarrow P\{T_s(K, \tau) = \infty\} > 0.$$

A state s is said simply to be *recurrent* if it is $\{s\}$ -recurrent, i.e.,

$$P\{T_s(\{s\}, \tau) < \infty\} = 1, \quad \tau \geq 0.$$

Therefore, a recurrent state is visited infinitely often (with probability = 1) if it is ever visited for a first time.

We label a state as being *transient* if it is not recurrent. Any visit to a transient state could be the last visit to that state. With probability = 1, there will be a last visit and only a finite number of visits will occur. Therefore, a state is transient if and only if it is temporary. This property ties recurrence to absorption, and it implies that the set of recurrent states can be partitioned into the minimal absorbing sets.

We should not associate "recurrent" with "good" and "transient" with "bad." In fact it is easy to generate a simple process having all states transient: let the stochastic process be discrete in time with $X(0), X(1), X(2), \dots$ being independent and identically distributed as a standard normal random variable. Transience is a consequence of each $X(t)$ being a continuous random variable.

We generalize the definition of a recurrent state to avoid the preceding triviality that may arise if S is nondenumerable. It is sufficient to define state s to be recurrent if s is *K-recurrent* for all sets K that have positive measure and contain s .

If state s is *K-recurrent*, then the process will eventually reach K after leaving state s . However, we have no idea how long it will take, and, on the

average, it may take nearly forever. A crude distinction between short-run and long-run recurrence is offered by the following definitions. If state s is K -recurrent, then the average value of $T_s(K, \tau)$, denoted $E[T_s(K, \tau)]$, is well defined mathematically but need not be finite in value. State s is defined to be *positive K-recurrent* if it is K -recurrent and also $E[T_s(K, \tau)] < \infty$. If s is K -recurrent but $E[T_s(K, \tau)] = \infty$, then state s is defined to be *null K-recurrent*. When $K = \{s\}$ the labels and notation are simplified to *positive recurrent*, *null recurrent*, and $T_s(\tau)$. We call $T_s(\tau)$ a *recurrence time*.

Examples of positive and null recurrence arise in the coin-tossing games of elementary probability. Let D_1, D_2, \dots be independent and identically distributed random variables with

$$p = P\{D_1 = +1\} = 1 - P\{D_1 = -1\};$$

let $S = \{0, 1, 2, \dots\}$; and let

$$X(t+1) = [X(t) + D_t]^+,$$

where the notation $(u)^+$ denotes the maximum of the number u and zero. If $p = \frac{1}{2}$, then every state in S is null recurrent; if $0 < p < \frac{1}{2}$, then every state is positive recurrent; and if $\frac{1}{2} < p < 1$, then every state is transient.

Example 7: Positive recurrent states invite the comparison of the distributions of their recurrence times. In the BWCA, for example, a state's mean recurrence time is generally increased if the interval between successive fires is unnaturally extended. In this sense, the forest's stability is decreased by retarding the advent of fire.

Other kinds of comparisons of recurrence times concern variability. The objective is to use a variability criterion that permits a partial ordering of the set of distribution functions of recurrence times. Common criteria include (a) the variance and (b) the ratio of the standard deviation to the mean. Other stochastic orderings are useful, as well, and the interested reader is referred to Bessler and Veinott (1966, sec. 7).

Example 8: It is apparent from figure 1 and anecdotal accounts of Isle Royale National Park (see Section 6) that moose biomass is more variable than wolf biomass (even if both are normalized by their respective means) and so is less stable in this sense.

Our comments in Section 3 concerning finite-horizon models and normalization of persistence criteria extend straightforwardly to our definitions for stochastic models. However, we leave the details to the reader.

Perturbation: stochastic models.—Our discussion of perturbation in deterministic models (at the end of Section 3) extends directly to stochastic processes. For the unperturbed process, let S_R and S_T denote the sets of (stochastically) recurrent and transient states, respectively; of course, $S = S_R \cup S_T$ and $S_R \cap S_T$ is the empty set. Let S'_R denote the set of recurrent states in the perturbed process and let $S'_T = S - S'_R$. If S'_R contains fewer states than S_R , then we say that the perturbed process is *less recurrent* than the unperturbed process.

5. APPLICATIONS TO THE BOUNDARY WATERS CANOE AREA:
A PROBLEM IN COMMUNITY STRUCTURE

We shall demonstrate that the foregoing definitions can be applied usefully to both theoretical and applied problems in ecology. First we reconsider the BWCA.

The suppression of fire leads to the development of large spatially homogeneous areas. Whether unburned or severely burned, such areas are distinct from the complex mosaic of different successional stages coexisting on the presettlement landscape. Heinzelman (1973) writes that fire in the BWCA must be "... seen as just a perturbation within the system. It was an essential factor in maintaining the kind of long-term stability and diversity recorded in the pollen and charcoal diagrams." We shall attempt to clarify his statement. The landscape can be viewed as a matrix of points at which some measure of the ecosystem is made. In the presettlement landscape, this measure would yield much greater diversity than at present. The presettlement landscape provided the variety of communities and wildlife that people seem to desire in a "wilderness."

"Equilibrium" has no meaning in the BWCA because the forest, without manipulation, changes slowly with the climate, and we can speak only of its posterity or trajectory through time, not of its equilibrium. Therefore, in this context, static stability, i.e., the return to equilibrium following a perturbation, is meaningless. The specific trajectory of a small area, say 100 m², is a procession from fire to lichens and annual herbaceous plants to perennial plants and shrubs to jack pine-red pine to fire, or else to fir-spruce-birch and eventually to fire. Heinzelman (1973) defines a natural fire rotation as the "average number of years required to burn over and reproduce an area equal to the total area under consideration." This is nearly equivalent to the mean recurrence time of the jack pine-red pine state. It seems that the intentional suppression of fire induces a posterity whose mean recurrence times are longer than in the presettlement forest. Indeed, there may be a risk that the permanent removal of fire, or the occurrence of less frequent but more severe fires, causes some otherwise recurrent states to be transient. In Heinzelman's opinion, the jack pine-red pine mean recurrence time is 100 yr for the entire area and probably 20-60 yr for any local area.

For us, the recurrence of desirable states has greater priority than resting in a single equilibrium state. This preference contrasts sharply with the implicit arguments of ecologists earlier in this century that recurrence required an equilibrium. Further, we would suggest that maximizing the size of the state space which is recurrent (and secondarily minimizing mean recurrence times of "desirable" states) is equivalent to ensuring the aesthetically desirable wilderness status—an ecosystem having a maximum structural (species) diversity.

A Decision Model

The preceding considerations suggest a positive management approach to the role of fire in determining structural diversity in a forest. The operational

question is, Under what conditions should fires be permitted to burn (or be started deliberately!)? We shall describe a simplified model to aid in answering this question. A more general model and its detailed mathematical analysis are presented elsewhere (Sobel 1974). After the simplified model and its most important properties are described, we shall relate those properties to the notions of stability presented in Sections 3 and 4.

We assume that, at a given time, the species composition of the forest falls into exactly one classification among a number of categories that are at most denumerable, i.e., there are states $0, 1, 2, \dots$. Let $X(t)$, $t = 0, 1, 2, \dots$ be the stochastic process of states during successive years. The structure and decisions that govern the $X(\cdot)$ process are described below.

Suppose that, during a given year, the forest is in state i , and k yr have elapsed since the last fire occurred (either accidentally or deliberately set), $k = 0, 1, 2, \dots$. If the manager decides to start a fire (equivalently, to let a "natural" fire burn) during the given year, then the forest is immediately (in zero time) transformed to forest state j with probability m_{ij} ($m_{ij} \geq 0$ for all i, j and $\sum_{j=0}^{\infty} m_{ij} = 1$ for all i), and $k = 0$ yr will have passed since a fire. If the manager decides not to start a fire during the given year, then there is some risk that an accidental fire may occur. Let f denote the probability that fire accidentally occurs during a year. If an accidental fire *does* occur when the forest is in state i , and k yr have elapsed since the most recent fire, then next year's state is determined according to the probability vector $[q_{ij}(k)]$, where $q_{ij}(k) \geq 0$ for $i, j, k = 0, 1, \dots$, and $\sum_{j=0}^{\infty} q_{ij}(k) = 1$ for $i, k = 0, 1, \dots$. If an accidental fire does *not* occur, then next year's state is determined according to the probability vector p_{ij} , where $p_{ij} \geq 0$ for $i, j = 0, 1, \dots$, and $\sum_{j=0}^{\infty} p_{ij} = 1$ for all $i = 0, 1, \dots$.

Some states are more desirable than others, and the objective is, roughly, to maximize the proportion of years (proportion of a large areal forest) during which the forest state is particularly desirable. Suppose that the states have been labeled so that there is an integer d such that $\{i: i \geq d\}$ is the set of "particularly desirable" states. Let

$$r(i) = \begin{cases} 1 & \text{if } i \geq d, \\ 0 & \text{if } i < d, \end{cases} \quad \text{for } i = 0, 1, \dots$$

During the first T years, the proportion of years in which the forest is in particularly desirable states is

$$\frac{1}{T} \sum_{t=1}^T r[X(t)]. \quad (5)$$

This leads us to consider the criterion of maximizing the long-run average value of (5), or

$$\max \lim_{T \rightarrow \infty} E \left\{ \frac{1}{T} \sum_{t=1}^T r[X(t)] \right\}, \quad (6)$$

where E denotes expectation (in the sense of the mean value of a random variable).

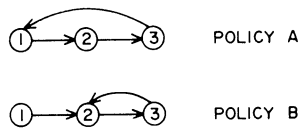


FIG. 2.—State transitions in example 9

The maximization in (6) is with respect to all rules for deciding when to start a fire. It is intuitive that attention can be confined to rules of the following kind:

$$\begin{aligned} &\text{For each state } i \text{ there is an integer } b(i) \text{ (possibly } +\infty) \\ &\quad \text{such that deliberate burning occurs if and only if} \\ &\quad b(i) \text{ or more years have elapsed since the last fire.} \end{aligned} \quad (7)$$

Under the following assumptions it has been shown (Sobel 1974) that there is a rule with the structure of (7) that attains the maximum in (6): for all generic states i and c and generic ages k , the probabilities satisfy

$$\sum_{j \geq c} q_{ij}(k+1) \leq \sum_{j \geq c} q_{ij}(k) \leq \sum_{j \geq c} q_{i+1,j}(k), \quad \text{for all } i, k, c; \quad (8a)$$

$$\sum_{j \geq c} p_{ij}(k+1) \leq \sum_{j \geq c} p_{ij}(k) \leq \sum_{j \geq c} p_{i+1,j}(k), \quad \text{for all } i, k, c; \quad (8b)$$

$$\sum_{j \geq c} m_{ij} \leq \sum_{j \geq c} m_{i+1,j}, \quad \text{for all } i, c. \quad (8c)$$

The assumptions in (8) have the following interpretation. The left inequalities in (8a) and (8b) assert that transitions to less favorable states will become more likely as the number of years since the last fire increases. Then (8c) and the right inequalities in (8a) and (8b) imply that transitions to more favorable states are more likely from favorable states than from unfavorable states. These assumptions seem reasonable to us in most contexts.

Example 9: The following trivial numerical example satisfies (8) and illustrates the superiority in some contexts of a policy that advocates deliberate burning in some states. Suppose that there are three states, $\{3\}$ is the set of desirable states, and a “natural” fire always occurs, so that $f = 1$ (the reader is reminded that f is the probability of accidental fire) and $\{p_{ij}(k)\}$ is irrelevant. We set values of

$$q_{12}(k) = q_{23}(k) = q_{31}(k) = m_{11} = m_{21} = m_{32} = 1, \quad \text{for all } k,$$

with other m_{ij} ’s and $q_{ij}(k)$ ’s equal to zero. The objective is (6), namely, to occupy state 3 as often as possible.

It is clearly suboptimal to burn when in states 1 and 2. Therefore, we compare policy *A* of not burning when in state 3 with policy *B* of burning when in state 3; both policies stipulate not burning in states 1 and 2. The state transitions generated by *A* and *B* are illustrated in figure 2.

Policy *A* causes state 3 to be occupied one-third of the time whereas policy *B*

causes it to be occupied one-half of the time. Therefore, in the sense of criterion (6), B is superior to A , and a fire ought to be set when the state is state 3.

6. APPLICATIONS TO MODELS OF PREDATOR-PREY INTERACTION

From the time of the first publication of the theoretical models of Lotka and Volterra, predator-prey interactions have intrigued many biologists. Many papers have discussed whether predator-prey interactions lead to stability of both populations. It has frequently been argued that predation leads to some kind of stability of the prey population not inherent in the dynamics of the prey population alone. While there have been many theoretical treatments of this problem, there have been few well-documented examples.

The interaction between wolves and moose at Isle Royale National Park, Michigan, provides one of the few comparatively well documented cases of real predator-prey interactions for large mammals in an undisturbed habitat (Mech 1966). Moose first appeared on the island in the early 1900s. In the absence of their only significant natural predator, the timber wolf, and in the presence of an abundance of preferred food plants, the moose population increased rapidly. Within 15 yr the browsing impact on the vegetation was striking, and moose die-offs, predicted by Murie (1934), occurred in the early 1930s.

Forest regeneration followed a major fire in 1936 and provided a new large supply of food for the moose. A second rapid population increase was followed in the mid-1940s by die-offs and marked suppression of forest growth (Krefting 1951). Wolves reached the island in 1947–1948; their population increased within a few years to an average of 23, a value which seemed to be maintained through the early 1970s. Also, until the early 1970s, wolf predation seemed to maintain the moose herd at a level below catastrophic die-offs but at a density higher than recorded elsewhere. During the 1960s the effect of the predator seemed to stabilize the population of the prey, and both moose and wolves seemed to exist in an apparent equilibrium. More recently, browsing impact has increased, and both moose and wolf populations appear to have increased.

It should be noted that estimates of population densities for large mammals in forested areas are notoriously inaccurate. Although the impact of the moose on the vegetation during the 1960s seemed constant, successive estimates of the moose population gave increasingly large numbers. However, it is unclear whether this apparent growth resulted from improved accuracy in survey techniques or from an increase in moose population.

Although long-term patterns in the wolf and moose populations cannot yet be ascertained from Isle Royale data, the observed history provides the following insights: (1) the moose population without predation experienced wide fluctuations; (2) predation damped these fluctuations, at least in the sense of increasing the time between maximum and minimum levels (it may also have damped them in the sense of decreasing the range of population size); and (3) predation does not seem to have brought the moose population to a fixed equilibrium.

Predator-prey interactions have often been modeled with the Lotka-Volterra

equations, and the ensuing discussions typically invoke the concept of static stability. The above examination of real predator-prey interactions at Isle Royale suggests that it is unproductive to interpret moose-wolf interactions with static stability. Instead, we shall apply the notions of recurrence and absorption to a variant of the Lotka-Volterra equations.

Markovian Predator-Prey Models

The Lotka-Volterra equations, as follows, comprise the classical model of predator-prey interaction:

$$\begin{aligned}\frac{dw(t)}{dt} &= w(t)[\beta m(t) - b]; \\ \frac{dm(t)}{dt} &= m(t)[a - \alpha w(t)].\end{aligned}\tag{9}$$

The quantity $w(t)$ is the size of the predator population of “wolves,” and $m(t)$ is the size of the prey population of “moose,” both at time $t > 0$. The initial populations $m(0)$ and $w(0)$ are specified at the outset. We shall consider a discrete-time analogue of (9) in which the states, i.e., the pairs $[m(t), w(t)]$, also are discretized. Let $X(0), X(1), \dots$ comprise a discrete-time stochastic process, with

$$X(t) = [M(t), W(t)],$$

specifying the random sizes of the moose population $M(t)$ and the wolf population $W(t)$. The set of states S is assumed to be all pairs of nonnegative integers (m, w) .

We assume that $X(0), X(1), X(2), \dots$ is a time-homogeneous *Markov Chain*, namely, that its future behavior is stochastically independent of its past history except through its present state.⁴ Therefore, the probabilistic structure is entirely specified by $X(0)$ and the *transition probabilities*

$$p_{xy} = P\{X(1) = y \mid X(0) = x\},$$

defined for all $x \in S$ and $y \in S$. The transition probabilities satisfy $p_{xy} \geq 0$ and

$$\sum_{y \in S} p_{xy} = 1, \quad \text{for all } x \in S.\tag{10}$$

To return to the moose and wolves, our first model is a simple generalization of Becker's (1973) Model 2. We assume

$$\begin{aligned}p_{(m,w),(m,w)} &+ p_{(m,w),(m+1,w)} + p_{(m,w),(m-1,w)} \\ &+ p_{(m,w),(m,w+1)} + p_{(m,w),(m,w-1)} = 1,\end{aligned}\tag{11}$$

for all (m, w) with m and w being positive integers. By analogy with the Lotka-Volterra equations in (9), let α , a , β , and b be positive numbers and γ a non-

⁴ The reader is referred to Karlin (1969) for a careful definition of a Markov Chain.

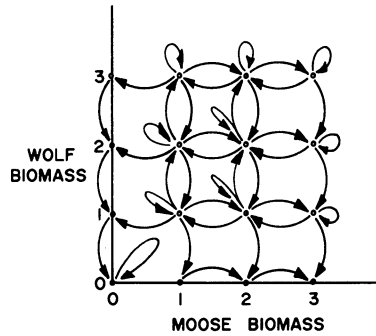


FIG. 3.—Transitions between states in the first model of moose-wolf interaction

negative number such that the transition probabilities when $m > 0$ and $w > 0$ are given by

$$\begin{aligned}
 p_{(m,w),(m+1,w)} &= \frac{a}{\alpha + a + \beta + b + \gamma}, \\
 p_{(m,w),(m-1,w)} &= \frac{\alpha}{\alpha + a + \beta + b + \gamma}, \\
 p_{(m,w),(m,w+1)} &= \frac{\beta}{\alpha + a + \beta + b + \gamma}, \\
 p_{(m,w),(m,w-1)} &= \frac{b}{\alpha + a + \beta + b + \gamma}, \\
 p_{(m,w),(m,w)} &= \frac{\gamma}{\alpha + a + \beta + b + \gamma},
 \end{aligned} \tag{12}$$

which satisfies (11). We note that $p_{(m,w),(m,w)}$ is zero or positive according to whether γ is zero or positive. It is assumed that $p_{(0,0),(0,0)} = 1$, $p_{(m,0),(m+1,0)} = 1$ if $m > 0$, and $p_{(0,w),(0,w-1)} = 1$ if $w > 0$. Therefore, $(0, 0)$ is an absorbing state and $\{(m, 0): m > 0\}$ and $\{(0, w): w > 0\}$ are sets of transient states. *Is any state except $(0, 0)$ recurrent?*

The transitions having positive probabilities are exhibited in figure 3. It follows from the theory of Markov Chains having denumerably many states (Karlin 1969) that, with probability = 1, whatever the initial state $X(0)$, the process will behave in one of the following ways: (1) it will reach the $(0, w)$ axis and thereafter be absorbed at $(0, 0)$; (2) it will reach the $(m, 0)$ axis and thereafter march out towards $(\infty, 0)$; or (3) it will drift out toward (∞, ∞) . In particular, *there is zero probability of persisting at positive finite numbers of either or both populations*. That is, for every subset of S , with probability = 1 there is a finite time t (finite but perhaps very large), such that either the process is at $(0, 0)$ or it will never again visit that subset. Equivalently, every state (m, w) for which $0 < mw < \infty$ is temporary and transient!

Our second predator-prey model embodies the assumption that resource

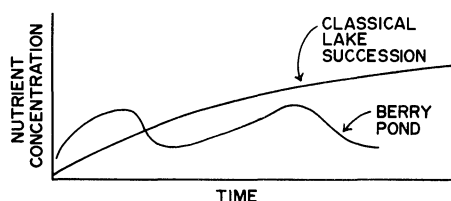


FIG. 5.—Comparison of Berry Pond (Whitehead et al. 1973) with classical lake succession (Likens and Davis, in press).

stability are applicable to both structural and functional properties of ecosystems. Suppose, for example, that our concern is with the “stability” of an ecosystem’s productivity, or its loss of some ion, or the rate of cycling of that ion. What concepts of stability are appropriate for these questions?

A convenient example to examine such problems is the postglacial history of Berry Pond, Massachusetts, as described by Whitehead et al. (1973). This is a small (3.9-hectare) pond lying in a forested watershed of approximately 28 hectares and having a number of species in common with the BWCA.

The history of Berry Pond contradicts the classic hypothetical pattern of pond succession. Rather than a unidirectional trend from oligotrophic to eutrophic conditions, and from lower to higher production, Berry Pond has cycled back and forth. Productivity reached a maximum 13,000–8,000 yr ago, then declined to a minimum 7,000–5,000 yr ago, then increased to a higher maximum and then declined again between 5,000 and 3,800 yr ago. According to Whitehead et al. (1973): “. . . The initial period of increasing productivity coincided with the development of coniferous forests (first spruce, then pine) in the region, [and] the decline with the establishment of northern hardwood forests. The second cycle of eutrophication coincided with a sharp decline of hemlock; increases of birch, oak, beech and other hardwoods; and a significant acceleration in the rate of delivery of leaf cuticle fragments to the pond.”

There are three points of interest in this history. First, the pond seems to have gone back and forth between oligotrophic and eutrophic stages. Second, the state of the pond depended on the state of the forested watershed, particularly on functional properties of the forest. Figure 5 illustrates the difference between the classical pattern of pond succession (Likens and Davis, in press) and the history of Berry Pond.

To put the problem in practical terms, if one wished to preserve the oligotrophic character of the pond, one would have to require that the loss of nutrients from the watershed remain below some maximum, and one would be interested only indirectly in the structural properties of the forest. The concern with forest structure would arise in this case only because the structure appeared to affect the functional properties, i.e., the loss of nutrients.

Such an argument is presented by Whitehead et al. (1973), who assert that, although boreal coniferous forests are generally lower in productivity, biomass, and rates of litter decomposition than northern hardwood forests, the boreal forests have a lower capacity to retain nutrients. Also, the boreal forests produce an acid litter that accentuates nutrient loss to streams and possibly have more rapid nitrification.

The history's third point of interest is that local states of the forest become important because the watershed for Berry Pond is small. A fire or storm that would be small in comparison to the size of the BWCA or Isle Royale National Park could completely alter the state of Berry Pond's 28-hectare watershed. It could produce extreme short-term changes even though the average, long-term trajectory of the pond might seem to remain in narrow limits.

This leads us to an important distinction in regard to the stability of ecosystems. Perhaps local and global stability of ecosystems, in both a temporal and spatial sense, cannot be achieved together. In fact, short-term stability may lead to long-term instability. For example, suppose that the forested watershed of Berry Pond had the same relation to fire as the BWCA forests so that the severity of a fire tended to increase with the time since the last fire. Then an attempt to ensure that the short-term trajectory of Berry Pond's watershed would remain within a small set of states might decrease the probability that, in the long-run, the pond and its watershed would remain within a desired group of states.

The graph of the concentration of an ion in a hypothetical pond is shown in figure 5 (in comparison with the same graph for Berry Pond). After an appropriate change of scale it could be fitted by the posterity $x(t) = 1 - e^{-t}$ with state set $S = (0, 1)$. As we observed in example 4, this posterity is Θ -persistent about $\frac{1}{2}$ for all $\Theta \geq \frac{1}{2}$, but every state in S is transient, so $S = S_T$.

The foregoing discussion of Berry Pond concerned functional properties of an ecosystem. Yet it utilized the notions of persistence and recurrence that we applied earlier to examine structural properties. Therefore, it appears that the same stability concepts, namely, persistence and recurrence, *are* applicable to both structural and functional properties of ecosystems.

8. CONCLUSIONS

Our initial objective was to formalize some notions suggested by connotations of "stability." Then we wished to see if the usefulness of these notions depended on the type of ecosystem process being discussed: population dynamics, ecosystem structure, or functional properties. A review of Sections 5–8 supports three tentative conclusions:

1. Several different stability notions are applicable to each type of ecosystem process, and they may lead to different insights.
2. A single notion of stability is applicable to the several types of ecosystem processes.
3. The concept of static stability frequently is inappropriate for the analysis of ecosystems, and, in such instances, alternative tractable notions of stability are available.

What do these conclusions signify for ecologists? First, they imply that data collected during research in the field and laboratory should be sufficiently varied to evaluate several stability notions. Second, theoretical analyses of stability, particularly its dependence on ecosystem complexity, should be broadened to include notions of stability besides the definition of static stability borrowed from statistical mechanics.

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