Resilience and Stability of Ecological Systems

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INTRODUCTION

Individuals die, populations disappear, and species become extinct. That is one view of the world. But another view of the world concentrates not so much on presence or absence as upon the numbers of organisms and the degree of constancy of their numbers. These are two very different ways of viewing the behavior of systems and the usefulness of the view depends very much on the properties of the system concerned. If we are examining a particular device designed by the engineer to perform specific tasks under a rather narrow range of predictable external conditions, we are likely to be more concerned with consistent nonvariable performance in which slight departures from the performance goal are immediately counteracted. A quantitative view of the behavior of the system is, therefore, essential. With attention focused upon achieving constancy, the critical events seem to be the amplitude and frequency of oscillations. But if we are dealing with a system profoundly affected by changes external to it, and continually confronted by the unexpected, the constancy of its behavior becomes less important than the persistence of the relationships. Attention shifts, therefore, to the qualitative and to questions of existence or not.

Our traditions of analysis in theoretical and empirical ecology have been largely inherited from developments in classical physics and its applied variants. Inevitably, there has been a tendency to emphasize the quantitative rather than the qualitative, for it is important in this tradition to know not just that a quantity is larger than another quantity, but precisely how much larger. 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.

Our traditional view of natural systems, therefore, might well be less a meaningful reality than a perceptual convenience. There can in some years be more owls and fewer mice and in others, the reverse. Fish populations wax and wane as a natural condition, and insect populations can range over extremes that only logarithmic

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transformations can easily illustrate. Moreover, over distinct areas, during long or short periods of time, species can completely disappear and then reappear. Different and useful insight might be obtained, therefore, by viewing the behavior of ecological systems in terms of the probability of extinction of their elements, and by shifting emphasis from the equilibrium states to the conditions for persistence.

An equilibrium centered view is essentially static and provides little insight into the transient behavior of systems that are not near the equilibrium. Natural, undisturbed systems are likely to be continually in a transient state; they will be equally so under the influence of man. As man's numbers and economic demands increase, his use of resources shifts equilibrium states and moves populations away from equilibria. The present concerns for pollution and endangered species are specific signals that the well-being of the world is not adequately described by concentrating on equilibria and conditions near them. Moreover, strategies based upon these two different views of the world might well be antagonistic. It is at least conceivable that the effective and responsible effort to provide a maximum sustained yield from a fish population or a nonfluctuating supply of water from a watershed (both equilibrium-centered views) might paradoxically increase the chance for extinctions.

The purpose of this review is to explore both ecological theory and the behavior of natural systems to see if different perspectives of their behavior can yield different insights useful for both theory and practice.

Some Theory

Let us first consider the behavior of two interacting populations: a predator and its prey, a herbivore and its resource, or two competitors. If the interrelations are at all regulated we might expect a disturbance of one or both populations in a constant environment to be followed by fluctuations that gradually decrease in amplitude. They might be represented as in Figure 1, where the fluctuations of each population over time are shown as the sides of a box. In this example the two populations in some sense are regulating each other, but the lags in the response generate a series of oscillations whose amplitude gradually reduces to a constant and sustained value for each population. But if we are also concerned with persistence we would like to know not just how the populations behave from one particular pair of starting values, but from all possible pairs since there might well be combinations of starting populations for which ultimately the fate of one or other of the populations is extinction. It becomes very difficult on time plots to show the full variety of responses possible, and it proves convenient to plot a trajectory in a phase plane. This is shown by the end of the box in Figure 1 where the two axes represent the density of the two populations.

The trajectory shown on that plane represents the sequential change of the two populations at constant time intervals. Each point represents the unique density of each population at a particular point in time and the arrows indicate the direction of change over time. If oscillations are damped, as in the case shown, then the trajectory is represented as a closed spiral that eventually reaches a stable equilibrium.

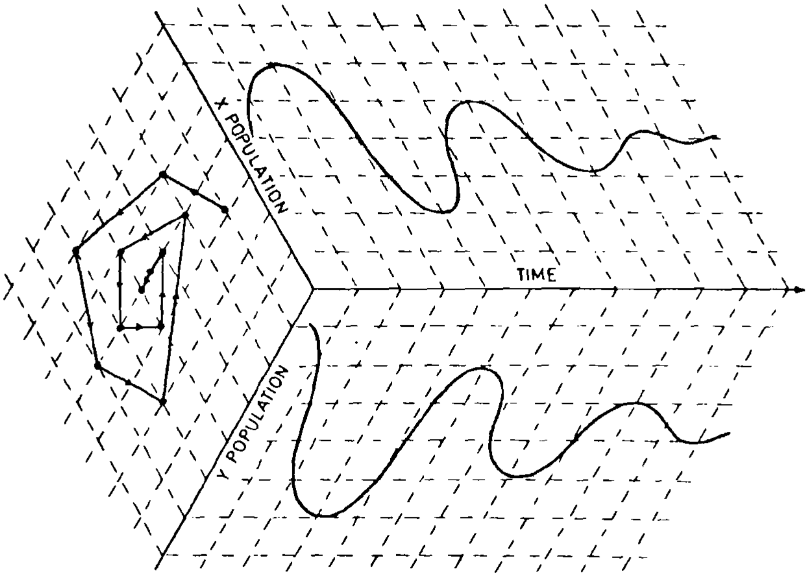

Figure 1 Derivation of a phase plane showing the changes in numbers of two populations over time.

We can imagine a number of different forms for trajectories in the phase plane (Figure 2). Figure 2a shows an open spiral which would represent situations where fluctuations gradually increase in amplitude. The small arrows are added to suggest that this condition holds no matter what combination of populations initiates the trajectory. In Figure 2b the trajectories are closed and given any starting point eventually return to that point. It is particularly significant that each starting point generates a unique cycle and there is no tendency for points to converge to a single cycle or point. This can be termed "neutral stability" and it is the kind of stability achieved by an imaginary frictionless pendulum.

Figure 2c represents a stable system similar to that of Figure 1, in which all possible trajectories in the phase plane spiral into an equilibrium. These three examples are relatively simple and, however relevant for classical stability analysis, may well be theoretical curiosities in ecology. Figures 2d–2f add some complexities. In a sense Figure 2d represents a combination of a and c, with a region in the center of the phase plane within which all possible trajectories spiral inwards to equilibrium. Those outside this region spiral outwards and lead eventually to extinction of one or the other populations. This is an example of local stability in contrast to the global stability of Figure 2c. I designate the region within which stability occurs as the domain of attraction, and the line that contains this domain as the boundary of the attraction domain.

The trajectories in Figure 2e behave in just the opposite way. There is an internal region within which the trajectories spiral out to a stable limit cycle and beyond

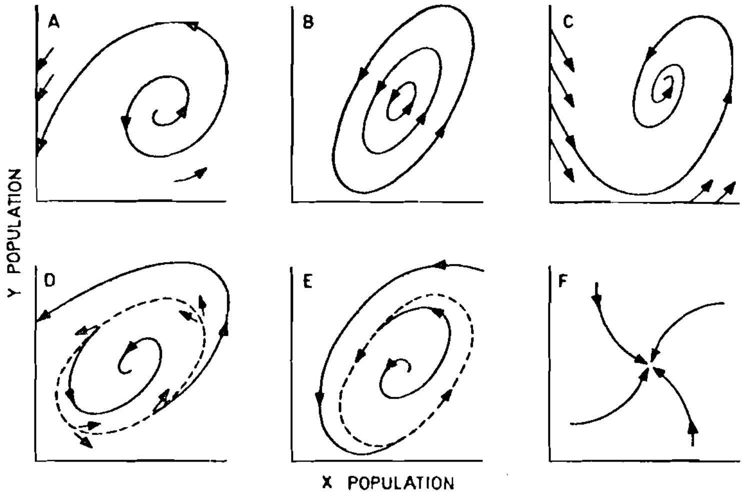

Figure 2 Examples of possible behaviors of systems in a phase plane; (a) unstable equilibrium, (b) neutrally stable cycles, (c) stable equilibrium, (d) domain of attraction, (e) stable limit cycle, (f) stable node.

which they spiral inwards to it. Finally, a stable node is shown in Figure 2f in which there are no oscillations and the trajectories approach the node monotonically. These six figures could be combined in an almost infinite variety of ways to produce several domains of attraction within which there could be a stable equilibrium, a stable limit cycle, a stable node, or even neutrally stable orbits. Although I have presumed a constant world throughout, in the presence of random fluctuations of parameters or of driving variables (Walters 39), any one trajectory could wander with only its general form approaching the shape of the trajectory shown. These added complications are explored later when we consider real systems. For the moment, however, let us review theoretical treatments in the light of the possibilities suggested in Figure 2.

The present status of ecological stability theory is very well summarized in a number of analyses of classical models, particularly May's (23–25) insightful analyses of the Lotka-Volterra model and its expansions, the graphical stability analyses of Rosenzweig (33, 34), and the methodological review of Lewontin (20).

May (24) reviews the large class of coupled differential equations expressing the rate of change of two populations as continuous functions of both. The behavior of these models results from the interplay between (*a*) stabilizing negative feedback or density-dependent responses to resources and predation, and (*b*) the destabilizing effects produced by the way individual predators attack and predator numbers respond to prey density [termed the functional and numerical responses, as in Holling (11)]. Various forms have been given to these terms; the familiar Lotka-Volterra model includes the simplest and least realistic, in which death of prey is caused only by predation, predation is a linear function of the product of prey and predator populations, and growth of the predator population is linearly proportional to the same product. This model generates neutral stability as in Figure 2b, but the assumptions are very unrealistic since very few components are included, there are no explicit lags or spatial elements, and thresholds, limits, and nonlinearities are missing.

These features have all been shown to be essential properties of the predation process (Holling 12, 13) and the effect of adding some of them has been analyzed by May (24). He points out that traditional ways of analyzing the stability properties of models using analytical or graphical means (Rosenzweig & MacArthur 33, Rosenzweig 34, 35) concentrate about the immediate neighborhood of the equilibrium. By doing this, linear techniques of analysis can be applied that are analytically tractable. Such analyses show that with certain defined sets of parameters stable equilibrium points or nodes exist (such as Figure 2c), while for other sets they do not, and in such cases the system is, by default, presumed to be unstable, as in Figure 2a. May (24), however, invokes a little-used theorem of Kolmogorov (Minorksy 26) to show that all these models have either a stable equilibrium point or a stable limit cycle (as in Figure 2e). Hence he concludes that the conditions presumed by linear analysis are unstable, and in fact must lead to stable limit cycles. In every instance, however, the models are globally rather than locally stable, limiting their behavior to that shown in either Figures 2c or 2e.

There is another tradition of models that recognizes the basically discontinuous features of ecological systems and incorporates explicit lags. Nicholson and Bailey initiated this tradition when they developed a model using the output of attacks and survivals within one generation as the input for the next (29). The introduction of this explicit lag generates oscillations that increase in amplitude until one or other of the species becomes extinct (Figure 2a). Their assumptions are as unrealistically simple as Lotka's and Volterra's; the instability results because the number of attacking predators at any moment is so much a consequence of events in the previous generation that there are "too many" when prey are declining and "too few" when prey are increasing. If a lag is introduced into the Lotka-Volterra formulation (Wangersky & Cunningham 40) the same instability results.

The sense one gains, then, of the behavior of the traditional models is that they are either globally unstable or globally stable, that neutral stability is very unlikely, and that when the models are stable a limit cycle is a likely consequence.

Many, but not all, of the simplifying assumptions have been relaxed in simulation models, and there is one example (Holling & Ewing 14) that joins the two traditions initiated by Lotka-Volterra and Nicholson and Bailey and, further, includes more realism in the operation of the stabilizing and destabilizing forces. These modifications are described in more detail later; the important features accounting for the difference in behavior result from the introduction of explicit lags, a functional response of predators that rises monotonically to a plateau, a nonrandom (or contagious) attack by predators, and a minimum prey density below which reproduction does not occur. With these changes a very different pattern emerges that conforms most closely to Figure 2d. That is, there exists a domain of attraction within which there is a stable equilibrium; beyond that domain the prey population becomes extinct. Unlike the Nicholson and Bailey model, the stability becomes possible, although in a limited region, because of contagious attack. [Contagious attack implies that for one reason or another some prey have a greater probability of being attacked than others, a condition that is common in nature (Griffiths & Holling 9).] The influence of contagious attack becomes significant whenever predators become abundant in relation to the prey, for then the susceptible prey receive the burden of attention, allowing more prey to escape than would be expected by random contact. This "inefficiency" of the predator allows the system to counteract the destabilizing effects of the lag.

If this were the only difference the system would be globally stable, much as Figure 2c. The inability of the prey to reproduce at low densities, however, allows some of the trajectories to cut this reproduction threshold, and the prey become extinct. This introduces a lower prey density boundary to the attraction domain and, at the same time, a higher prey density boundary above which the amplitudes of the oscillations inevitably carry the population below the reproduction threshold. The other modifications in the model, some of which have been touched on above, alter this picture in degree only. The essential point is that a more realistic representation of the behavior of interacting populations indicates the existence of at least one domain of attraction. It is quite possible, within this domain, to imagine stable equilibrium points, stable nodes, or stable limit cycles. Whatever the detailed configuration, the existence of discrete domains of attraction immediately suggests important consequences for the persistence of the system and the probability of its extinction.

Such models, however complex, are still so simple that they should not be viewed in a definitive and quantitative way. They are more powerfully used as a starting point to organize and guide understanding. It becomes valuable, therefore, to ask what the models leave out and whether such omissions make isolated domains of attraction more or less likely.

Theoretical models generally have not done well in simultaneously incorporating realistic behavior of the processes involved, randomness, spatial heterogeneity, and an adequate number of dimensions or state variables. This situation is changing very rapidly as theory and empirical studies develop a closer technical partnership. In what follows I refer to real world examples to determine how the four elements that tend to be left out might further affect the behavior of ecological systems.

SOME REAL WORLD EXAMPLES

Self-Contained Ecosystems

In the broadest sense, the closest approximation we could make of a real world example that did not grossly depart from the assumptions of the theoretical models would be a self-contained system that was fairly homogenous and in which climatic fluctuations were reasonably small. If such systems could be discovered they would reveal how the more realistic interaction of real world processes could modify the patterns of systems behavior described above. Very close approximations to any of these conditions are not likely to be found, but if any exist, they are apt to be fresh water aquatic ones. Fresh water lakes are reasonably contained systems, at least within their watersheds; the fish show considerable mobility throughout, and the properties of the water buffer the more extreme effects of climate. Moreover, there have been enough documented man-made disturbances to liken them to perturbed systems in which either the parameter values or the levels of the constituent populations are changed. In a crude way, then, the lake studies can be likened to a partial exploration of a phase space of the sorts shown in Figure 2. Two major classes of disturbances have occurred: first, the impact of nutrient enrichment from man's domestic and industrial wastes, and second, changes in fish populations by harvesting.

The paleolimnologists have been remarkably successful in tracing the impact of man's activities on lake systems over surprisingly long periods. For example, Hutchinson (17) has reconstructed the series of events occurring in a small crater lake in Italy from the last glacial period in the Alps (2000 to 1800 BC) to the present. Between the beginning of the record and Roman times the lake had established a trophic equilibrium with a low level of productivity which persisted in spite of dramatic changes in surroundings from *Artemesia* steppe, through grassland, to fir and mixed oak forest. Then suddenly the whole aquatic system altered. This alteration towards eutrophication seems to have been initiated by the construction of the Via Cassia about 171 BC, which caused a subtle change in the hydrographic regime. The whole sequence of environmental changes can be viewed as changes in parameters or driving variables, and the long persistence in the face of these major changes suggests that natural systems have a high capacity to absorb change without dramatically altering. But this resilient character has its limits, and when the limits are passed, as by the construction of the Roman highway, the system rapidly changes to another condition.

More recently the activities of man have accelerated and limnologists have recorded some of the responses to these changes. The most dramatic change consists of blooms of algae in surface waters, an extraordinary growth triggered, in most instances, by nutrient additions from agricultural and domestic sources.

While such instances of nutrient addition provide some of the few examples available of perturbation effects in nature, there are no controls and the perturbations are exceedingly difficult to document. Nevertheless, the qualitative pattern seems consistent, particularly in those lakes (Edmundson 4, Hasler 10) to which sewage has been added for a time and then diverted elsewhere. This pulse of disturbance characteristically triggers periodic algal blooms, low oxygen conditions, the sudden disappearance of some plankton species, and appearance of others. As only one example, the nutrient changes in Lake Michigan (Beeton 2) have been accompanied by the replacement of the cladoceran *Bosmina coregoni* by *B. Longirostris*, *Diaptomus oregonensis* has become an important copepod species, and a brackish water copepod *Eurytemora affinis* is a new addition to the zooplankton.

In Lake Erie, which has been particularly affected because of its shallowness and intensity of use, the mayfly *Hexagenia*, which originally dominated the benthic community, has been almost totally replaced by oligochetes. There have been blooms of the diatom *Melosira binderana*, which had never been reported from the

United States until 1961 but now comprises as much as 99% of the total phytoplankton around certain islands. In those cases where sewage has been subsequently diverted there is a gradual return to less extreme conditions, the slowness of the return related to the accumulation of nutrients in sediments.

The overall pattern emerging from these examples is the sudden appearance or disappearance of populations, a wide amplitude of fluctuations, and the establishment of new domains of attraction.

The history of the Great Lakes provides not only some particularly good information on responses to man-made enrichment, but also on responses of fish populations to fishing pressure. The eutrophication experience touched on above can be viewed as an example of systems changes in driving variables and parameters, whereas the fishing example is more an experiment in changing state variables. The fisheries of the Great Lakes have always selectively concentrated on abundant species that are in high demand. Prior to 1930, before eutrophication complicated the story, the lake sturgeon in all the Great Lakes, the lake herring in Lake Erie, and the lake whitefish in Lake Huron were intensively fished (Smith 37). In each case the pattern was similar: a period of intense exploitation during which there was a prolonged high level harvest, followed by a sudden and precipitous drop in populations. Most significantly, even though fishing pressure was then relaxed, none of these populations showed any sign of returning to their previous levels of abundance. This is not unexpected for sturgeon because of their slow growth and late maturity, but it is unexpected for herring and whitefish. The maintenance of these low populations in recent times might be attributed to the increasingly unfavorable chemical or biological environment, but in the case of the herring, at least, the declines took place in the early 1920s before the major deterioration in environment occurred. It is as if the population had been shifted by fishing pressure from a domain with a high equilibrium to one with a lower one. This is clearly not a condition of neutral stability as suggested in Figure 2b since once the populations were lowered to a certain point the decline continued even though fishing pressure was relaxed. It can be better interpreted as a variant of Figure 2d where populations have been moved from one domain of attraction to another.

Since 1940 there has been a series of similar catastrophic changes in the Great Lakes that has led to major changes in the fish stocks. Beeton (2) provides graphs summarizing the catch statistics in the lakes for many species since 1900. Lake trout, whitefish, herring, walleye, sauger, and blue pike have experienced precipitous declines of populations to very low values in all of the lakes. The changes generally conform to the same pattern. After sustained but fluctuating levels of harvest the catch dropped dramatically in a span of a very few years, covering a range of from one to four orders of magnitude. In a number of examples particularly high catches were obtained just before the drop. Although catch statistics inevitably exaggerate the step-like character of the pattern, populations must have generally behaved in the way described.

The explanations for these changes have been explored in part, and involve various combinations of intense fishing pressure, changes in the physical and chemical environment, and the appearance of a foreign predator (the sea lamprey) and foreign competitors (the alewife and carp). For our purpose the specific cause is of less interest than the inferences that can be drawn concerning the resilience of these systems and their stability behavior. The events in Lake Michigan provide a typical example of the pattern in other lakes (Smith 37). The catch of lake trout was high, but fluctuated at around six million pounds annually from 1898 to 1940. For four years catches increased noticeably and then suddenly collapsed to near extinction by the 1950s due to a complete failure of natural reproduction. Lake herring and whitefish followed a similar pattern (Beeton 2: Figure 7). Smith (37) argues that the trigger for the lake trout collapse was the appearance of the sea lamprey that had spread through the Great Lakes after the construction of the Welland Canal. Although lamprey populations were extremely small at the time of the collapse, Smith argues that even a small mortality, added to a commercial harvest that was probably at the maximum for sustained yield, was sufficient to cause the collapse. Moreover, Ricker (31) has shown that fishing pressure shifts the age structure of fish populations towards younger ages. He demonstrates that a point can come where only slight increases in mortality can trigger a collapse of the kind noted for lake trout. In addition, the lake trout was coupled in a network of competitive and predatory interconnections with other species, and pressures on these might have contributed as well.

Whatever the specific causes, it is clear that the precondition for the collapse was set by the harvesting of fish, even though during a long period there were no obvious signs of problems. The fishing activity, however, progressively reduced the resilience of the system so that when the inevitable unexpected event occurred, the populations collapsed. If it had not been the lamprey, it would have been something else: a change in climate as part of the normal pattern of fluctuation, a change in the chemical or physical environment, or a change in competitors or predators. These examples again suggest distinct domains of attraction in which the populations forced close to the boundary of the domain can then flip over it.

The above examples are not isolated ones. In 1939 an experimental fishery was started in Lake Windermere to improve stocks of salmonids by reducing the abundance of perch (a competitor) and pike (a predator). Perch populations were particularly affected by trapping and the populations fell drastically in the first three years. Most significantly, although no perch have been removed from the North Basin since 1947, populations have still not shown any tendency to return to their previous level (Le Cren et al 19).

The same patterns have even been suggested for terrestrial systems. Many of the arid cattle grazing lands of the western United States have gradually become invaded and dominated by shrubs and trees like mesquite and cholla. In some instances grazing and the reduced incidence of fire through fire prevention programs allowed invasion and establishment of shrubs and trees at the expense of grass. Nevertheless, Glendening (8) has demonstrated, from data collected in a 17-year experiment in which intensity of grazing was manipulated, that once the trees have gained sufficient size and density to completely utilize or materially reduce the moisture supply, elimination of grazing will not result in the grassland reestablishing itself. In short, there is a level of the state variable "trees" that, once achieved, moves the system from one domain of attraction to another. Return to the original domain can only be made by an explicit reduction of the trees and shrubs.

These examples point to one or more distinct domains of attraction in which the important point is not so much how stable they are within the domain, but how likely it is for the system to move from one domain into another and so persist in a changed configuration.

This sampling of examples is inevitably biased. There are few cases well documented over a long period of time, and certainly some systems that have been greatly disturbed have fully recovered their original state once the disturbance was removed. But the recovery in most instances is in open systems in which reinvasion is the key ingredient. These cases are discussed below in connection with the effects of spatial heterogeneity. For the moment I conclude that distinct domains of attraction are not uncommon within closed systems. If such is the case, then further confirmation should be found from empirical evidence of the way processes which link organisms operate, for it is these processes that are the cause of the behavior observed.

Process Analysis

One way to represent the combined effects of processes like fecundity, predation, and competition is by using Ricker's (30) reproduction curves. These simply represent the population in one generation as a function of the population in the previous generation, and examples are shown in Figures 3a, c, and e. In the simplest form, and the one most used in practical fisheries management (Figure 3a), the reproduction curve is dome-shaped. When it crosses a line with slope 1 (the straight line in the figures) an equilibrium condition is possible, for at such cross-overs the popula-

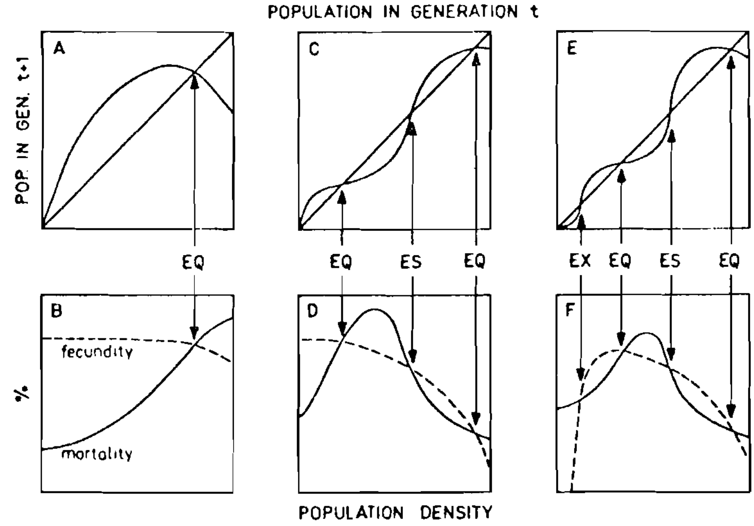

Figure 3 Examples of various reproduction curves (a, c, and e) and their derivation from the contributions of fecundity and mortality (b, d, and f).

tion in one generation will produce the same number in the next. It is extremely difficult to detect the precise form of such curves in nature, however; variability is high, typically data are only available for parts of any one curve, and the treatment really only applies to situations where there are no lags. It is possible to deduce various forms of reproduction curves, however, by disaggregating the contributions of fecundity and mortality. The three lower graphs in Figure 3b, 3d, and 3f represent this disaggregation of their counterpart reproduction curves. The simplest types of reproduction curve (Figure 3a) can arise from a mortality that regularly increases with density and either a constant fecundity or a declining one. With fecundity expressed as the percentage mortality necessary to just balance reproduction, the cross-over point of the curves represents the equilibrium condition. But we know that the effects of density on fecundity and mortality can be very much more complicated.

Mortality from predation, for example, has been shown to take a number of classic forms (Holling 11, 13). The individual attack by predators as a function of prey density (the functional response to prey density) can increase with a linear rise to a plateau (type 1), a concave or negatively accelerated rise to a plateau (type 2), or an S-shaped rise to a plateau (type 3) The resulting contribution to mortality from these responses can therefore show ranges of prey density in which there is direct density dependence (negative feedback from the positively accelerated portions of the type 3 response), density independence (the straight line rise of type 1), and inverse dependence (the positive feedback from the negatively accelerated and plateau portions of the curves). There are, in addition, various numerical responses generated by changes in the number of predators as the density of their prey increases. Even for those predators whose populations respond by increasing, there often will be a limit to the increase set by other conditions in the environment When populations are increasing they tend to augment the negative feedback features (although with a delay), but when populations are constant, despite increasing prey density, the percent mortality will inevitably decline since individual attack eventually saturates at complete satiation (the plateaux of all three functional responses). In Figures 3d and 3f the mortality curves shown summarize a common type. The rising or direct density-dependent limb of the curve is induced by increasing predator populations and by the reduced intensity of attack at low densities, shown by the initial positively accelerated portion of the S-shaped type 3 response Such a condition is common for predators with alternate prey, both vertebrates (Holling 14) and at least some invertebrates (Steele 38). The declining inverse density-dependent limb is induced by satiation of the predator and a numerical response that has been reduced or stopped.

Fecundity curves that decline regularly over a very wide range of increasing population densities (as in Figure 3d) are common and have been referred to as *Drosophila*-type curves (Fujita 6). This decline in fecundity is caused by increased competition for oviposition sites, interference with mating, and increased sterility. The interaction between a dome-shaped mortality curve and a monotonically decreasing fecundity curve can generate equilibrium conditions (Figure 3d). Two stable equilibria are possible, but between these two is a transient equilibrium designated as the escape threshold (ES in Figure 3). Effects of random changes on populations or parameters could readily shift densities from around the lower equilibrium to above this escape threshold, and in these circumstances populations would inevitably increase to the higher equilibrium.

The fecundity curves are likely to be more complex, however, since it seems inevitable that at some very low densities fecundity will decline because of difficulties in finding mates and the reduced effect of a variety of social facilitation behaviors. We might even logically conclude that for many species there is a minimum density below which fecundity is zero. A fecundity curve of this Allee-type (Fujita 6) has been empirically demonstrated for a number of insects (Watt 42) and is shown in Figure 3f. Its interaction with the dome-shaped mortality curve can add another transient equilibrium, the extinction threshold (EX in Figure 3f) With this addition there is a lower density such that if populations slip below it they will proceed inexorably to extinction. The extinction threshold is particularly likely since it has been shown mathematically that each of the three functional response curves will intersect with the ordinate of percent predation at a value above zero (Holling 13).

Empirical evidence, therefore, suggests that realistic forms to fecundity and mortality curves will generate sinuous reproduction curves like those in Figures 3c and 3e with the possibility of a number of equilibrium states, some transient and some stable. These are precisely the conditions that will generate domains of attraction, with each domain separated from others by the extinction and escape thresholds. This analysis of process hence adds support to the field observations discussed earlier.

The behavior of systems in phase space cannot be completely understood by the graphical representations presented above. These graphs are appropriate only when effects are immediate; in the face of the lags that generate cyclic behavior the reproduction curve should really produce two values for the population in generation $t + 1$ for each value of the population in generation t. The graphical treatment of Rosenzweig & MacArthur (33) to a degree can accommodate these lags and cyclic behavior. In their treatment they divide phase planes of the kind shown in Figure 2 into various regions of increasing and decreasing x and y populations. The regions are separated by two lines, one representing the collection of points at which the prey population does not change in density ($dx/dt = 0$, the prey isocline) and one in which the predator population does not so change ($dy/dt = 0$, the predator isocline). They deduce that the prey isocline will be dome-shaped for much the same reason as described for the fecundity curves of Figure 3f. The predator isocline, in the simplest condition, is presumed to be vertical, assuming that only one fixed level of prey is necessary to just maintain the predator population at a zero instantaneous rate of change.

Intersection of the two isoclines indicates a point where both populations are at equilibrium. Using traditional linear stability analysis one can infer whether these equilibrium states are stable (Figure 2c) or not (Figure 2a). Considerable importance is attached to whether the predator isocline intersects the rising or falling portion of the prey isocline. As mentioned earlier these techniques are only appropriate near equilibrium (May 24), and the presumed unstable conditions in fact generate stable limit cycles (Figure 2e). Moreover, it is unlikely that the predator isocline is a vertical one in the real world, since competition between predators at high predator densities would so interfere with the attack process that a larger number of prey would be required for stable predator populations. It is precisely this condition that was demonstrated by Griffiths & Holling (9) when they showed that a large number of species of parasites distribute their attacks contagiously. The result is a "squabbling predator behavior" (Rosenzweig 34, 35) that decreases the efficiency of predation at high predator/prey ratios. This converts an unstable system (Figure 2a) to a stable one (Figure 2c); it is likely that stability is the rule, rather than the exception, irrespective of where the two isoclines cross.

The empirical evidence described above shows that realistic fecundity and mortality (particularly predation) processes will generate forms that the theorists might tend to identify as special subsets of more general conditions. But it is just these special subsets that separate the real world from all possible ones, and these more realistic forms will modify the general conclusions of simpler theory. The ascending limb of the Allee-type fecundity curve will establish, through interaction with mortality, a minimum density below which prey will become extinct. This can at the same time establish an upper prey density above which prey will become extinct because the amplitude of prey fluctuations will eventually carry the population over the extinction threshold, as shown in the outer trajectory of Figure 2d. These conditions alone are sufficient to establish a domain of attraction, although the boundaries of this domain need not be closed. Within the domain the contagious attack by predators can produce a stable equilibrium or a stable node. Other behaviors of the mortality agents, however, could result in stable limit cycles.

More realistic forms of functional response change this pattern in degree only. For example, a negatively accelerated type of functional response would tend to make the domain of attraction somewhat smaller, and an S-shaped one larger. Limitations in the predator's numerical response and thresholds for reproduction of predators, similar to those for prey, could further change the form of the domain. Moreover, the behaviors that produce the sinuous reproduction curves of Figures 3c and 3e can add additional domains. The essential point, however, is that these systems are not globally stable but can have distinct domains of attraction. So long as the populations remain within one domain they have a consistent and regular form of behavior. If populations pass a boundary to the domain by chance or through intervention of man, then the behavior suddenly changes in much the way suggested from the field examples discussed earlier.

The Random World

To this point, I have argued as if the world were completely deterministic. In fact, the behavior of ecological systems is profoundly affected by random events. It is important, therefore, to add another level of realism at this point to determine how the above arguments may be modified. Again, it is applied ecology that tends to supply the best information from field studies since it is only in such situations that data have been collected in a sufficiently intensive and extensive manner. As one example, for 28 years there has been a major and intensive study of the spruce budworm and its interaction with the spruce-fir forests of eastern Canada (Morris

27). There have been six outbreaks of the spruce budworm since the early 1700s (Baskerville 1) and between these outbreaks the budworm has been an exceedingly rare species. When the outbreaks occur there is major destruction of balsam fir in all the mature forests, leaving only the less susceptible spruce, the nonsusceptible white birch, and a dense regeneration of fir and spruce. The more immature stands suffer less damage and more fir survives. Between outbreaks the young balsam grow, together with spruce and birch, to form dense stands in which the spruce and birch, in particular, suffer from crowding. This process evolves to produce stands of mature and overmature trees with fir a predominant feature.

This is a necessary, but not sufficient, condition for the appearance of an outbreak; outbreaks occur only when there is also a sequence of unusually dry years (Wellington 43). Until this sequence occurs, it is argued (Morris 27) that various natural enemies with limited numerical responses maintain the budworm populations around a low equilibrium. If a sequence of dry years occurs when there are mature stand of fir, the budworm populations rapidly increase and escape the control by predators and parasites. Their continued increase eventually causes enough tree mortality to force a collapse of the populations and the reinstatement of control around the lower equilibrium. The reproduction curves therefore would be similar to those in Figures 3c or 3e.

In brief, between outbreaks the fir tends to be favored in its competition with spruce and birch, whereas during an outbreak spruce and birch are favored because they are less susceptible to budworm attack. This interplay with the budworm thus maintains the spruce and birch which otherwise would be excluded through competition. The fir persists because of its regenerative powers and the interplay of forest growth rates and climatic conditions that determine the timing of budworm outbreaks.

This behavior could be viewed as a stable limit cycle with large amplitude, but it can be more accurately represented by a distinct domain of attraction determined by the interaction between budworm and its associated natural enemies, which is periodically exceeded through the chance consequence of climatic conditions. If we view the budworm only in relation to its associated predators and parasites we might argue that it is highly unstable in the sense that populations fluctuate widely. But these very fluctuations are essential features that maintain persistence of the budworm, together with its natural enemies and its host and associated trees. By so fluctuating, successive generations of forests are replaced, assuring a continued food supply for future generations of budworm and the persistence of the system.

Until now I have avoided formal identification of different kinds of behavior of ecological systems. The more realistic situations like budworm, however, make it necessary to begin to give more formal definition to their behavior. It is useful to distinguish two kinds of behavior. One can be termed stability, which represents the ability of a system to return to an equilibrium state after a temporary disturbance; the more rapidly it returns and the less it fluctuates, the more stable it would be. But there is another property, termed resilience, that is a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables. In this sense, the budworm forest community is highly unstable and it is because of this instability that it has an enormous resilience. I return to this view frequently throughout the remainder of this paper.

The influence of random events on systems with domains of attraction is found in aquatic systems as well. For example, pink salmon populations can become stabilized for several years at very different levels, the new levels being reached by sudden steps rather than by gradual transition (Neave 28). The explanation is very much the same as that proposed for the budworm, involving an interrelation between negative and positive feedback mortality of the kinds described in Figures 3d and 3f, and random effects unrelated to density. The same pattern has been described by Larkin (18) in his simulation model of the Adams River sockeye salmon. This particular run of salmon has been characterized by a regular four-year periodicity since 1922, with one large or dominant year, one small or subdominant, and two years with very small populations. The same explanation as described above has been proposed with the added reality of a lag. Essentially, during the dominant year limited numerical responses produce an inverse density-dependent response as in the descending limb of the mortality curves of Figure 3d and 3f. The abundance of the prey in that year is nevertheless sufficient to establish populations of predators that have a major impact on the three succeeding low years. Buffering of predation by the smolts of the dominant year accounts for the larger size of the subdominant. These effects have been simulated (Larkin 18), and when random influences are imposed in order to simulate climatic variations the system has a distinct probability of flipping into another stable configuration that is actually reproduced in nature by sockeye salmon runs in other rivers. When subdominant escapement reaches a critical level there is about an equal chance that it may become the same size as the dominant one or shrivel to a very small size.

Random events, of course, are not exclusively climatic. The impact of fires on terrestrial ecosystems is particularly illuminating (Cooper 3) and the periodic appearance of fires has played a decisive role in the persistence of grasslands as well as certain forest communities. As an example, the random perturbation caused by fires in Wisconsin forests (Loucks 21) has resulted in a sequence of transient changes that move forest communities from one domain of attraction to another. The apparent instability of this forest community is best viewed not as an unstable condition alone, but as one that produces a highly resilient system capable of repeating itself and persisting over time until a disturbance restarts the sequence.

In summary, these examples of the influence of random events upon natural systems further confirm the existence of domains of attraction. Most importantly they suggest that instability, in the sense of large fluctuations, may introduce a resilience and a capacity to persist. It points out the very different view of the world that can be obtained if we concentrate on the boundaries to the domain of attraction rather than on equilibrium states. Although the equilibrium-centered view is analytically more tractable, it does not always provide a realistic understanding of the systems' behavior. Moreover, if this perspective is used as the exclusive guide to the management activities of man, exactly the reverse behavior and result can be produced than is expected.

The Spatial Mosaic

To this point, I have proceeded in a series of steps to gradually add more and more reality. I started with self-contained closed systems, proceeded to a more detailed explanation of how ecological processes operate, and then considered the influence of random events, which introduced heterogeneity over-time.

The final step is now to recognize that the natural world is not very homogeneous over space, as well, but consists of a mosaic of spatial elements with distinct biological, physical, and chemical characteristics that are linked by mechanisms of biological and physical transport. The role of spatial heterogeneity has not been well explored in ecology because of the enormous logistic difficulties. Its importance, however, was revealed in a classic experiment that involved the interaction between a predatory mite, its phytophagous mite prey, and the prey's food source (Huffaker et al 15). Briefly, in the relatively small enclosures used, when there was unimpeded movement throughout the experimental universe, the system was unstable and oscillations increased in amplitude. When barriers were introduced to impede dispersal between parts of the universe, however, the interaction persisted. Thus populations in one small locale that suffer chance extinctions could be reestablished by invasion from other populations having high numbers—a conclusion that is confirmed by Roff's mathematical analysis of spatial heterogeneity (32).

There is one study that has been largely neglected that is, in a sense, a much more realistic example of the effects of both temporal and spatial heterogeneity of a population in nature (Wellington 44, 45). There is a peninsula on Vancouver Island in which the topography and climate combine to make a mosaic of favorable locales for the tent caterpillar. From year to year the size of these locales enlarges or contracts depending on climate; Wellington was able to use the easily observed changes in cloud patterns in any year to define these areas. The tent caterpillar, to add a further element of realism, has identifiable behavioral types that are determined not by genetics but by the nutritional history of the parents. These types represent a range from sluggish to very active, and the proportion of types affects the shape of the easily visible web the tent caterpillars spin. By combining these defined differences of behavior with observations on changing numbers, shape of webs, and changing cloud patterns, an elegant story of systems behavior emerges. In a favorable year locales that previously could not support tent caterpillars now can, and populations are established through invasion by the vigorous dispersers from other locales. In these new areas they tend to produce another generation with a high proportion of vigorous behavioral types. Because of their high dispersal behavior and the small area of the locale in relation to its periphery, they then tend to leave in greater numbers than they arrive. The result is a gradual increase in the proportion of more sluggish types to the point where the local population collapses. But, although its fluctuations are considerable, even under the most unfavorable conditions there are always enclaves suitable for the insect. It is an example of a population with high fluctuations that can take advantage of transient periods of favorable conditions and that has, because of this variability, a high degree of resilience and capacity to persist.

A further embellishment has been added in a study of natural insect populations by Gilbert & Hughes (7). They combined an insightful field study of the interaction between aphids and their parasites with a simulation model, concentrating upon a specific locale and the events within it under different conditions of immigration from other locales. Again the important focus was upon persistence rather than degree of fluctuation. They found that specific features of the parasite-host interaction allowed the parasite to make full use of its aphid resources just short of driving the host to extinction. It is particularly intriguing that the parasite and its host were introduced into Australia from Europe and in the short period that the parasite has been present in Australia there have been dramatic changes in its developmental rate and fecundity. The other major difference between conditions in Europe and Australia is that the immigration rate of the host in England is considerably higher than in Australia. If the immigration rate in Australia increased to the English level, then, according to the model the parasite should increase its fecundity from the Australian level to the English to make the most of its opportunity short of extinction. This study provides, therefore, a remarkable example of a parasite and its host evolving together to permit persistence, and further confirms the importance of systems resilience as distinct from systems stability.

SYNTHESIS

Some Definitions

Traditionally, discussion and analyses of stability have essentially equated stability to systems behavior. In ecology, at least, this has caused confusion since, in mathematical analyses, stability has tended to assume definitions that relate to conditions very near equilibrium points. This is a simple convenience dictated by the enormous analytical difficulties of treating the behavior of nonlinear systems at some distance from equilibrium. On the other hand, more general treatments have touched on questions of persistence and the probability of extinction, defining these measures as aspects of stability as well. To avoid this confusion I propose that the behavior of ecological systems could well be defined by two distinct properties: resilience and stability.

Resilience determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist. In this definition resilience is the property of the system and persistence or probability of extinction is the result. Stability, on the other hand, is the ability of a system to return to an equilibrium state after a temporary disturbance. The more rapidly it returns, and with the least fluctuation, the more stable it is. In this definition stability is the property of the system and the degree of fluctuation around specific states the result.

Resilience versus Stability

With these definitions in mind a system can be very resilient and still fluctuate greatly, i.e. have low stability. I have touched above on examples like the spruce budworm forest community in which the very fact of low stability seems to introduce high resilience. Nor are such cases isolated ones, as Watt (41) has shown in his analysis of thirty years of data collected for every major forest insect throughout Canada by the Insect Survey program of the Canada Department of the Environment. This statistical analysis shows that in those areas subjected to extreme climatic conditions the populations fluctuate widely but have a high capability of absorbing periodic extremes of fluctuation. They are, therefore, unstable using the restricted definition above, but highly resilient. In more benign, less variable climatic regions the populations are much less able to absorb chance climatic extremes even though the populations tend to be more constant. These situations show a high degree of stability and a lower resilience. The balance between resilience and stability is clearly a product of the evolutionary history of these systems in the face of the range of random fluctuations they have experienced.

In Slobodkin's terms (36) evolution is like a game, but a distinctive one in which the only payoff is to stay in the game. Therefore, a major strategy selected is not one maximizing either efficiency or a particular reward, but one which allows persistence by maintaining flexibility above all else. A population responds to any environmental change by the initiation of a series of physiological, behavioral, ecological, and genetic changes that restore its ability to respond to subsequent unpredictable environmental changes. Variability over space and time results in variability in numbers, and with this variability the population can simultaneously retain genetic and behavioral types that can maintain their existence in low populations together with others that can capitalize on chance opportunities for dramatic increase. The more homogeneous the environment in space and time, the more likely is the system to have low fluctuations and low resilience. It is not surprising, therefore, that the commerical fishery systems of the Great Lakes have provided a vivid example of the sensitivity of ecological systems to disruption by man, for they represent climatically buffered, fairly homogeneous and self-contained systems with relatively low variability and hence high stability and low resilience. Moreover, the goal of producing a maximum sustained yield may result in a more stable system of reduced resilience.

Nor is it surprising that however readily fish stocks in lakes can be driven to extinction, it has been extremely difficult to do the same to insect pests of man's crops. Pest systems are highly variable in space and time; as open systems they are much affected by dispersal and therefore have a high resilience. Similarly, some Arctic ecosystems thought of as fragile may be highly resilient, although unstable. Certainly this is not true for some subsystems in the Arctic, such as Arctic frozen soil, self-contained Arctic lakes, and cohesive social populations like caribou, but these might be exceptions to a general rule.

The notion of an interplay between resilience and stabilty might also resolve the conflicting views of the role of diversity and stability of ecological communities. Elton (5) and MacArthur (22) have argued cogently from empirical and theoretical points of view that stability is roughly proportional to the number of links between species in a trophic web. In essence, if there are a variety of trophic links the same flow of energy and nutrients will be maintained through alternate links when a species becomes rare. However, May's (23) recent mathematical analyses of models of a large number of interacting populations shows that this relation between increased diversity and stability is not a mathematical truism. He shows that randomly assembled complex systems are in general less stable, and never more stable, than less complex ones. He points out that ecological systems are likely to have evolved to a very small subset of all possible sets and that MacArthur's conclusions, therefore, might still apply in the real world. The definition of stability used, however, is the equilibrium-centered one. What May has shown is that complex systems might fluctuate more than less complex ones. But if there is more than one domain of attraction, then the increased variability could simply move the system from one domain to another. Also, the more species there are, the more equilibria there may be and, although numbers may thereby fluctuate considerably, the overall persistence might be enhanced. It would be useful to explore the possibility that instability in numbers can result in more diversity of species and in spatial patchiness, and hence in increased resilience.

Measurement

If there is a worthwhile distinction between resilience and stability it is important that both be measurable. In a theoretical world such measurements could be developed from the behavior of model systems in phase space. Just as it was useful to disaggregate the reproduction curves into their constituent components of mortality and fecundity, so it is useful to disaggregate the information in a phase plane. There are two components that are important: one that concerns the cyclic behavior and its frequency and amplitude, and one that concerns the configuration of forces caused by the positive and negative feedback relations.

To separate the two we need to imagine first the appearance of a phase space in which there are no such forces operating. This would produce a referent trajectory containing only the cyclic properties of the system. If the forces were operating, departure from this referent trajectory would be a measure of the intensity of the forces. The referent trajectories that would seem to be most useful would be the neutrally stable orbits of Figure 2b, for we can arbitrarily imagine these trajectories as moving on a flat plane. At least for more realistic models parameter values can be discovered that do generate neutrally stable orbits. In the complex predator-prey model of Holling (14), if a range of parameters is chosen to explore the effects of different degrees of contagion of attack, the interaction is unstable when attack is random and stable when it is contagious. We have recently shown that there is a critical level of contagion between these extremes that generates neutrally stable orbits. These orbits, then, have a certain frequency and amplitude and the departure of more realistic trajectories from these referent ones should allow the computation of the vector of forces. If these were integrated a potential field would be represented with peaks and valleys. If the whole potential field were a shallow bowl the system would be globally stable and all trajectories would spiral to the bottom of the bowl, the equilibrium point. But if, at a minimum, there were a lower extinction threshold for prey then, in effect, the bowl would have a slice taken out of one side, as suggested in Figure 4. Trajectories that initiated far up on the side of the bowl would have amplitude that would carry the trajectory over the slice cut out of it. Only those

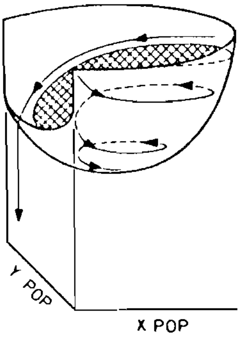

Figure 4 Diagramatic representation showing the feedback forces as a potential field upon which trajectories move. The shaded portion is the domain of attraction.

trajectories that just avoided the lowest point of the gap formed by the slice would spiral in to the bowl's bottom. If we termed the bowl the basin of attraction (Lewontin 20) then the domain of attraction would be determined by both the cyclic behavior and the configuration of forces. It would be confined to a smaller portion of the bottom of the bowl, and one edge would touch the bottom portion of the slice taken out of the basin.

This approach, then, suggests ways to measure relative amounts of resilience and stability. There are two resilience measures: Since resilience is concerned with probabilities of extinction, firstly, the overall area of the domain of attraction will in part determine whether chance shifts in state variables will move trajectories outside the domain. Secondly, the height of the lowest point of the basin of attraction (e.g. the bottom of the slice described above) above equilibrium will be a measure of how much the forces have to be changed before all trajectories move to extinction of one or more of the state variables.

The measures of stability would be designed in just the opposite way from those that measure resilience. They would be centered on the equilibrium rather than on the boundary of the domain, and could be represented by a frequency distribution of the slopes of the potential field and by the velocity of the neutral orbits around the equilibrium.

But such measures require an immeanse amount of knowledge of a system and it is unlikely that we will often have all that is necessary. Hughes & Gilbert (16), however, have suggested a promising approach to measuring probabilities of extinction and hence of resilience. They were able to show in a stochastic model that the distribution of surviving population sizes at any given time does not differ significantly from a negative binomial. This of course is just a description, but it does provide a way to estimate the very small probability of zero, i.e. of extinction, from the observed mean and variance. The configuration of the potential field and the cyclic behavior will determine the number and form of the domains of attraction, and these will in turn affect the parameter values of the negative binomial or of any other distribution function that seems appropriate. Changes in the zero class of the distribution, that is, in the probability of extinction, will be caused by these parameter values, which can then be viewed as the relative measures of resilience. It will be important to explore this technique first with a number of theoretical models so that the appropriate distributions and their behavior can be identified. It will then be quite feasible, in the field, to sample populations in defined areas, apply the appropriate distribution, and use the parameter values as measures of the degree of resilience.

APPLICATION

The resilience and stability viewpoints of the behavior of ecological systems can yield very different approaches to the management of resources. The stability view emphasizes the equilibrium, the maintenance of a predictable world, and the harvesting of nature's excess production with as little fluctuation as possible. The resilience view emphasizes domains of attraction and the need for persistence. But extinction is not purely a random event; it results from the interaction of random events with those deterministic forces that define the shape, size, and characteristics of the domain of attraction. The very approach, therefore, that assures a stable maximum sustained yield of a renewable resource might so change these deterministic conditions that the resilience is lost or reduced so that a chance and rare event that previously could be absorbed can trigger a sudden dramatic change and loss of structural integrity of the system.

A management approach based on resilience, on the other hand, would emphasize the need to keep options open, the need to view events in a regional rather than a local context, and the need to emphasize heterogeneity. Flowing from this would be not the presumption of sufficient knowledge, but the recognition of our ignorance; not the assumption that future events are expected, but that they will be unexpected. The resilience framework can accommodate this shift of perspective, for it does not require a precise capacity to predict the future, but only a qualitative capacity to devise systems that can absorb and accommodate future events in whatever unexpected form they may take.

Literature Cited

1. Baskerville, G. L. 1971. *The Fir-Spruce-Birch Forest and the Budworm.* Forestry Service, Canada Dept. Environ., Fredericton, N. B. Unpublished
2. Beeton, A. D. 1969. Changes in the environment and biota of the Great Lakes. *Eutrophication: Causes, Consequences, Correctives.* Washington DC: Nat. Acad. Sci.
3. Cooper, C. F. 1961. The ecology of fire. *Sci. Am.* 204:150-6, 158, 160
4. Edmondson, W. T. 1961. Changes in Lake Washington following increase in nutrient income. *Verh. Int. Ver. Limnol.* 14:167-75
5. Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants.* London: Methuen
6. Fujita, H. 1954. An interpretation of the changes in type of the population density effect upon the oviposition rate. *Ecology* 35:253-7
7. Gilbert, N., Hughes, R. D. 1971. A model of an aphid population—three adventures. *J. Anim. Ecol.* 40:525-34

8. Glendening, G. 1952. Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. *Ecology* 33:319–28
9. Griffiths, K. J., Holling, C. S. 1969. A competition submodel for parasites and predators. *Can. Entomol.* 101:785–818
10. Hasler, A. D. 1947. Eutrophication of lakes by domestic sewage. *Ecology* 28: 383–95
11. Holling, C. S. 1961. Principles of insect predation. *Ann. Rev. Entomol.* 6:163–82
12. Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48: 1–86
13. Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulations. *Mem. Entomol. Soc. Can.* 45: 1–60
14. Holling, C. S., Ewing, S. 1971. Blind man's buff: exploring the response space generated by realistic ecological simulation models. *Proc. Int. Symp. Statist. Ecol.* New Haven, Conn.: Yale Univ. Press 2:207–29
15. Huffaker, C. D., Shea, K. P., Herman, S. S. 1963. Experimental studies on predation. Complex dispersion and levels of food in an acarine predator-prey interaction. *Hilgardia* 34:305–30
16. Hughes, R. D., Gilbert, N. 1968. A model of an aphid population —a general statement. *J. Anim. Ecol.* 40:525–34
17. Hutchinson, G. E. 1970. Ianula: an account of the history and development of the Lago di Monterosi, Latium, Italy. *Trans. Am. Phil. Soc.* 60:1–178
18. Larkin, P. A. 1971. Simulation studies of the Adams River Sockeye Salmon *(Oncarhynchus nerka). J. Fish. Res. Bd. Can.* 28:1493–1502
19. Le Cren, E. D., Kipling, C., McCormack, J. C. 1972. Windermere: effects of exploitation and eutrophication on the salmonid community. *J. Fish. Res. Bd. Can.* 29:819–32
20. Lewontin, R. C. 1969. The meaning of stability. *Diversity and Stability of Ecological Systems, Brookhaven Symp. Biol.* 22:13–24
21. Loucks, O. L. 1970. Evolution of diversity, efficiency and community stability. *Am. Zool.* 10:17–25
22. MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–6
23. May, R. M. 1971. Stability in multi-species community models. *Math. Biosci.* 12:59–79
24. May, R. M. 1972. Limit cycles in predator-prey communities. *Science* 177: 900–2
25. May, R. M. 1972. Will a large complex system be stable? *Nature* 238:413–14
26. Minorsky, N. 1962. *Nonlinear Oscillations.* Princeton, N.J.: Van Nostrand
27. Morris, R. F. 1963. The dynamics of epidemic spruce budworm populations. *Mem. Entomol. Soc. Can.* 31:1–332
28. Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. *J. Fish. Res. Bd. Can.* 9:450–91
29. Nicholson, A. J., Bailey, V. A. 1935. The balance of animal populations—Part I. *Proc. Zool. Soc. London* 1935: 551–98
30. Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.* 11:559–623
31. Ricker, W. E. 1963. Big effects from small causes: two examples from fish population dynamics. *J. Fish. Res. Bd. Can.* 20:257–84
32. Roff, D. A. 1973. Spatial heterogeneity and the persistence of populations. *J. Theor. Pop. Biol.* In press
33. Rosenzweig, M. L., MacArthur, R. H. 1963. Graphical representation and stability condition of predator-prey interactions. *Am. Natur.* 97:209–23
34. Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–7
35. Rosenzweig, M. L. 1972. Stability of enriched aquatic ecosystems. *Science* 175: 564–5
36. Slobodkin, L. B. 1964. The strategy of evolution. *Am. Sci.* 52:342–57
37. Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. *J. Fish. Res. Bd. Can.* 25:667–93
38. Steele, J. H. 1971. Factors controlling marine ecosystems. *The Changing Chemistry of the Oceans,* ed. D. Dryssen, D. Jaquer, 209–21. Nobel Symposium 20, New York: Wiley
39. Walters, C. J. 1971. Systems ecology: the systems approach and mathematical models in ecology. *Fundamentals of Ecology,* ed. E. P. Odum. Philadelphia: Saunders. 3rd ed.
40. Wangersky, P. J., Cunningham, W. J. 1957. Time lag in prey-predator population models. *Ecology* 38:136–9
41. Watt, K. E. F. 1968. A computer approach to analysis of data on weather, population fluctuations, and disease. *Biometeorology, 1967 Biology Colloquium,* ed. W. P. Lowry. Corvallis, Oregon: Oregon State Univ. Press

42. Watt, K. E. F. 1960. The effect of population density on fecundity in insects. *Can. Entomol.* 92:674–95
43. Wellington, W. G. 1952. Air mass climatology of Ontario north of Lake Huron and Lake Superior before outbreaks of the spruce budworm and the forest tree caterpillar. *Can. J. Zool.* 30:114–27
44. Wellington, W. G. 1964. Qualitative changes in populations in unstable environments. *Can. Entomol.* 96:436–51
45. Wellington, W. G. 1965. The use of cloud patterns to outline areas with different climates during population studies. *Can. Entomol.* 97:617–31