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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

1

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2 HOLLING

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.

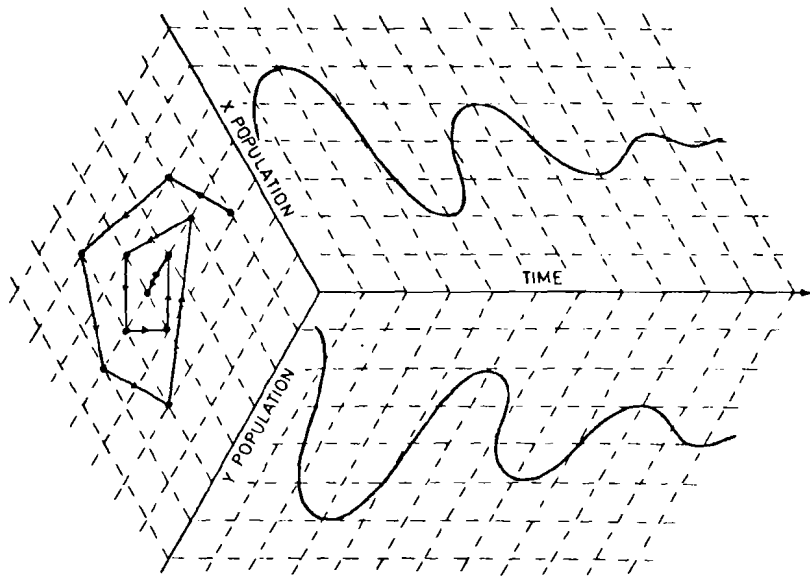


Figure 1 Derivation of a phase plane showing the changes in numbers of two populations over time.

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

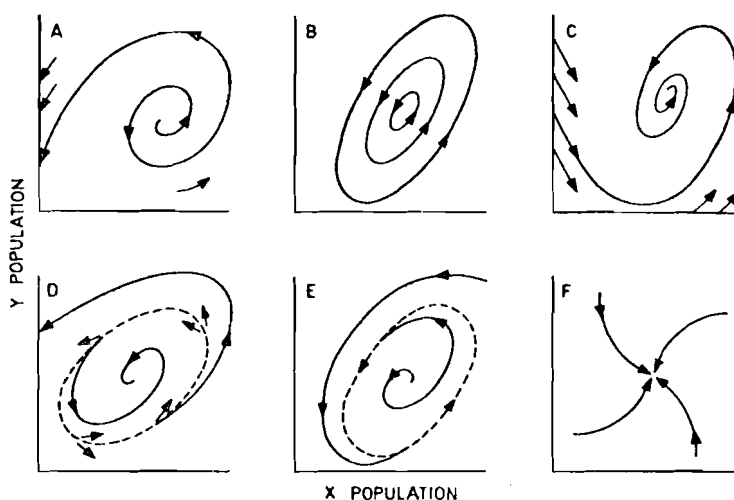


Figure 2 Examples of possible behaviors of systems in a phase plane: (a) unstable equilibrium, (b) neutrally stable cycles, (c) stable equilibrium, (d) domain of attraction, (e) stable limit cycle, (f) stable node.

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 (Minorsky 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-

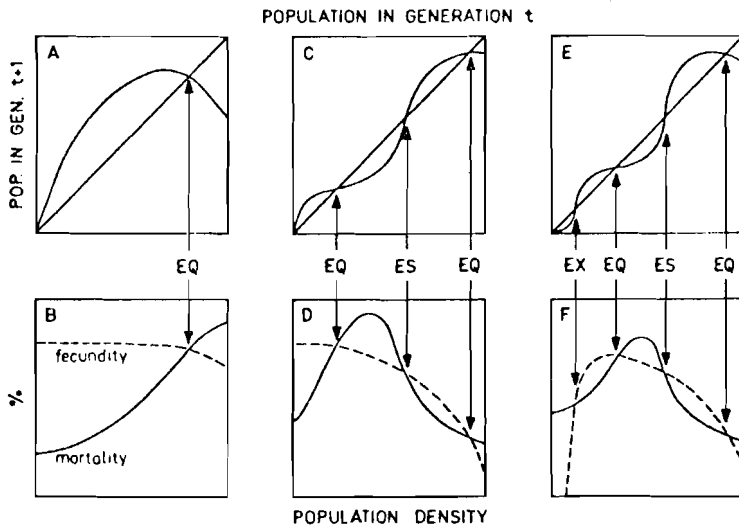


Figure 3 Examples of various reproduction curves (a, c, and e) and their derivation from the contributions of fecundity and mortality (b, d, and f).

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 stands 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 intro-

duce 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 commercial 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 stability 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

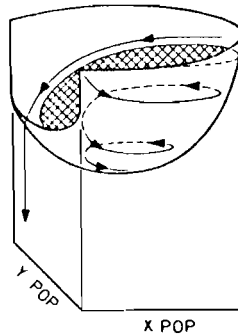


Figure 4 Diagrammatic representation showing the feedback forces as a potential field upon which trajectories move. The shaded portion is the domain of attraction.

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 immense 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.

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Understanding the Complexity of Economic, Ecological, and Social Systems

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ABSTRACT

Hierarchies and adaptive cycles comprise the basis of ecosystems and social-ecological systems across scales. Together they form a panarchy. The panarchy describes how a healthy system can invent and experiment, benefiting from inventions that create opportunity while being kept safe from those that destabilize because of their nature or excessive exuberance. Each level is allowed to operate at its own pace, protected from above by slower, larger levels but invigorated from below by faster, smaller cycles of innovation. The whole panarchy is therefore both creative and conserving. The interactions between cycles in a panarchy combine learning with

continuity. An analysis of this process helps to clarify the meaning of “sustainable development.” Sustainability is the capacity to create, test, and maintain adaptive capability. Development is the process of creating, testing, and maintaining opportunity. The phrase that combines the two, “sustainable development,” thus refers to the goal of fostering adaptive capabilities and creating opportunities. It is therefore not an oxymoron but a term that describes a logical partnership.

Key words: hierarchy; adaptive cycles; multiple scales; resilience; sustainability.

INTRODUCTION

The ecological status of nations and regions is a current item for assessment and action on the agenda of several organizations. In the United States, the National Academy of Sciences and the Heinz Center have issued guidelines to identify sustainability indicators. Internationally, the Species Survival Commission of the World Conservation Union (IUCN) has stated that sustainability, either in a region or of a species, depends on interactions among internal and external factors. The internal factors may be social, political, ecological, or economic; the external factors include foreign debt, structural poverty, global environmental problems,

and social/political/economic conflicts. Indicators of sustainability have been identified for all the internal factors, while issues of concern have been suggested for the external ones. One unpublished report cited 76 specific sustainability indicators for the internal factors and a more diffuse set of attributes for the external factors.

All of these indicators and all of the attributes make sense. The problem is not that they are wrong, or that they are not useful. They are, if anything, incomplete. Rather, they suggest a complexity that can overwhelm understanding, even when, in specific situations, only a subset of these entities are relevant. There are two approaches to complexity.

One of them, which has been explored thoroughly and incisively by Emory Roe (1998), views complexity as anything we do not understand, because there are apparently a large number of inter-

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acting elements. The appropriate approach, according to Roe, is to embrace the complexity and resulting uncertainty and analyze different subsets of interactions, each of which seem relevant from a number of fundamentally different operational and philosophical perspectives. A recent article in *Conservation Ecology* offered a review of this thesis from four different disciplinary and policy perspectives and a commentary on the reviews by the author (www.consecol.org/Journal/vol4/iss2/index.html).

An alternative view (Holling 2000; Gunderson and Holling 2001) suggests that the complexity of living systems of people and nature emerges not from a random association of a large number of interacting factors rather from a smaller number of controlling processes. These systems are self-organized, and a small set of critical processes create and maintain this self-organization. ("Self-organization" is a term that characterizes the development of complex adaptive systems, in which multiple outcomes typically are possible depending on accidents of history. Diversity and the individuality of components, localized interactions among components, and an autonomous process that uses the outcomes of those local interactions to select a subset of those components for enhancement are characteristics of complex adaptive systems [Levin 1999]). These processes establish a persistent template upon which a host of other variables exercise their influence. Such "subsidiary" variables or factors can be interesting, relevant, and important, but they exist at the whim of the critical controlling factors or variables. If sustainability means anything, it has to do with the small set of critical self-organized variables and the transformations that can occur in them during the evolutionary process of societal development.

But these two views of complexity require alternative perspectives and competing models and hypotheses. The goal of each approach is to mobilize evidence that can distinguish among competing explanations so that multiple lines of evidence begin to define what is known, what is uncertain, and what is unknown. We are always left with best judgments, not certainties.

The view presented here argues that there is a requisite level of simplicity behind the complexity that, if identified, can lead to an understanding that is rigorously developed but can be communicated lucidly. It holds that if you cannot explain or describe the issue of concern using at least a handful of causes, then your understanding is too simple. If you require many more than a handful of causes, then your understanding is unnecessarily complex. That level of understanding is built upon a founda-

tion of adequate integrative theory, rigorously developed. This theory is rooted in empirical reality and communicated with metaphor and example. The first requirement is to begin to integrate the essence of ecological, economic, and social science theory and to do so with the goal of being, in Einstein's words, "as simple as possible but no simpler."

The purpose of this paper is to summarize a theoretical framework and process for understanding complex systems. This concept has recently been developed and expanded into a book-length thesis (Gunderson and Holling 2001). In its expanded version, it provides a means of assessing information about the internal factors and external influences that interact to determine systemic sustainability. To be useful, such a framework and process must satisfy the following criteria:

- Be "as simple as possible but no simpler" than is required for understanding and communication.
- Be dynamic and prescriptive, not static and descriptive. Monitoring of the present and past is static unless it connects to policies and actions and to the evaluation of different futures.
- Embrace uncertainty and unpredictability. Surprise and structural change are inevitable in systems of people and nature.

AN INTEGRATIVE THEORY

Background

The theory was developed under the auspices of the "Resilience Project", a 5-year collaboration among an international group of ecologists, economists, social scientists, and mathematicians. The project was initiated to search for an integrative theory and integrative examples of practice. Its goal was to develop and test the elements of an integrative theory that had the degree of simplicity necessary for understanding but also the complexity required to develop policy for sustainability. The results of that project are summarized in the final report to the MacArthur Foundation found at <http://www.resalliance.org/reports>.

The heart of the work has now been amplified in *Panarchy: Understanding Transformations in Human and Natural Systems* (Gunderson and Holling, 2001). This book expands the theory and explores its implications for ecological, political, institutional, and management systems. It was intended to deepen our understanding of linked ecological/economic/decision systems through the use of a set of interactive models, several analyses of institutions that

Table 1. Table of Contents for *Panarchy: Understanding Transformations in Human and Natural Systems*

Part I. Introduction	
Chapter 1. In Quest of a Theory of Adaptive Change.	C.S. Holling, L.H. Gunderson, and D. Ludwig
Part II. Theories of Change	
Chapter 2. Resilience and Adaptive Cycles.	C.S. Holling and L.H. Gunderson
Chapter 3. Sustainability and Panarchies.	C.S. Holling, L.H. Gunderson, and G.D. Peterson
Chapter 4. Why Are Systems of People and Nature not just Ecological or Social Systems?	F. Westley, S.R. Carpenter, W.A. Brock, C.S. Holling, and L.H. Gunderson
Chapter 5. Back to the Future: Ecosystem Dynamics and Local Knowledge.	F. Berkes and C. Folke
Chapter 6. The Dynamics of Political Discourse in Seeking Sustainability.	L. Pritchard Jr. and S.E. Sanderson
Part III. Myths, Models, and Metaphors	
Chapter 7. Collapse, Learning, and Renewal.	S.R. Carpenter, W.A. Brock, and D. Ludwig
Chapter 8. Dynamic Interaction of Societies and Ecosystems: Linking Theories from Ecology, Economy, and Sociology.	M. Scheffer, F. Westley, W.A. Brock, and M. Holmgren
Chapter 9. A Future of Surprises.	M. Janssen
Chapter 10. Resilience and Sustainability: The Economic Analysis of Non-Linear Dynamic Systems.	W.A. Brock, K.G. Mäler, and C. Perrings
Part IV. Linking Theory to Practice	
Chapter 11. Resilient Rangelands — Adaptation in Complex Systems.	B. Walker and N. Abel
Chapter 12. Surprises and Sustainability Cycles of Renewal in the Everglades.	L.H. Gunderson, C.S. Holling, and G.D. Peterson
Chapter 13. The Devil in the Dynamics: Adaptive Management on the Front Lines.	F. Westley
Chapter 14. Planning for Resilience: Scenarios, Surprises, and Branch Points.	G. C. Gallopin
Part V. Summary and Synthesis	
Chapter 15. Discoveries for Sustainable Futures.	C. S. Holling, S. R. Carpenter, W. A. Brock, and L. H. Gunderson
Chapter 16. Towards an Integrative Synthesis.	R. Yorque, B. Walker, C. S. Holling, L. H. Gunderson, C. Folke, S. R. Carpenter, and W. A. Brock

link people and nature, and an extensive exploration of two prototypical systems, the savannas and grasslands of Australia and the Everglades of Florida. Table 1 summarizes the book's contents.

"Panarchy" is the term we use to describe a concept that explains the evolving nature of complex adaptive systems. Panarchy is the hierarchical structure in which systems of nature (for example, forests, grasslands, lakes, rivers, and seas), and humans (for example, structures of governance, settlements, and cultures), as well as combined human-nature systems (for example, agencies that control natural resource use) (Gunderson and others 1995) and social-ecological systems (for instance, co-evolved systems of management) (Folke and others 1998), are interlinked in never-ending adaptive cycles of growth, accumulation, restructuring, and renewal. These transformational cycles take place in nested sets at scales ranging from a leaf to the biosphere over periods from days to geologic epochs, and from the scales of a family to a socio-political region over periods from years to centuries. If we can understand these cycles and their scales, it seems possible to evaluate their contribution to sustainability and to identify the points at which a system is capable of accepting positive change and

the points where it is vulnerable. It then becomes possible to use those leverage points to foster resilience and sustainability within a system.

The idea of panarchy combines the concept of space/time hierarchies with a concept of adaptive cycles. I will deal with each in turn and then show the consequence of combining them in a synthesis.

Hierarchies

Simon (1974) was one of the first to describe the adaptive significance of hierarchical structures. He called them "hierarchies", but not in the sense of a top-down sequence of authoritative control. Rather, semi-autonomous levels are formed from the interactions among a set of variables that share similar speeds (and, we would add, geometric/spatial attributes). Each level communicates a small set of information or quantity of material to the next higher (slower and coarser) level. Figure 1 shows an example for a forested landscape, Figure 2 shows a wetland system, and Figure 3 shows a social system.

As long as the transfer from one level to the other is maintained, the interactions within the levels themselves can be transformed, or the variables changed, without the whole system losing its integ-

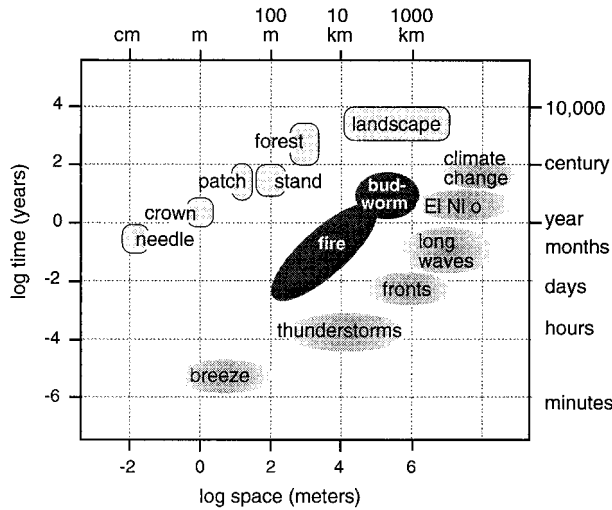


Figure 1. Time and space scales of the boreal forest (Holling 1986) and the atmosphere (Clark 1985) and their relationship to some of the processes that structure the forest. Contagious meso-scale processes, such as insect outbreaks and fire, mediate the interaction between faster atmospheric processes and slower vegetation processes. (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

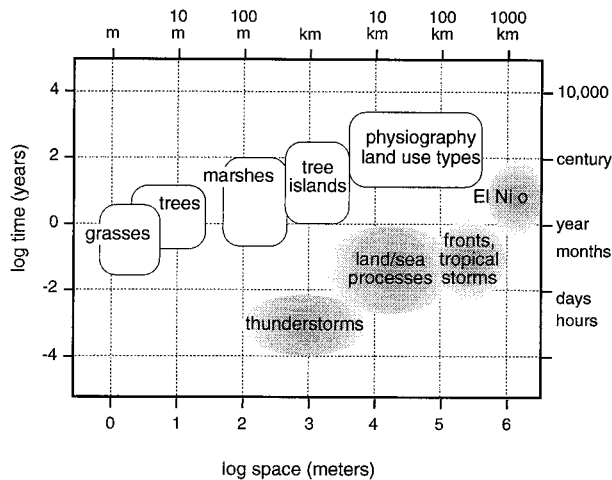


Figure 2. Time and space scales of levels of a hierarchy in the Everglades. (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

As a consequence, this structure allows wide latitude for experimentation within levels, thereby greatly increasing the speed of evolution.

Ecologists were inspired by Simon’s seminal article to apply the term “hierarchy” to ecological systems and develop its significance for a variety of ecological relationships and structures. In particular, Allen and Starr (1982) and O’Neill and others (1986) stimulated a major expansion of theoretical

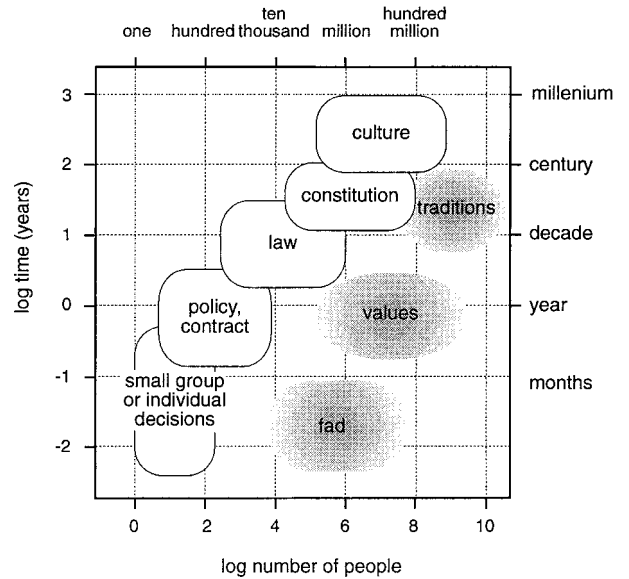


Figure 3. Institutional hierarchy of rule sets. In contrast to ecological hierarchies, this hierarchy is structured along dimensions of the number of people involved in rule sets and approximate turnover times (Gunderson and others 1995; Westley and others 2001). (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

understanding by shifting attention from the small-scale view that characterized much of biological ecology to a multiscale and landscape view that recognized that biotic and abiotic processes could develop, mutually re-enforcing relationships over distinct ranges of scale. More recently, Levin (1999) has expanded that representation of cross-scale dynamics in a way that greatly deepens our understanding of the self-organized features of terrestrial ecosystems.

Simon’s key arguments are that each of the levels of a dynamic hierarchy serves two functions. One is to conserve and stabilize conditions for the faster and smaller levels; the other is to generate and test innovations by experiments occurring within a level. It is this latter, dynamic function we call “an adaptive cycle” (Holling 1986). It is a heuristic model, a fundamental unit that contributes to the understanding of the dynamics of complex systems from cells, to ecosystems, to societies, to cultures.

The Adaptive Cycle

There are three properties that shape the adaptive cycle and the future state of a system:

- The inherent potential of a system that is available for change, since that potential determines

the range of future options possible. This property can be thought of, loosely, as the “wealth” of a system.

- The internal controllability of a system; that is, the degree of connectedness between internal controlling variables and processes, a measure that reflects the degree of flexibility or rigidity of such controls, such as their sensitivity or not to perturbation.
- The adaptive capacity; that is, the resilience of the system, a measure of its vulnerability to unexpected or unpredictable shocks. This property can be thought of as the opposite of the vulnerability of the system.

These three properties—wealth, controllability, and adaptive capacity—are general ones, whether at the scale of the cell or the biosphere, the individual or the culture. In case examples of regional development and ecosystem management (Gunderson and others 1995), they are the properties that shape the responses of ecosystems, agencies, and people to crisis.

Potential, or wealth, sets limits for what is possible—it determines the number of alternative options for the future. Connectedness, or controllability, determines the degree to which a system can control its own destiny, as distinct from being caught by the whims of external variability. Resilience, as achieved by adaptive capacity, determines how vulnerable the system is to unexpected disturbances and surprises that can exceed or break that control.

A stylized representation of an adaptive cycle is shown in Figure 4 for two of these properties—potential and connectedness. The trajectory alternates between long periods of slow accumulation and transformation of resources (from exploitation to conservation, or r to K), with shorter periods that create opportunities for innovation (from release to reorganization, or Ω to α). That potential includes accumulated ecological, economic, social, and cultural capital as well as unexpressed chance mutations and inventions. During the slow sequence from exploitation to conservation, connectedness and stability increase and capital is accumulated. Ecosystem capital, for example, includes nutrients, biomass, and physical structure. Although this accumulated capital is sequestered for the growing, maturing ecosystem, it also represents a gradual increase in the potential for other kinds of ecosystems and futures. For an economic or social system, the accumulating potential could as well derive from the skills, networks of human relationships, and mutual trust that are developed incrementally

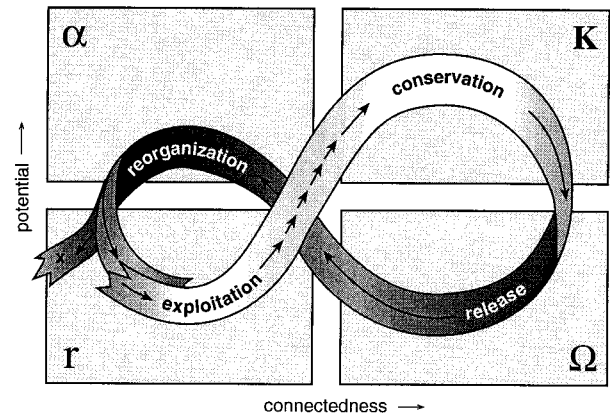


Figure 4. A stylized representation of the four ecosystem functions (r , K , Ω , α) and the flow of events among them. The arrows show the speed of the flow in the cycle. Short, closely spaced arrows indicate a slowly changing situation; long arrows indicate a rapidly changing situation. The cycle reflects changes in two properties: the y axis (the potential that is inherent in the accumulated resources of biomass and nutrients) and the x axis (the degree of connectedness among controlling variable). The exit from the cycle indicated at the left of the figure suggests, in a stylized way, the stage where the potential can leak away and where a flip into a less productive and less organized system is most likely (Holling 1986). (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

and integrated during the progression from r to K . They also represent a potential that was developed and used in one setting but could be available in transformed ones.

As the progression to the K phase proceeds in an ecosystem, for example, the accumulating nutrient and biomass resources become more and more tightly bound within existing vegetation, preventing other competitors from utilizing them. The potential for other use is high, but it is expropriated and controlled by the specific biota and processes of the ecosystem in place. That is, the system's connectedness increases, eventually becoming over-connected and increasingly rigid in its control. It becomes an accident waiting to happen.

The actual change is triggered by agents of disturbance, such as wind, fire, disease, insect outbreak, and drought. The resources accumulated and sequestered in vegetation and soil are then suddenly released and the tight organization is lost. Human enterprises can exhibit similar behavior, as, for example, when corporations such as IBM, AT&T, or General Motors accumulate rigidities to the point of crisis and then attempt to restructure (Hurst and Zimmerman 1994; Hurst 1995; Holling

and others 2001). The Soviet Union is a societal example of accumulated rigidities that precipitate a sudden collapse. The proximate agents of disturbance in these cases can be stakeholder revolts, public-interest attacks through the legal system, or more extreme societal revolts.

The phase from Ω to α is a period of rapid reorganization during which novel recombinations can unexpectedly seed experiments that lead to innovations in the next cycle. The economist J. A. Schumpeter (1950) appropriately called this phase “creative destruction.” Initially, the “front loop” of the trajectory, from r to K , becomes progressively more predictable as it develops. In contrast, the “back loop” of the adaptive cycle, from Ω to α , is inherently unpredictable and highly uncertain. At that stage, the previously accumulated mutations, inventions, external invaders, and capital can become reassorted into novel combinations, some of which nucleate new opportunity.

It is as if two separate objectives are functioning, but in sequence. The first maximizes production and accumulation; the second maximizes invention and reassortment. The two objectives cannot be maximized simultaneously but only occur sequentially. And the success in achieving one inexorably sets the stage for its opposite. The adaptive cycle therefore embraces two opposites: growth and stability on the one hand, change and variety on the other.

Figure 5 adds the third dimension, resilience, to the adaptive cycle. The appearance of a figure 8 in the path of the adaptive cycle, as in Figure 4, is the consequence of the projection of a three-dimensional object onto a two-dimensional plane. We can view that three-dimensional object from different perspectives, emphasizing one property or another. Figure 5 rotates the object to expose the resilience axis.

This orientation of the figure shows that as the phases of the adaptive cycle proceed, a system’s ecological resilience expands and contracts. The conditions that occasionally foster novelty and experiment occur during periods in the back loop of the cycle, when connectedness, or controllability, is low and resilience is high (that is, during the α phase). The low connectedness, or weak control, permits novel reassortments of elements that were previously tightly connected to others in isolated sets of interactions. The high resilience allows tests of those novel combinations because the system-wide costs of failure are low. The result is the condition needed for creative experimentation. This recognition of resilience varying within a cycle adds an element that can reconcile the delicious para-

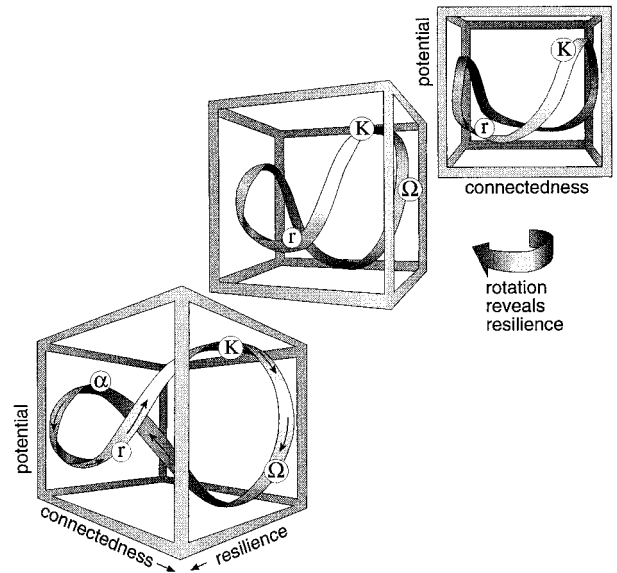


Figure 5. Resilience is another dimension of the adaptive cycle. A third dimension, resilience, is added to the two-dimensional box of Figure 4 to show how resilience expands and contracts throughout the cycle. Resilience shrinks as the cycle moves towards K , where the system becomes more brittle. It expands as the cycle shifts rapidly into a back loop to reorganize accumulated resources for a new initiation of the cycle. The appearance of a figure 8 in Figure 4 is the consequence of viewing a three-dimensional object in a two-dimensional plane. (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

doxes of conservative nature vs creative nature; sustainability vs creative change.

The α phase is the stage that is least examined and the least known. It is the beginning of a process of reorganization that provides the potential for subsequent growth, resource accumulation, and storage. At this stage, ecological resilience is high, as is potential. But connectedness is low and internal regulation is weak. There is a wide stability region, with weak regulation around equilibria, low connectivity among variables, and a substantial amount of potential available for future options. Because of those features, it is a fertile environment for experiments, for the appearance and initial establishment of entities that would otherwise be out-competed. As in good experiments, many will fail, but in the process, the survivors will accumulate the fruits of change. It is a time of both crisis and opportunity.

In summary, there are four key features that characterize an adaptive cycle, with its properties of growth and accumulation on the one hand and of

novelty and renewal on the other. All of them are measurable in specific situations:

1. Potential (that is, wealth as expressed in ecosystem structure, productivity, human relationships, mutations, and inventions) increases incrementally in conjunction with increased efficiency but also in conjunction with increased rigidity. This is the phase from r to K in Figure 4.
2. As potential increases, slow changes gradually expose an increasing vulnerability (decreased resilience) to such threats as fire, insect outbreak, competitors, or opposition groups. The system becomes an accident waiting to happen. A break can trigger the release of accumulated potential in what the economist Schumpeter called "creative destruction" (1950). The trajectory then moves abruptly into a back loop from K to Ω .
3. Innovation occurs in pulses or surges of innovation when uncertainty is great, potential is high, and controls are weak, so that novel recombinations can form. This is the phase of reorganization represented in α (Figure 4) where low connectedness allows unexpected combinations of previously isolated or constrained innovations that can nucleate new opportunity.
4. Those innovations are then tested. Some fail, but others survive and adapt in a succeeding phase of growth from r to K .

Not All Adaptive Cycles Are the Same

Efforts to find exceptions that might invalidate the preceding representation have identified different classes of systems that represent distinct variants of, or departures from, that cycle. Examples of these exceptions include:

- Physical systems where the lack of invention and mutation limits the potential for evolutionary change. Examples: tectonic plate dynamics, and Per Bak's (1996) sand pile experiments demonstrating "organized criticality" from K to Ω).
- Ecosystems and communities of plants and animals that are strongly influenced by uncontrollable or unpredictable episodic external inputs and have little internal regulation and highly adaptive responses to opportunity. Examples: exploited arid rangelands, pelagic biotic communities. These systems tend to remain largely in the lower left quadrant of the cycle, oscillating in

the α and r phases, dominated by trophic dynamics (Walker and Abel 2001).

- Ecosystems and human organizations with predictable but variable inputs and some significant internal regulation of external variability over certain scale ranges. For example, productive temperate forests and grasslands, large bureaucracies. These systems represent the full cycle of boom-and-bust dynamics shown in Figure 4 (Holling and Gunderson 2001).
- Biological entities with strong and effective homeostatic internal regulation of external variability. Examples: cells and ionic regulation, "warm-blooded" organisms with endothermic control of temperature. System variables remain near an equilibrium and the individual is freed to exploit a wider range of opportunities within a community or ecosystem. This is an example of local control that can release external opportunity and variability at a different scale—a transfer of the full adaptive cycle to the larger arena of a higher level in the hierarchy.
- Human systems with foresight and active adaptive methods that stabilize variability and exploit opportunity. Examples: entrepreneurial businesses, futures markets and resource scarcity, some traditional cultures. The high variability of the adaptive cycle can be transferred from the society to an individual entrepreneur or, in a traditional culture, to a "wise person" (Westley and others 2001; Berkes and Folke 2001).

THE PANARCHY: A SYNTHESIS

Because the word "hierarchy" is so burdened by the rigid, top-down nature of its common meaning, we decided to look for another term that would capture the adaptive and evolutionary nature of adaptive cycles that are nested one within each other across space and time scales. Our goal was to rationalize the interplay between change and persistence, between the predictable and the unpredictable. We therefore melded the image of the Greek god Pan as the epitoma of unpredictable change with the notion of hierarchies across scales to invent a new term that could represent structures that sustain experiment, test its results, and allow adaptive evolution. Hence, "panarchy".

A panarchy is a representation of a hierarchy as a nested set of adaptive cycles. The functioning of those cycles and the communication between them determines the sustainability of a system. That synthesis will be explored in this section.

The adaptive cycle, as shown in Figures 4 and 5,

transforms hierarchies from fixed static structures to dynamic, adaptive entities whose levels are sensitive to small disturbances at the transition from growth to collapse (the Ω phase) and the transition from reorganization to rapid growth (the α phase). At other times, the processes are stable and robust, constraining the lower levels and immune to the buzz of noise from small and faster processes. It is at the two-phase transitions between gradual and rapid change and vice versa that the large and slow entities become sensitive to change from the small and fast ones.

However, the structural, top-down aspect of hierarchies has tended to dominate theory and application, reinforced by the standard dictionary definition of hierarchy as a system of vertical authority and control. Therefore, the dynamic and adaptive nature of such nested structures has tended to be lost.

It is certainly true that slower and larger levels set the conditions within which faster and smaller ones function. Thus, a forest stand moderates the climate within the stand to narrow the range of temperatures experienced by its individuals constituents. Similarly, cultures of different people establish norms that guide the actions of human individuals. But this representation has no way of accounting for the dynamics of each level as symbolized in the four-phase cycle of birth, growth and maturation, death, and renewal.

This adaptive cycle captures in a heuristic fashion the engine that periodically generates the variability and novelty upon which experimentation depends. As a consequence of the periodic, but transient, phases of creative destruction (Ω stage) and renewal (α stage), each level of a system's structure and processes can be reorganized. This reshuffling in the back loop of the cycle allows the possibility of new system configurations and opportunities utilizing the exotic and entirely novel entrants that had accumulated in earlier phases. The adaptive cycle opens transient windows of opportunity so that novel assortments can be generated.

For organisms, those novel entrants are mutated genes or, for some bacteria, exotic genes that are transferred occasionally between species. For ecosystems, the novel entrants are exotic, potentially invasive species or species "in the wings" waiting for more appropriate conditions. For economic systems, these novel entrants are inventions, creative ideas, and innovative people. The adaptive cycle explicitly initiates a slow period of growth during which mutations, invasions, and inventions can accumulate, followed by a briefer period when they undergo rearrangements. This process can occur

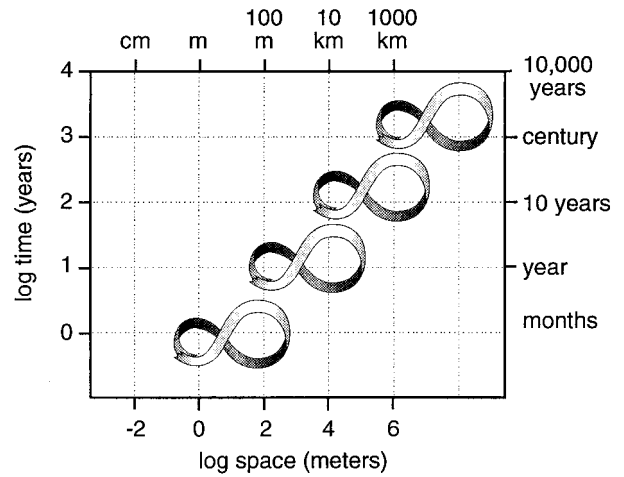


Figure 6. A stylized panarchy. A panarchy is a cross-scale, nested set of adaptive cycles that indicates the dynamic nature of structures depicted in the previous plots. (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

periodically within each hierarchical level, in a way that partially isolates the resulting experiments, reducing the risk to the integrity of the whole structure.

The organization and functions that form biological, ecological, and human systems can therefore be viewed as a nested set of four-phase adaptive cycles. Within these cycles, there are opportunities for periodic reshuffling within levels, which maintain adaptive opportunity, while simple interactions across levels maintain integrity. One major difference among biological, ecological, and human systems is the way that inventions are accumulated and transferred over time. But more on that later.

There are two features that distinguish the panarchical representation from traditional hierarchical ones. The first, as discussed earlier, is the importance of the adaptive cycle and, in particular, the α phase as the engine of variety and the generator of new experiments within each level. The various levels of the panarchy can be seen as a nested set of adaptive cycles (Figure 6).

The second feature is the connections between levels. There are potentially multiple connections between phases at one level and phases at another level. But two of these connections are particularly significant to our search for the meaning of sustainability. They are labeled as "revolt" and "remember" in Figure 7, where three levels of a panarchy are represented. The revolt and remember connections become important at times of change in the adaptive cycles.

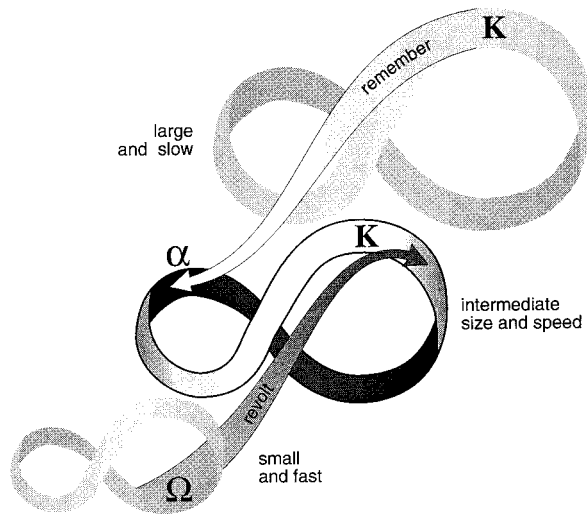


Figure 7. Panarchical connections. Three selected levels of a panarchy are illustrated to show the two connections that are critical in creating and sustaining adaptive capability. One is the “revolt” connection, which can cause a critical change in one cycle to cascade up to a vulnerable stage in a larger and slower one. The other is the “remember” connection which facilitates renewal by drawing on the potential that has been accumulated and stored in a larger, slower cycle. An example of the sequence from small and fast through larger and slower and thence to largest and slowest for a boreal forest ecosystem includes needles, tree crowns, and patches. For institutions, those three speeds might be operational rules, collective choice rules, and constitutional rules (Ostrom 1992); for economies, they might be individual preferences, markets, and social institutions (Whitaker 1987); for developing nations, they might be markets, infrastructure, and governance (Barro 1997); for societies, they might be allocation mechanisms, norms, and myths (Westley 1995); for knowledge systems, they might be local knowledge, management practice, and world view (Gadgil and others 1993; Berkes 1999; Holling and others 2001). (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

When a level in the panarchy enters its Ω phase of creative destruction, the collapse can cascade to the next larger and slower level by triggering a crisis. Such an event is most likely if the slower level is at its K phase, because at this point the resilience is low and the level is particularly vulnerable. The “revolt” arrow in Figure 7 suggests this effect, one where fast and small events overwhelm slow and large ones. Once triggered, the effect can cascade to still higher, slower levels, particularly if those levels have also accumulated vulnerabilities and rigidities.

An ecological version of this situation occurs when conditions in a forest allow a local ignition to create a small ground fire that spreads first to the

crown of a tree, then to a patch in the forest, and then to a whole stand of trees. Each step in that cascade moves the transformation to a larger and slower level. A societal version occurs when local activists succeed in their efforts to transform regional organizations and institutions, because the latter have become broadly vulnerable. Such a change occurred in New Brunswick, Canada when a few small groups opposed to spraying insecticide over the forest were able to transform this region’s vulnerable forest management policies and practices (Baskerville 1995).

The arrow labeled “remember” in Figure 7 indicates a second type of cross-scale interaction that is important at times of change and renewal. Once a catastrophe is triggered at one level, the opportunities for, or constraints against, the renewal of the cycle are strongly influenced by the K phase of the next slower and larger level. After a forest fire, for example, the processes and resources that have accumulated at a larger level slow the leakage of nutrients that have been mobilized and released into the soil. At the same time, the options for renewal include the seed bank, physical structures, and surviving species, which comprise biotic legacies (Franklin and MacMahon 2000) that have accumulated in the course of the forest’s growth. Similarly, for its reorganization and renewal, a coral reef hit by a storm draws on its own legacies and the memory of the seascape of which it is a part (Nyström and Folke 2001). It is as if this connection draws on the accumulated wisdom and experiences of maturity; hence, the word “remember.”

In a similar vein, Stewart Brand, in his marvelous meditation on buildings (1994), described them as adaptive, hierarchical entities. Buildings of enduring character are a reflection of seasoned maturity—the culmination of a series of idiosyncratic, wise, and thought-provoking experiments in the form and content of a mature, evolved structure. In *The Clock of the Long Now*, Brand (1999) extends these ideas and generalizes the concept of fast and slow processes to society as a whole. His work resonates with features reminiscent of panarchy theory. Similarly, Levin’s *Fragile Dominion* (1999) is an accessible and effective disquisition on self-organization as it characterizes adaptive, complex ecological systems.

The panarchy is a representation of the ways in which a healthy social-ecological system can invent and experiment, benefiting from inventions that create opportunity while it is kept safe from those that destabilize the system because of their nature or excessive exuberance. Each level is allowed to operate at its own pace, protected from above by

slower, larger levels but invigorated from below by faster, smaller cycles of innovation. The whole panarchy is therefore both creative and conserving. The interactions between cycles in a panarchy combine learning with continuity.

This process can serve to clarify the meaning of “sustainable development”. Sustainability is the capacity to create, test, and maintain adaptive capability. Development is the process of creating, testing, and maintaining opportunity. The phrase that combines the two, “sustainable development”, therefore refers to the goal of fostering adaptive capabilities while simultaneously creating opportunities. It is therefore not an oxymoron but a term that describes a logical partnership.

Collapsing Panarchies

Stochastic events external to a cycle can trigger spasmodic collapses, particularly if they encounter vulnerabilities within an adaptive cycle. Extremely large events can overwhelm the sustaining properties of panarchies, destroying levels, and triggering destructive cascades down the successive levels of a panarchy. The cataclysmic loss of biological diversity that occurred some 65 million years ago, destroying about 70% of Earth’s species; Jablonski 1995), for example, is likely to have been caused by the impact of an asteroid (Alvarez and others 1980). That event, which may also be associated with massive volcanic eruptions that occurred around the same time, unraveled the web of interactions within and between panarchical levels over scales from biomes to species.

Since recovery from these events is so delayed, it is likely that mass extinction events eliminate not only species but also ecological niches. For their continued existence, species depend on an environment that is created by life. Because they destroy most species, mass extinction events concomitantly eliminate many ecological niches. The recovery of biodiversity from such cataclysmic events requires the reconstruction of these niches, as new species evolve to fill them.

Notably, different families, orders, and species dominated the new assemblages after recovery; novel inventions and new ways of living emerged. The dinosaurs became extinct during the collapse that occurred 65 million years ago; the mammals, inconspicuous before that time, exploded in a diversification that created new opportunity. The conservative nature of established panarchies certainly slows change, while at the same time accumulating potential that can be released periodically if the decks are cleared of constraining influences by large, extreme events.

Similarly, a long view of human history reveals not regular change but spasmodic, catastrophic disruptions followed by long periods of reinvention and development. In contrast to the sudden collapses of biological panarchies, there are long periods of ruinous reversal, followed by slow recovery and the restoration of lost potential. Robert Adams’s magnificent reconstruction of Mesopotamian societies (1966, 1978) and a later review of other archaeological sequences at regional or larger scales (R. M. Adams unpublished) led him to identify two trends in human society since the Pleistocene. The first is an overall increase in the hierarchical differentiation and complexity of societies. That is, levels in the panarchy are added over time. If enough potential accumulates at one level, it can pass a threshold and establish another, slower and larger level. The second trend is defined by the occurrence of rapid discontinuous shifts, interspersed by much longer periods of relative stability. A number of scholars have focused on the study of such societal dynamics in more recent history. For example, Goldstone (1991) examined the wave of revolutions that occurred in Eurasia after a period of calm in the 17th century. He hypothesized that political breakdown occurs when there are simultaneous crises at several different organizational levels in society. In other words, adaptive cycles at different levels in a panarchy become aligned at the same phase of vulnerability. Thus, he explicitly posits a cascading, panarchical collapse.

In *The Great Wave*, David Fischer (1996) presents a somewhat similar model of political breakdown that focuses less on social stratification and revolutionary dynamics than on empirical price data and inflation. According to Fischer, at least three waves of social unrest swept Eurasia, first in the 14th century and later in the 17th and late 18th centuries. He argues that currency mismanagement and the outbreak of diseases aggravated the destabilizing effects of an inflation that in turn was driven by population growth.

In effect, both of these models of societal change propose that slow dynamics inform social organization. Periods of success carry the seeds of subsequent downfall, because they allow stresses and rigidities to accumulate. Organizations and institutions often fail to cope with these slow changes either because the changes are invisible to them, or they are so complex and highly contested that no action can be agreed upon.

Modern democratic societies are clearly vulnerable to the same process, but they have invented ways to diffuse large episodes of creative destruction by creating smaller cycles of renewal and

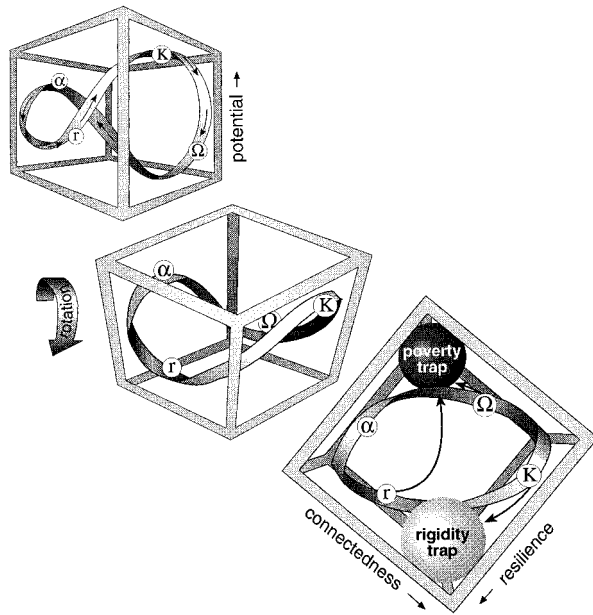


Figure 8. Maladaptive systems. A poverty trap and a rigidity trap are illustrated as departures from an adaptive cycle. If an adaptive cycle collapses because the potential and diversity have been eradicated due to misuse or an external force, an impoverished state can result, with low connectedness, low potential, and low resilience, thus creating a poverty trap. A system with high potential, connectedness, and resilience is represented by the rigidity trap. It is suggestive of the maladaptive conditions present in hierocracies, such as large bureaucracies (Holling and others 2001). (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

change through periodic political elections. So long as there is a literate and attentive citizenry, the painful lessons learned from the episodic collapses of whole societal panarchies can be transferred to faster learning at smaller scales. Various designs in business, from the creation of “skunk works” to the introduction of total quality management, serve the same purpose.

Poverty Traps and Rigidity Traps

Collapsing panarchies begin to decline within specific adaptive cycles that have become maladaptive. Earlier, I described the path of an adaptive cycle as oscillating between conditions of low connectedness, low potential, and high resilience to their opposites. Could there be systems with other combinations of those three attributes in which variability is sharply constrained and opportunity is limited? We suggest two such possibilities in Figure 8. If an adaptive cycle collapses because the potential and diversity have been eradicated through misuse

or due to an external force, an impoverished state can result, with low connectedness, low potential, and low resilience, thus creating a poverty trap.

This condition can then propagate downward through levels of the panarchy, collapsing levels as it goes. An ecological example is the productive savanna that, through human overuse and misuse, flips into an irreversible, eroding state, beginning with sparse vegetation. Thereafter, subsequent drought precipitates further erosion, and economic disincentives maintain sheep production. The same persistent collapse might also occur in a society traumatized by social disruption or conflict, so that its cultural cohesion and adaptive abilities are lost. In such a situation, the individual members of the society would be able to depend only on themselves and perhaps their immediate family members.

Some such societies might continue to exist in this degraded state of bare subsistence, barely able to persist as a group, but unable to accumulate enough potential to form the larger structures and sustaining properties of a complete panarchy. Others might simply collapse into anarchy. Berkes (1999) and Folke and others (1998) tried to determine how far such erosion must progress before recovery becomes impossible. When recovery is possible, it would be useful to know what critical attributes need to be reinvented and reestablished from the residual memory stored in slowly fading traditions and myths to recreate a new, sustaining panarchy.

Figure 8 also suggests that it is possible to have a sustainable but maladaptive system. Imagine a situation of great wealth and control, where potential is high, connectedness great and—in contrast to the phase where those conditions exist in an adaptive cycle—resilience is high; that is, a wealthy, tightly regulated, and resilient system. The high resilience would mean that the system had a great ability to resist external disturbances and persist, even beyond the point where it is adaptive and creative. It would have a kind of perverse resilience, preserving a maladaptive system. The high potential would be measured in accumulated wealth or abundant natural capital. The high connectedness would be created by efficient methods of social control, in which any novelty is either smothered or its inventor ejected. It would represent a rigidity trap.

We see signs of such sustained but maladaptive conditions in great “hierocracies,” such as societies that operate under rigid and apparently immutable caste systems. Other examples occur in regions of the developing world that have abundant natural resources but are subject to the rigid control of corrupt political regimes. But all such systems are

likely to have the seeds of their own destruction built in, as was the case with the totalitarian bureaucracy of the now defunct Soviet Union (Levin and others 1998).

What Distinguishes Human Systems?

Human systems exhibit at least three features that are unique—features that change the character and location of variability within the panarchy and that can dramatically enhance the potential of the panarchies themselves. Those three features are foresight, communication, and technology.

Foresight and intentionality. Human foresight and intentionality can dramatically reduce or even eliminate the boom and bust character of some cycles. Predictions of looming economic crises and collapses caused by resource scarcity, for example, are an important issue in debates about sustainability. The economist R. Solow (1973) provided a withering critique of such doomsday scenarios, pointing out that they ignore the forward-looking behaviors of people. These behaviors play a role in transmitting future scarcities into current prices, thereby inducing conservation behaviors in the real economic world. This forward-looking process functions through futures markets and the strategic purchase and holding of commodities. They provide very large incentives for some people to forecast the coming scarcity better than the rest of the market and to take a position to profit from it. But what one market participant can do, all can do; thus, this process transmits information to the market as a whole.

But there limits to this process, as described by Carpenter and others (1999, 2001). These limits are illustrated in specific examples of models that combine ecosystem simulations with economic optimization and decision processes. These models suggest that even when knowledge is total, a minimally complex ecosystem model, together with stochastic events, can thwart the forward-looking economic and decision-making capacity to eliminate booms and busts. These minimal requirements for the system are the same ones that characterize the ecosystem panarchy—that is, at least three speeds of variables, separation among those speeds, and nonlinear, multistable behavior.

That analysis is the source of our conclusion that ecosystems have a minimal complexity we call the “Rule of Hand” whose features make linear policies more likely to produce temporary solutions and a greater number of escalating problems. Only an actively adaptive approach can minimize the consequences.

Finally, how can we explain the common ten-

dency for large organizations to develop rigidities, thus precipitating major crises that initiate restructuring in a larger social, ecological, economic setting? Or, the many examples of long-term, ruinous reversals in the development of societies? These collapses seem to be more extreme and require much longer recovery than the internally generated cycles of ecosystem panarchies.

Certainly, in management agencies, the exercise of foresight and intentionality is often brilliantly directed to protect the positions of individuals rather than to further larger societal goals. The foresight that maintains creativity and change when connected to an appropriate economic market can lead to rigid organizations that are maintained even when that particular market no longer exists. The market in these cases is a market for political power of the few, not a free market for the many (Pritchard and Sanderson 2001). Foresight and intentionality can therefore precipitate ruinous reversals if they are not connected to a market with essential liberal and equitable properties.

Communication. Organisms transfer, test, and store experience in a changing world genetically. Ecosystems transfer, test, and store experience by forming self-organized patterns that repeat themselves. These patterns are formed and refined by a set of interacting variables that function over specific scale ranges and form a mutually reinforcing core of relationships. In fact, an ecosystem is developed out of a few such sets that establish a reproducing, discontinuous template to provide niches for species diversification and the adaptation of individual organisms.

In human systems, the same self-organized patterns are strongly developed, but humans uniquely add the ability to communicate ideas and experience. As they are tested, these ideas can become incorporated into slower parts of the panarchy, such as cultural myths, legal constitutions, and laws. Many sources of information, including television, movies, and the Internet, are global in their connectedness and influence. These media are contributing to a transformation of culture, beliefs, and politics at global scales.

Technology. The scale of the influence exerted by every animal other than humans is highly restricted. But technology amplifies the actions of humans so that they affect an astonishing range of scales from the submicroscopic to global and—however modestly at the moment—even extend beyond Earth itself.

As human technology has evolved over the last hundred thousand years, it has progressively accelerated, changing the rules and context of the pan-

archies in the process. The specialized tools, habitation, and weapons of hunter-gatherers, for example, together with the domestication of canines for use as hunting companions, created opportunities over wide scales. The use of fire by early humans made them part of the ecological structuring process. In temperate North America and Australia, for example, they became capable of transforming mosaics of grasslands and woods into extensive regions of contiguous grasslands or forests (Flannery 1994).

Progressively, the horse, train, automobile, and aircraft have extended the ambit for human choices from local to regional and thence to planetary scales, but the time allotted for each of these choices has changed little, or even decreased. Trips between home and work, for example, have always been largely limited to less than an hour or so, although the spatial scale has expanded from a maximum of a few kilometers by foot to potentially a few hundred kilometers by commuter aircraft. The slope of the decision panarchy for humans, if plotted in the same space as in Figures 1–3, now angles sharply upward, intersecting and dominating other panarchies of nature.

Assessing Sustainability

The current state of our understanding of panarchies is summarized in Table 2. The theory is sufficiently new that its practical application to regional questions or the analysis of specific problems has just begun. Panarchy theory focuses on the critical features that affect or trigger reorganization and transformation in a system. First, the back-loop of the cycles is the phase where resilience and opportunity is maintained or created, via “release” and “reorganization” (Figures 4 and 5). Second, the connections between levels of the panarchy are where persistence (via “remembrance”) and evolvability (via “revolt”) (Figure 7) are maintained.

These four phases or processes make up the four R’s of sustainability and development: release, reorganization, remembrance, and revolt. They provide new categories that can be used to organize the more specific indicators and attributes discussed in documents aimed at finding ways to evaluate sustainability and development.

To summarize: The panarchy describes how a healthy socioecological system can invent and experiment, benefiting from inventions that create opportunity while it is kept safe from those that destabilize the system due to their nature or excessive exuberance. Each level is allowed to operate at its own pace, protected from above by slower, larger levels but invigorated from below by faster, smaller

cycles of innovation. The whole panarchy is therefore both creative and conserving. The interactions between cycles in a panarchy combines learning with continuity.

The four R’s, then, represent the critical processes that manage the balance and tension between change and sustainability.

It is often useful to begin the analysis of a specific problem with a historical reconstruction of the events that have occurred, focusing on the surprises and crises that have arisen as a result of both external influences and internal instabilities. In essence, a sequence of adaptive cycles can be described, for the so-called natural system, the economy, management agencies, users, and politics. We think it is necessary to consider three scale ranges for each system, although the particular scales might be different for different subsystems. One of the principal aims is to define where in their respective adaptive cycles each of the subsystems is now. Actions that would be appropriate at one phase of the cycle might not be appropriate at other phases. Knowing where you are helps you to define what action needs to be taken.

In many instances, the motive for an assessment is a crisis or transformation that has already occurred or is anticipated. In these situations, the conditions of the back loop of the adaptive cycle (Figure 4) dominate. However, it is these times of greatest threat that offer the greatest opportunity, because many constraints have been removed. In an insightful analysis of local communities as seen from this perspective, Berkes and Folke (2001) showed that local societies often develop reserves that are necessary during back-loop restructuring. In the same book, Westley (2001) presented an equally incisive analysis of a sequence of decisions and actions taken in specific examples of problem solving by a resource manager. Figure 9 provides an example of the kind of analysis that is possible.

Such transformations across scales are qualitatively different from the incremental changes that occur during the growth phase of the adaptive cycle. They are also qualitatively different from the potentially more extreme changes and frozen accidents that can occur during the more revolutionary shift from creative destruction (Ω) to renewal (α). These transformations cascade and transform the whole panarchy along with its constituent adaptive cycles.

Because a unique combination of separate developments has to conspire to occur simultaneously, extreme events are rare. Some developments emerge within adaptive cycles during the back loop of the cycle, when recombinations and external

Table 2. Summary Findings from the Assessment of Resilience in Ecosystems, Economies, and Institutions

Statement	Brief Explanation
Multistable states are common in many systems.	Abrupt shifts among a multiplicity of very different stable domains are plausible in regional ecosystems, some economic systems, and some political systems.
The adaptive cycle is a fundamental unit of dynamic change.	An adaptive cycle that aggregates resources and that periodically restructures to create opportunities for innovation is a fundamental unit for understanding complex systems, from cells to ecosystems to societies to cultures.
Not all adaptive cycles are the same and some are maladaptive.	Variants to the adaptive cycle are present in different systems. These include physical systems (because of the absence of mutations of elements), ecosystems strongly influenced by external pulses, and human systems with foresight and adaptive methods to stabilize variability. Some systems are maladaptive and trigger poverty and rigidity traps.
Sustainability requires both change and persistence.	We propose that sustainability is maintained by relationships that can be interpreted as a nested set of adaptive cycles arranged as a dynamic hierarchy in space and time—the panarchy.
Self-organization shapes long-term change.	Self-organization of ecological systems establishes the arena for evolutionary change. Self-organization of human institutional patterns establishes the arena for future sustainable opportunity.
There are three types of learning.	Panarchies identify three types of change, each of which can generate a different kind of learning: (a) incremental (r to K , Figure 4), (b) lurching, (Ω to α , Figure 4), and (c) transforming.
The world is lumpy.	Attributes of biological and human entities form clumped patterns that reflect panarchical organization, create diversity, and contribute to resilience and sustainability.
Functional diversity builds resilience.	Functional groups across size classes of organisms maintain ecosystem resilience.
Tractability comes from a “Rule of Hand.”	The minimal complexity needed to understand a panarchy and its adaptive cycles requires at least three to five key interacting components, three qualitatively different speeds, nonlinear causation. Vulnerability and resilience change with the slow variables; spatial contagion and biotic legacies generate self-organized patterns over scales in space and time.
Emergent behavior emerges from integrated systems.	Linked ecological, economic, and social systems can behave differently from their parts. Integrated systems exhibit emergent behavior if they have strong connectivity between the human and ecological components and if they have key characteristics of nonlinearity and complexity as suggested in the “Rule of Hand.”
Management must take surprise and unpredictability into consideration.	Managing complex systems requires confronting multiple uncertainties. These can arise from technical considerations, such as models or analytic frameworks. The examples suggest that as much complexity exists in the social dimensions as in the ecological ones and that managers must juggle shifting objectives.
Is adaptive management an answer?	For linked ecological/social/economic systems, slow variables, multistable behaviors, and stochasticity cause active adaptive management to outperform optimization approaches that seek stable targets.

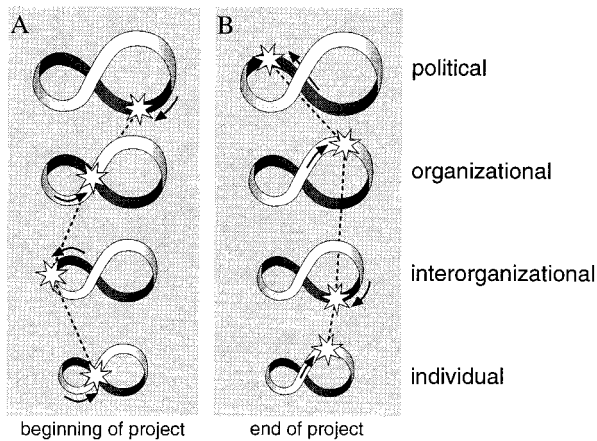


Figure 9. Separate adaptive cycles are used to depict phases of issues as interpreted in four systems—political, organizational, interorganizational, and individual. Managers' actions and solutions must account for these dynamics of these systems (Westley 2001). (Reprinted from Gunderson and Holling 2001 with permission of Island Press)

influences can generate unexpected new seeds of opportunity that can nucleate and modify the subsequent phase of growth. So long as connections are maintained with other levels, those innovations are contained and do not propagate to other levels.

But if these recombinations and inventions accumulate independently in a number of adjacent levels, a time will come when the phases of several neighboring cycles become coincident, and each becomes poised as an accident waiting to happen in a shift from Ω to α . Windows open that can then allow those independent inventions and adaptations to interact, producing a cascade of novel self-organized patterns across a panarchy and creating fundamental new opportunity. There is an "alignment of the stars." Such a coincidence in phases of vulnerability at multiple scales is quite rare. That is, true revolutionary transformations are rare, whether in systems of people or systems in nature.

Under conditions of crisis in a region, the elements of a prescription for facilitating constructive change are as follows:

- Identify and reduce destructive constraints and inhibitions on change, such as perverse subsidies.
- Protect and preserve the accumulated experience on which change will be based.
- Stimulate innovation and communicate the results in a variety of fail-safe experiments designed to probe possible directions in a way that is low in costs in terms of human careers and organizational budgets.

- Encourage new foundations for renewal that build and sustain the capacity of people, economies, and nature to deal with change.
- Encourage programs to expand an understanding of change and communicate it to citizens, businesses, and people at different levels of administration and governance, engaging them in the process of change.

A principal conclusion from the Resilience Project is that the era of ecosystem management via incremental increases in efficiency is over. We are now in an era of transformation, in which ecosystem management must build and maintain ecological resilience as well as the social flexibility needed to cope, innovate, and adapt.

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