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2

Models and Metaphors of Sustainability, Stability, and Resilience

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Humans are dependent upon natural systems for the necessities of life, such as air and water, as well as for resources that are essential to modern societies (Odum 1993). As humans have imposed greater and greater demands upon natural systems, Arrow et al. (1995) and many others have raised concerns about the sustainability of the resource flows from these systems. The purpose of this exposition is to review some theoretical concepts and present specific examples to illustrate the variety of possible behaviors that natural systems may display under exploitation. The concepts stem from our informal understanding of the ideas of stability, sustainability, and resilience, but clarity requires a more detailed classification of behaviors. The examples that we present do not exhaust the supply of possible behaviors, but each is “generic,” in the mathematical sense that small changes in parameter values do not change the qualitative behavior of the system. This implies that the qualitative behavior of each example is typical of a whole class of systems.

Equilibrium

A mechanical system is at equilibrium if the forces acting on it are in balance. For example, when a body floats, the force of gravity is balanced by the buoyant force due to displacement of the liquid. The “balance of nature” (Pimm 1991) is an extension of this idea to the natural world. The concept usually refers to steady flows of energy and materials rather than to systems whose components do not change.

Resilience and Stability

We are interested in characterizing natural systems that are resilient, or, in other words, that tend to maintain their integrity when subject to disturbance (Holling 1973). This is related to the idea of stability. The informal concept of stability refers to the tendency of a system to return to a position of equilibrium when disturbed. If a weight is added suddenly to a raft floating on water, the usual response is for the weighted raft to oscillate, but the oscillations gradually decrease in amplitude as the energy of the oscillations is dissipated in waves and, eventually, in heat. The weighted raft will come to rest in a different position than the unweighted raft, but we think of the new configuration as essentially the same as the old one. The system is stable.

If we gradually increase the weight on the raft, eventually the configuration will change. If the weight is hung below the raft, the raft will sink deeper and deeper into the water as more and more displacement is required to balance the higher gravitational force. Eventually, the buoyant force cannot balance the gravitational force and the whole configuration sinks: the system is no longer stable. On the other hand, if the weight is placed on top of the raft, the raft may flip over suddenly and lose the weight and its other contents long before the point at which the system, as a whole, would sink. This sudden loss of stability may be more dangerous than the gradual sinking, because there may be little warning or opportunity to prepare for it. We may think of the raft system as losing its resilience as more weight is placed on it.

Suppose that we accept the "balance of nature" and the steady flows of resources that it implies. As we demand more and more products of natural systems, and as we load these systems with more and more of our waste products, are we likely to experience a gradual loss of stability or a sudden one? In order to clarify such questions, we must refine our terminology. To decide whether a system is stable or not, we must first specify what we mean by a change in configuration or loss of integrity. If we don't care whether the raft flips over when weighted, then there is no problem of sudden loss of stability for the floating raft. We must also specify the types and quantities of disturbances that may affect the system. Suppose that a fixed weight is placed on top of an occupied raft. If the occupants of the raft move about, the raft may float at a slightly different angle, but if they move too far or all at once, the raft may tip. The range of possible movements of the occupants that do not lead to tipping is called the *domain of stability*, or *domain of attraction*, of the upright state. If the amount of the fixed weight is gradually increased, the balance becomes more precarious and, hence, the domain of attraction will shrink. Eventually, the weight becomes large enough so that there is no domain of attraction at all, and the raft will flip over no matter what its occupants do.

The preceding example makes a distinction between the weight loading the raft and the positions of the occupants. If the amount of the weight changes very slowly or not at all, we may think of the "system" as consisting of the raft and weight. The occupants change position relatively quickly, and these changes may be thought of as disturbances of the system. On the other hand, we may adopt a more comprehensive point of view, seeing the raft, the weight, and the occupants as a single system. If the occupants organize themselves to anticipate and correct for external disturbances, then the system may be able to maintain its integrity long enough for them to achieve their objectives. Another possible response to disturbance might be to restructure the raft itself. If it were constructed of several loosely coupled subunits, then excessive weighting or a strong disturbance might flip one part of the system but leave the rest intact. Such a structure might not require as much vigilance to maintain as the single raft, and it might be able to withstand a greater variety of external disturbances. On the other hand, if the bindings that link the subunits become stiff, then the structure may become brittle and, hence, more prone to failure. This simple example illustrates how the notion of resilience of a system depends upon our objectives, the time scale of interest, the character and magnitude of disturbances, the underlying structure of the system, and the sort of control measures that are feasible.

The section that follows presents the main ideas of stability and resilience for simple, one-dimensional prototype systems. Calculations can be done explicitly for these prototype systems, but their qualitative behavior holds for much more complicated examples. The third section in this chapter illustrates the ideas of bistable equilibria, hard loss of stability, hysteresis, and resilience, with a model for the spruce budworm. There are qualitative similarities between the behavior of the budworm model and a variety of ecological systems, particularly lake ecosystems, the Baltic Sea, and boreal forests, although no attempt is made here to provide a formal model for these systems. Such a model is given in the fourth section, for a competitive grazing system. This system has qualitative behavior analogous to a one-dimensional model, and it also exhibits hysteresis and hard loss of stability. An analogous system that involves fire as a regulating process is presented in the fifth section. The latter system also exhibits regular oscillations. The Appendix presents a detailed account of the relationship between return times for a disturbed system and its resilience. There are two conflicting definitions of resilience, which may cause some confusion. The definition of Pimm (1991) applies only to behavior of a linear system or behavior of a nonlinear system in the immediate vicinity of a stable equilibrium where a linear approximation is valid. For Pimm, loss of resilience is due to slow dynamics near a stable equilibrium. The definition of Holling (1973), which we use in this volume,

refers to behavior of a nonlinear system near the boundary of a domain of attraction. Loss of resilience, in our sense, is associated with slow dynamics in a region that separates domains of attraction.

A Simple Prototype for Stability and Resilience

In order to understand complicated systems, it is often convenient to consider a simpler system that exhibits the type of behavior of interest. A full theory of the floating raft would require a combination of the theories of hydrodynamics and of rigid body dynamics, but the essential features can be captured in a one-dimensional model. We are mainly concerned with the notion of stability and the fact that the domain of attraction of a stable equilibrium may depend upon slowly varying parameters. These features are present in a one-dimensional system.

Global Stability

The concept of the balance of nature might be taken to imply that the system will maintain its integrity under any sort of perturbation. Such an assumption may be made (often unconsciously) when we make large modifications to natural systems. Our expectation is that things will proceed more or less as before and that the response of the system will be approximately proportional to the perturbation. Such behavior is shown by the simplest linear models. Some might argue that a principle of parsimony dictates that such models be used in the absence of strong evidence to the contrary. The following linear model illustrates the property of global stability, which implies that the system will always return to a certain equilibrium regardless of how far it is displaced from that equilibrium.

Suppose that the dynamics are given by a relation of the form

$$\frac{dx}{dt} = h(\alpha) - x \quad (2.1)$$

where $h(\alpha)$ is a smoothly varying function of an external variable α and x is the quantity of interest. Then $dx/dt = 0$ if $x = h(\alpha)$; the system has a single equilibrium there. This equilibrium is stable, since $dx/dt > 0$ if $x < h(\alpha)$ and $dx/dt < 0$ if $x > h(\alpha)$. These relations imply that the system approaches the equilibrium, no matter what the starting point.

A system such as equation (2.1) cannot fail us or surprise us. It returns to an equilibrium, no matter how far it is displaced, and the position of the equilib-

rium changes smoothly with the exogenous variable α . Such a system is not suitable for a discussion of possible collapses of natural systems, since such collapses are excluded by assumptions such as equation (2.1). Mathematical theory provides numerous examples of different behavior, and our goal is to investigate their plausibility. Unfortunately, much theory (including most economic theory) has been based upon assumptions analogous to equation (2.1). In particular, "resilience" has been defined by Pimm (1991) in terms of the system equation (2.1), and this very special assumption may mislead the unwary. There is a mathematical theory that shows that systems such as (2.1) are good approximations to general systems with a stable equilibrium, but that theory implies that the approximation holds only in the immediate vicinity of the equilibrium: the approximation is valid only locally. Details are provided in the appendix.

Bifurcation

In order to explore the differences between local and global stability, we must examine nonlinear models, meaning models in which the state variable appears in functions more complicated than linear ones. The following example has three equilibria instead of a single one. Such a complication requires a cubic or more complicated dependence upon the x variable, for example equation (2.2).

$$\frac{dx}{dt} = f(x) = x(x^2 - \alpha) \quad (2.2)$$

Here, α is a parameter or a slowly varying quantity whose dynamics are not of immediate concern. The equilibria of the system are the states where $f(x) = 0$. These are the states where either of the two factors in equation (2.2) vanishes. Hence, they are points where

$$x = 0 \quad \text{or} \quad x^2 = \alpha \quad (2.3)$$

If $\alpha > 0$, then there are three equilibria (equation [2.4]):

$$x = 0, \quad x = \sqrt{\alpha}, \quad \text{or} \quad x = -\sqrt{\alpha} \quad (2.4)$$

If $\alpha \leq 0$, then there is only the single equilibrium at $x = 0$. Such a change in the configuration or stability of equilibria is called a *bifurcation* (Guckenheimer and Holmes 1983). It implies a change in the qualitative behavior of the system. To explore this feature, we must discuss some additional concepts.

Local Stability and Domain of Attraction

In order to determine the stability of equilibria, it suffices to examine the sign of the velocity of x . For example, if $\alpha < 0$, the second factor in equation (2.2) is always positive and, hence, $dx/dt > 0$ if $x > 0$, and $dx/dt < 0$ if $x < 0$. In this case, the system always moves away from the state where $x = 0$. We conclude that the equilibrium at $x = 0$ is unstable if $\alpha < 0$. On the other hand, if $\alpha > 0$, then dx/dt changes sign at three places:

$$\frac{dx}{dt} > 0 \text{ if } x > \sqrt{\alpha} \quad (2.5)$$

$$\frac{dx}{dt} < 0 \text{ if } 0 < x < \sqrt{\alpha} \quad (2.6)$$

$$\frac{dx}{dt} > 0 \text{ if } -\sqrt{\alpha} < x < 0 \quad (2.7)$$

$$\frac{dx}{dt} < 0 \text{ if } x < -\sqrt{\alpha} \quad (2.8)$$

The equilibrium where $x = \sqrt{\alpha}$ is unstable, because the system always moves away from that point if nearby (according to equations [2.5] and [2.6]). Similarly, the equilibrium where $x = -\sqrt{\alpha}$ is unstable (according to equations [2.7] and [2.8]). On the other hand, the equilibrium where $x = 0$ is stable (according to equations [2.6] and [2.7]), because the motion from nearby points is toward that point. However, if the system starts outside the interval $(-\sqrt{\alpha}, \sqrt{\alpha})$, it moves away from the equilibrium at $x = 0$. Therefore, the equilibrium at $x = 0$ is locally stable, but not globally stable. The system returns to $x = 0$ if small perturbations are made, but larger perturbations take the system into an unstable domain. The interval $(-\sqrt{\alpha}, \sqrt{\alpha})$ is called the *domain of attraction* of the point $x = 0$, because trajectories that start within that interval eventually return to $x = 0$, but not those that start outside.

It is clear that the domain of attraction of the stable equilibrium at $x = 0$ shrinks as α decreases toward zero. The three equilibria collapse into one where $\alpha = 0$, and only a single unstable equilibrium remains when $\alpha < 0$. This information is summarized in figure 2.1. The diagram looks like a branch, and, for this reason, it is called a *bifurcation diagram*. The domain of attraction of the point $x = 0$ is contained within the two curved branches, and there is no other domain of attraction.

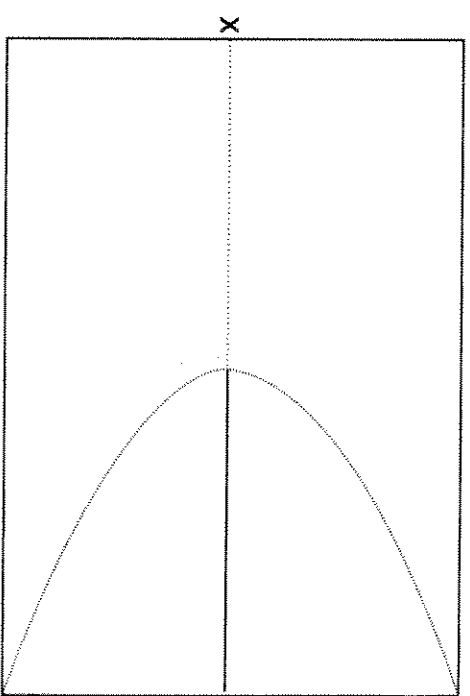


Figure 2.1. The parameter α is plotted on the horizontal axis and the corresponding equilibria in x for equation (2.2) are plotted on the vertical axis.

Disturbances and Slow Parameter Changes

We have seen that if $\alpha > 0$ then this system approaches the stable equilibrium at $x = 0$ if it is started within the domain of attraction. If we envisage disturbances that displace the system a distance x_1 from the stable equilibrium, they will not affect the integrity of the system (its tendency to return to the 0 state) as long as $x_1^2 < \alpha$. Now, if we allow the parameter α to decrease slowly toward x_1^2 , the system will take longer and longer to return to the state $x = 0$ when x is displaced to x_1 because motion is very slow near $x = \sqrt{\alpha}$, and a disturbance of magnitude x_1 may take the system into the region of slow dynamics. We may think of the decrease in α as causing a loss of resilience, because the integrity of the system is threatened more and more by disturbances of a given magnitude. A symptom of loss of resilience may be that it takes longer and longer to return to the vicinity of $x = 0$ after disturbance. The connection between return times and resilience is not completely straightforward; we address it in some detail in the appendix.

Two Domains of Attraction

The preceding system is not a believable model for natural systems, because it predicts that the state variable may approach infinity under some circumstances.

A more plausible scenario is one in which the system may change from having a single stable equilibrium to one with two stable equilibria. We next consider a number of such “bistable” systems.

We obtain a simple prototype for such systems by changing the sign of dx/dt in equation (2.2). If the direction of time is reversed, the stable and unstable equilibria are interchanged. If $\alpha < 0$, then the single equilibrium at $x = 0$ is globally stable; the system always returns to that equilibrium no matter where it starts. Instead of two unstable equilibria when $\alpha > 0$ (as in the former case), there will be two stable equilibria. The new system is

$$\frac{dx}{dt} = -f(x) = -x(x^2 - \alpha) \quad (2.9)$$

If $\alpha > 0$ for this system, we have

$$\frac{dx}{dt} < 0 \text{ if } x > \sqrt{\alpha} \quad (2.10)$$

$$\frac{dx}{dt} > 0 \text{ if } 0 < x < \sqrt{\alpha} \quad (2.11)$$

$$\frac{dx}{dt} < 0 \text{ if } -\sqrt{\alpha} < x < 0 \quad (2.12)$$

$$\frac{dx}{dt} > 0 \text{ if } x < -\sqrt{\alpha} \quad (2.13)$$

If $x > 0$ initially, then x heads toward the equilibrium at $x = \sqrt{\alpha}$, but if $x < 0$ initially, then x heads toward the equilibrium at $x = -\sqrt{\alpha}$. Thus, the domain of attraction of the point $x = \sqrt{\alpha}$ is the positive x -axis, and the domain of attraction of $x = -\sqrt{\alpha}$ is the negative x -axis. Each of the stable equilibria is locally stable, but not globally stable. This system can be flipped from one stable state to another by crossing the unstable line where $x = 0$. Because this line separates the two domains of attraction, it is called a *separatrix*. The equilibria in x are plotted in figure 2.2.

Increasing evidence has accumulated for the existence of multistable states in nature: coral reefs (Done 1992; Hughes 1994; McClanahan et al. 1996), African rangelands (Dublin et al. 1990), shallow lakes (Schindler 1990; Carpenter and Levitt 1991; Scheffer et al. 1993; Carpenter et al. 1999), kelp forests (Estes and Duggins 1995), and grasslands (D'Antonio and Vitousek 1992; Zimov et al. 1995).

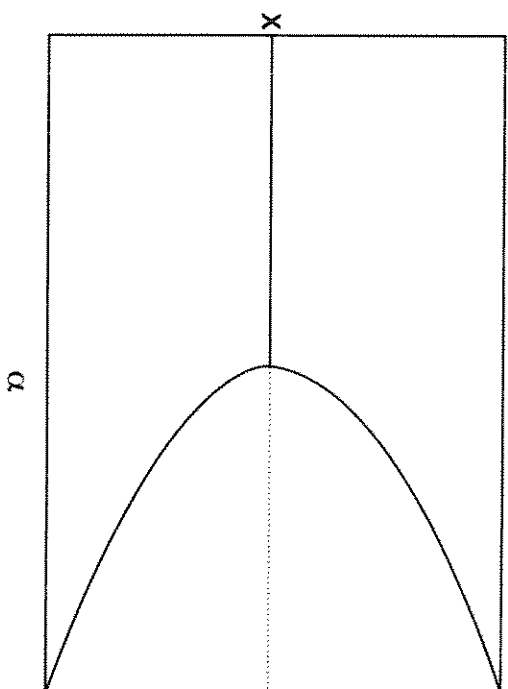


Figure 2.2. Equilibria in x for equation (2.9) are plotted against α , as in figure 2.1.

Disturbances and Slow Parameter Changes

The bifurcation diagram in figure 2.2 implies a great deal about the response of the system to disturbance. If $\alpha < 0$, then the system will return to the stable equilibrium at $x = 0$ no matter how large the disturbance—there is nowhere else for it to go. However, if $\alpha > 0$, and the system starts near the lower branch, it will tend to return there if displaced by a small amount. As α decreases toward zero, the distance between the stable equilibria and the unstable one decreases. Hence, disturbances of a given magnitude take the system closer and closer to the unstable equilibrium. Dynamics are slow near the unstable equilibrium and, hence, the time to return to the vicinity of the lower branch increases sharply for trajectories that approach the unstable equilibrium. This point about return times can be made precise by a calculation analogous to that given in the appendix.

For a higher level of disturbance and $\alpha > 0$, the system may be moved across the separatrix at $x = 0$ and may approach the upper branch of stable equilibria. Under a random pattern of disturbances, we may expect to see the system spend long periods of time in the vicinity of one or the other of the stable equilibria. Every now and then, the random disturbances may combine and send the system to the other stable equilibrium. The *Allee effect* studied by ecologists pro-

vides an example of a bistable system. A population may suffer reduced survival or reproductive success at low numbers. For example, schooling fishes tend to suffer low per capita mortality if their numbers are high enough relative to the capacity of their predators. If such fish are reduced in numbers through fishing pressure or environmental degradation, the population may decline and eventually become extinct locally. On the other hand, a large population may sustain itself over long periods. Dynamics of this sort might explain the occasional flips between dominance of sardine and anchovy as revealed by deposits of their scales off the coast of California. A similar pattern appears in such geophysical features as the polarity of the earth's magnetic field, the ocean circulation involving the Gulf Stream, and climate fluctuations, but some of these fluctuations may be too regular to be completely random. For larger values of α one would expect flips from one equilibrium to the other to be extremely rare. Thus, we may associate an increase in α with an increase in resilience.

Hard Loss of Stability and Hysteresis

The two preceding examples illustrate a so-called *soft loss of stability*. As the exogenous variable changes, the location of the stable equilibria changes smoothly. The state variable may move from one domain of attraction to another, but such changes are slow because dynamics are slow near an unstable equilibrium or a separatrix. The possibility of such behavior would not ordinarily be cause for alarm, because slow dynamics may allow for adjustments to new behavior. There are natural systems, such as outbreaking insect populations, that sometimes show more abrupt changes.

The following model was used by Ludwig et al. (1978) to understand the dynamics of the spruce budworm. The quantity B represents budworm density, measured in larvae per acre. This density is assumed to vary in time according to equation (2.14):

$$\frac{dB}{dt} = r_b B \left(1 - \frac{B}{K_b}\right) - \beta \frac{B^2}{\alpha^2 + B^2} \quad (2.14)$$

where r_b is an intrinsic growth rate at low densities, K_b is a carrying capacity for the budworm in the absence of predation, and the second term in equation (2.14) is a predation rate. The predators are assumed to have a Holling type-III functional response, with a maximum predation rate of β and a half-saturation budworm density of α . This functional form implies that predators have their greatest influence upon dynamics at intermediate ranges of budworm densities. At low densities, the predators search for alternate prey because returns from for-

aging for budworm are relatively low. At high densities, budworms swamp their predators; thus, the predators have a small per capita effect, just as predators have a small per capita effect on large schools of fish. The parameter α is proportional to a measure of foliage density, because the predators search foliage for the budworms and their response is mediated by the number of budworms per unit of foliage. Hence, α is actually a state variable that generally changes on a slower time scale than that of the budworm. For the moment, we regard α as a constant.

Some algebra supplied in Ludwig et al. (1978) shows that there are either two or four equilibria for the budworm, depending upon the sizes of the dimensionless parameters R and Q , given by relations in equation (2.15).

$$R = \frac{r_b \alpha}{\beta}, \quad Q = \frac{K_b}{\alpha} \quad (2.15)$$

These equilibria satisfy equation (2.16),

$$R \left(1 - \frac{b}{Q}\right) - \frac{b^2}{1 + b^2} = 0 \quad (2.16)$$

where $b = B/\alpha$. The equilibrium $b = 0$ is always unstable, because $db/dt > 0$ if b is small and positive. The highest equilibrium is always stable, because $db/dt < 0$ if b is very large and positive. Thus, if there are only two equilibria, budworm density always moves toward the upper equilibrium. When there are four equilibria, they alternate in stability. A typical case is shown in figure 2.3. If R is between R_1 and R_2 , then b may approach either the high equilibrium or the low equilibrium, depending upon whether the starting position of b is above or below the unstable equilibrium, which is the separatrix.

Hard Loss of Stability

Imagine that the parameter α begins at a low value and gradually increases as the forest grows. It turns out that Q does not change with forest growth; hence, figure 2.3 applies. Because R is proportional to α , R will increase. At first (when $R < R_1$), budworm numbers will remain low, since the only stable equilibrium is the low one. Even when R increases beyond R_1 , the budworm numbers will remain low, because they lie below the unstable equilibrium, which determines the domain of attraction of the low equilibrium. The stability of the low equilibrium becomes precarious as R approaches R_2 , because the domain of attraction shrinks. Finally, at $R = R_2$, the lower two equilibria disappear and budworm density jumps to the high value: an outbreak occurs. This abrupt change

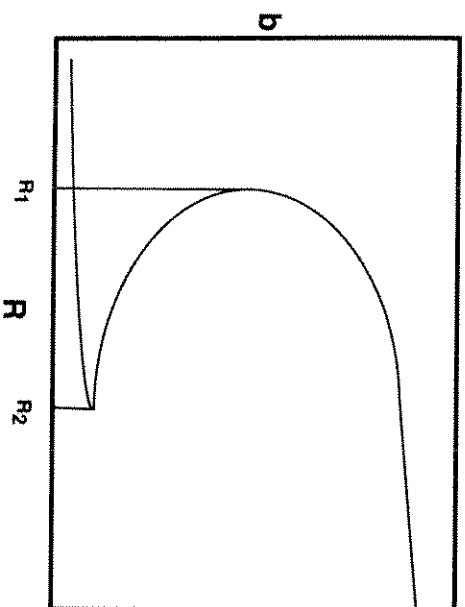


Figure 2.3. The equilibria in b for equation (2.16) are plotted against R for $Q = 20$.

in the attracting state is called a *hard loss of stability*. It should be contrasted with the soft loss of stability displayed by the system in equation (2.9). In the case of the budworm, once density has reached the high equilibrium there is no easy way to reduce it to the lower equilibrium. If the variable R is reduced below R_2 , the budworm remains at the high equilibrium. As R is further reduced, there is a second hard loss of stability as R declines below R_1 . In this case, there is a jump down to the low equilibrium, which is not reversed as R increases again.

Hysteresis and Cycles

If we now connect the dynamics of the trees and the dynamics of the budworm, a new phenomenon appears. If the system starts with low foliage density and low budworm numbers, the foliage density slowly increases until it surpasses R_2 . At this point, an outbreak occurs, as shown previously. High budworm numbers eventually cause death of trees, so R begins to decrease when the budworm has an outbreak. Budworm numbers remain high even though R declines, because budworm density lies above the separatrix. As R continues to decline to R_1 , budworm density declines slowly and then jumps to a low value when R decreases below R_1 . The different paths followed by the total system for increasing versus decreasing R constitute the *hysteresis effect*. The combination of budworm and

forest dynamics produces stable cycles with long periods. Such stable cycles that are maintained through alternations of rapid transitions and slow changes are called *relaxation oscillations*. They are common in many physical, chemical, and physiological systems (Edelstein-Keshet 1988).

Disturbances and Resilience

If the objective of management is to keep budworm numbers and foliage damage low, the loss of stability as R increases beyond R_2 may be regarded as a loss of resilience. This model suggests that small disturbances near the lower stable equilibrium may exhibit long return times if they approach the unstable branch. Such long return times may be a useful diagnostic indicator. However, because R increases as trees grow, a loss of stability accompanied by a budworm outbreak seems inevitable.

We may adopt a different perspective and regard periodic budworm outbreaks as part of a stable system that renews the forest from time to time. Indeed, systems analogous to the budworm-forest system frequently appear as stable oscillators. The advantage of such oscillators is that they continue to oscillate more or less with the same frequency and amplitude under a wide variety of disturbances. Hence, physiological oscillators are important in maintaining integrity of the organism, which is another kind of resilience. According to this perspective, an attempt to halt the oscillations may lead to a disastrous breakdown in the long term. Will human interventions to increase productivity in natural systems suffer a similar fate?

Lake Dynamics

Carpenter and Cottingham (chapter 3, and 1997) have discussed the applicability of these ideas to lake ecosystems. They characterize lake dynamics as either "normal" or "pathological." Normal lakes have high numbers of game fish, effective grazing upon phytoplankton, and low incidence of algal blooms. The normal system maintains its integrity when subjected to perturbations such as phosphorus pulses, because phosphorus moves rapidly into the higher trophic levels (Carpenter and Kitchell 1993) and humics constrain algal growth (Jones 1992). However, heavy phosphate loading, removal of macrophytes, overfishing, and removal of wetlands and riparian vegetation may lead to the pathological state in which there are few game fish, less grazing, no macrophytes, and extensive and frequent algal blooms (Harper 1992). This may be a rapid transition and it is not easily reversed (National Research Council 1992).

This situation appears to fit the definition of a hard loss of stability, because the change is rapid and large, and is sometimes not reversed even if phosphate loads are decreased (National Research Council 1992). One may say that the normal lake is resilient because it maintains its integrity under perturbation, but resilience is lost as phosphate loading and other stresses are increased. If critical levels of phosphate and other environmental variables could be identified, we might attempt to measure resilience in terms of the difference from the critical levels (Vollenweider 1976). Perhaps the question of whether or not the lake ecosystem fits our definitions may be answered by statistical analysis of long-term data.

The Baltic Sea

Jansson and Jansson (chapter 4) and Jansson and Velner (1995) describe the Baltic system in terms that show many similarities to the lake system. The Baltic Sea is partially enclosed and, consequently, has a residence time of water on the order of twenty years. Algae form the base of a diverse food web, with higher trophic levels occupied by commercially important species such as herring, flounder pike, and perch. There may be long periods when there is weak vertical mixing of the water column due to lack of inflow from the North Sea. During such periods, oxygen levels at greater depths may be very low and sulphur bacteria may predominate. The latter put large quantities of phosphorus into solution, which then upwell and cause plankton blooms.

In historical times, the Baltic has experienced several extended anoxic periods, but the system had not been permanently altered. Since the industrial revolution, the Baltic has been loaded with increasing amounts of phosphorus, and there are indications of a change of configuration to a detritus-based system. This would imply more turbid water and a fish community consisting mainly of sluggish species such as bream, roach, and ruffe, which are much less valuable than those previously listed. The possibility exists that the Baltic might reach a point at which even reducing phosphate inputs might not return the system to its earlier, more desirable state. Such a turn of events would correspond to a hard loss of stability, analogous to the behavior of the lake ecosystem. Unfortunately, there are no replicates of the Baltic system; hence, we have only analogies to guide action. A purposeful demonstration that the Baltic is actually capable of a sudden change corresponding to a hard loss of stability is unthinkable as an experiment. Nevertheless, it may be occurring as a result of human negligence. The earlier ability of the Baltic to recover from anoxic periods may correspond to resilience, but we cannot be sure whether this resilience is being lost.

The Boreal Forest

Carpenter et al. (1978) characterize the boreal forest as a system with relatively few species and complicated interactions and dynamics. In upland regions, forests dominated by aspen and birch alternate with forests dominated by spruce and fir. Browsing by moose over a period of twenty to forty years can convert an aspen stand into one dominated by conifers. As stands of conifers mature, they become increasingly favorable for reproduction of the spruce budworm. Eventually, outbreaks occur and portions of the system are converted into early successional aspen. The budworm outbreak corresponds to a hard loss of stability, and the combined upland system undergoes stable, long-period oscillations analogous to those described previously.

As the upland regions undergo these oscillations, the valley bottoms alternate between flooded plains and moist meadows. The flooded state is maintained by beavers, which cut aspen bordering streams for food and dam the streams to create ponds. When the supply of aspen is insufficient, the beavers abandon their dams, the dams break, and the ponds are soon replaced by meadows. This relatively rapid change, a consequence of decreasing supply of aspen, may be thought of as a hard loss of stability. The upland and lowland cycles tend to entrain each other because of the interaction between beavers and aspen. Fires also play a role in synchronizing cycles over large spatial areas, because conifers killed by the spruce budworm provide an abundance of fuel.

Although this system undergoes large alterations, sometimes very quickly, it may be thought of as resilient, maintaining its character over many centuries. Conditions at any given site may change abruptly, but the system is usually a mosaic of patches at differing stages of the cycle. When considered as a whole, it maintains considerable diversity.

A Competitive Grazing System

In this section, we describe a natural system that may be bistable. Competition between grasses and woody vegetation in a semi-arid environment is described in chapter 7 and in Walker et al. (1981). Suppose that either the grass or the woody vegetation has an advantage when at high densities relative to the other. In such a case, the system has stable equilibria that correspond to high levels of grass and woody vegetation, respectively. The competition is also influenced by the stocking rate of cattle, which consume grass but not woody vegetation. We shall regard the two plant forms as the dynamic state variables and the stocking rate as a slowly varying parameter.

Imagine starting with high levels of grass and low levels of woody vegetation.

At low levels of stocking, there is only a small difference from the ungrazed system: if the system starts out with grass dominant, grass will continue to dominate. As stocking increases, the competition may favor woody vegetation. Eventually, there may be a collapse of the grass, and woody vegetation will dominate. Thus, the effect of grazing is to move the system from a state in which grass dominates to one in which woody vegetation dominates. Even when grazing pressure is relaxed, there may be little change in composition, because of the advantage enjoyed by woody vegetation over grass when the former is dominant. The effect of grazing is to move the system into the domain of attraction of woody vegetation for the ungrazed system.

If one plots grass density versus the stocking level, the behavior may appear to be inexplicable: the grass level declines as grazing increases but does not return to former levels when grazing returns to its former level. The apparent paradox is resolved if we realize that the density of grass depends not only on the stocking level, but also on competition with woody vegetation. These phenomena may be illustrated by a modification of the Lotka-Volterra competition model.

Let g represent the density of grass, and let w represent the density of woody vegetation. The rate of change of grass density is assumed to be represented in equation (2.17).

$$\frac{dg}{dt} = r_g g (1 - s - c_{gg} g - c_{wg} w) \quad (2.17)$$

In equation (2.17), r_g is a growth rate, and c_{gg} and c_{wg} are competition coefficients. The parameter s is determined by the stocking rate of cattle. The rate of increase of the woody vegetation is assumed to be represented by equation (2.18).

$$\frac{dw}{dt} = r_w [a + w (1 - c_{gw} g - c_{ww} w)] \quad (2.18)$$

In equation (2.18), r_w is a growth rate, c_{gw} and c_{ww} are competition coefficients, and a is a source term. In the illustrations that follow, the parameters were chosen as indicated in equation (2.19).

$$r_w = 1, \quad r_g = 1.5, \quad c_{gg} = 7, \quad c_{wg} = 1, \quad c_{gw} = 2, \quad \alpha = .03, \quad c_{ww} = 1 + a \quad (2.19)$$

The case of light grazing corresponds to $s = 1/10$.

In order to understand the behavior of this system, it is helpful to plot some curves in the g - w plane, as in figure 2.4. In the phase plane, the direction and

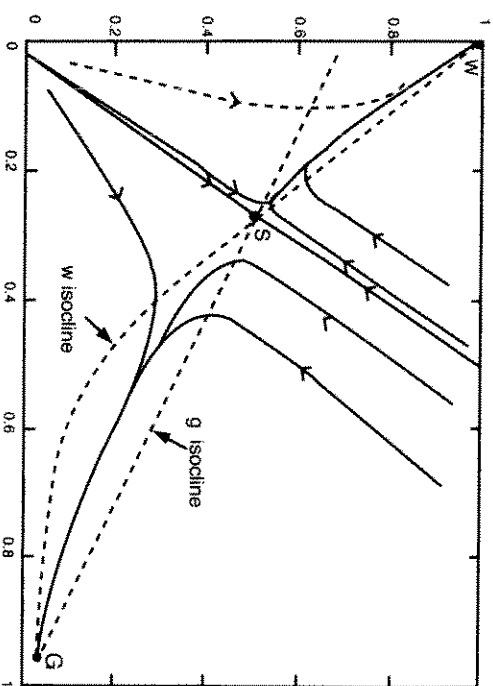


Figure 2.4. The phase plane for grass and trees derived from equations (2.17)–(2.19).

speed of change of the system are given by the vector $(dg/dt, dw/dt)$. This vector is vertical on the curve where $dg/dt = 0$ (the null g isocline), and it is horizontal on the curve where $dw/dt = 0$ (the null w isocline). As can be seen, $dg/dt = 0$, where either $g = 0$, or the relationship holds in equation (2.20):

$$c_{gg} g + c_{wg} w = 1 - s \quad (2.20)$$

This locus is a straight line, and it shifts to the left as s increases. The null w isocline is a hyperbola according to equation (2.18). One of the asymptotes is the w -axis, and the locus passes through the point $g = 0, w = 1$, labeled "W." This locus is independent of the stocking parameter s . Figure 2.4 shows in detail how a system may approach more than one steady state, depending upon the starting conditions. Although this system is much more complicated than equation (2.9), its qualitative behavior is the same if $\alpha > 0$. This illustrates how the very simple one-dimensional models may, nevertheless, be a valuable heuristic guide.

We now turn to the effect of increased stocking. The effect of an increase in s is to shift the null g -isocline down and to the left. Hence, the points S and G will approach each other along the w null isocline. Because the separatrix passes through the point S, the domain of attraction of G must shrink, whereas the domain of attraction of W will expand. Qualitatively, the representation of fig-

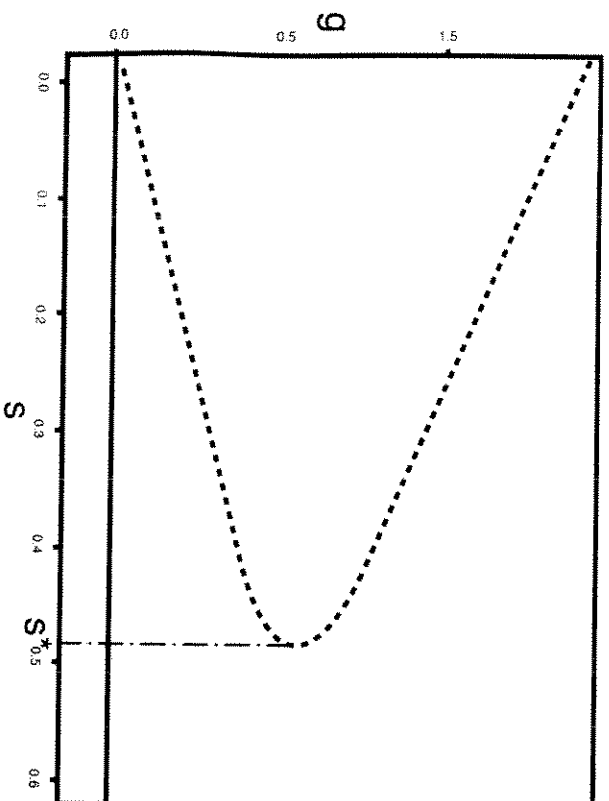


Figure 2.5. A bifurcation diagram showing grass equilibria as a function of the grazing parameter s for the system as described in equations (2.17)–(2.19).

ure 2.4 still holds. For a still-higher value, $s = s^*$ the points S and G coincide. The values of g corresponding to the roots S and G are shown in figure 2.5. A similar diagram could be drawn to show the corresponding values of w . This is a bifurcation diagram analogous to figure 2.3. If the stocking rate changes slowly, we may expect the grass density to be given by the upper curve in figure 2.5. However, if $s > s^*$, the grass density must crash, since there is no stable equilibrium with a nonzero grass density. This is a hard loss of stability, and indeed there is a striking similarity between figures 2.5 and 2.3.

For values of $s > s^*$, the qualitative form of figure 2.6 applies. The only equilibrium is point W , and all trajectories approach W . The domain of attraction of W is the whole quadrant, where $g > 0$ and $w > 0$.

We may imagine the system beginning with the stocking rate $s = 0$. According to figure 2.5, the unstable equilibrium S and the stable equilibrium W are very close together. Hence, the separatrix in a figure analogous to figure 2.4 is in the extreme upper left corner: virtually any initial combination of g and w will lead to a high density of g , given by the upper branch in figure 2.5, with a cor-

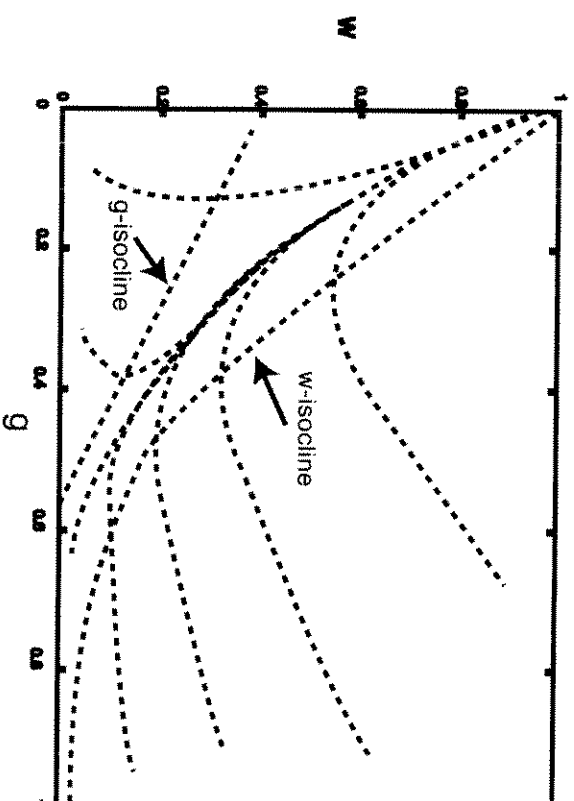


Figure 2.6. The phase plane for grass and trees for the system in equations (2.17)–(2.19), with $S = 0.6$.

respondingly small density of w . Now, if s is increased slowly, the density of g will move downward along the upper branch until the bifurcation point s^* is reached. Beyond that point, the grass density must crash, and woody plants will dominate. Even if grazing pressure is withdrawn ($s = 0$), the grass cannot recover because it will be to the left of the separatrix. This is the hysteresis effect.

Fire in a Savanna System

The preceding model does not describe most savanna systems for two reasons: (1) Generally, neither grass nor woody vegetation can completely exclude the other. Instead, there is a single stable equilibrium for the system (which changes over time, depending upon rainfall, grazing, and fire) where grass and trees coexist. (2) Woody vegetation cannot exclude grass indefinitely: after a long period of low grazing, the grass may return. This is due to a combination of two effects. First, the older woody vegetation may die and leave gaps that may be colonized by grass, and then fire gets into the system. Second, woody vegetation dies back very quickly in dry years but recovers only slowly in wet years—too slowly to use all the water. Grass, on the other hand, can increase ten-fold in a season, quickly

enough to fully use all of the available water. Because of this, the combination of wet and dry years keeps woody vegetation at lower levels than the average rain would sustain and permits grass to remain in the system in significant amounts.

When viewed at a long time scale, a brief period of grazing may cause a rapid collapse of the grass followed by a slow recovery. When viewed at a short time scale, there appears to be an equilibrium with high woody vegetation. However, when this system is viewed over a longer time scale, it is apparent that the system merely spends a long time in this state. This sort of qualitative behavior is analogous to "excitable systems." Such systems are best known as models of the nerve impulse according to the theory of Hodgkin and Huxley as modified by Fitzhugh. The system has a single stable equilibrium, but when perturbed in an appropriate direction it may undergo a very large excursion (firing of the neuron), followed by a long recovery (refractory) period. Details are given in Edelstein-Keshet (1988).

To model aging properly is complicated, but for present purposes it suffices to find a simple system that has the required qualitative behavior. We do not contend that the following model is an accurate representation of the true dynamics. We must keep track of surplus grass that may serve as fuel for fires. Hence, we let gross grass production be given by g_p as in equation (2.21).

$$g_p = r_g g + a_g \quad (2.21)$$

In equation (2.21) a_g is a source term, and r_g is the rate of grass production available for grazing. The grass not consumed by grazing cattle is potential fuel for fires and is denoted by g_f , as defined in equation (2.22)

$$g_f = g_p \exp(-s g) \quad (2.22)$$

The parameter s determines the proportion of grass consumed by cattle. Now equation (2.17) is replaced by equation (2.23).

$$\frac{dg}{dt} = g_f - g_p (c_{gg} g + c_{wg} w) \quad (2.23)$$

The dynamics of w will be influenced by fires, and the age of trees influences their susceptibility to fire. Let a new variable b denote the product of the woody plant density and the average age of the woody plants. A first approximation yields $db/dt = w$, but that relationship neglects the influence of fire on the average age. The dynamics of w and b are given by equations (2.24) and (2.25), respectively.

$$\frac{dw}{dt} = r_w w (1 - c_{gw} g - c_{ww} w) - f w + a_w \quad (2.24)$$

$$\frac{db}{dt} = w - r_f f b \quad (2.25)$$

The fire risk f is defined as follows: let the fire potential p be proportional to the available fuel as shown in equation (2.26).

$$p = \begin{cases} c_f g_f & \text{if } b > 20 \\ c_f g_f b/20 & \text{otherwise} \end{cases} \quad (2.26)$$

We assume that the fire risk f is given by equation (2.27).

$$f = p \frac{b^\alpha}{(w w_0)^\alpha + b^\alpha} \quad (2.27)$$

In equation (2.27), the parameter a_o is an age at which the fire risk is half of its maximum, and the parameter α determines the sharpness of the increase of fire risk with age. We have used $\alpha = 9$ to give a sharp increase, and $a_o = 60$. The remaining parameters are given in equation (2.28).

$$\begin{aligned} r_g &= .5, c_{wg} = .8, c_{gg} = 1, a_g = .02, c_f = .4, \\ r_w &= .3, c_{gw} = .8, c_{ww} = 1, a_w = .02 \end{aligned} \quad (2.28)$$

The stocking rate s may be chosen as a parameter or control variable. In the following, we chose $s = .5$.

Because there are three state variables in this system, one cannot make a meaningful phase plot. However, if the age variable b is fixed, we may gain an impression of the dynamics. Figure 2.7 shows how a low value of b leads the system to an equilibrium with high w . On the other hand, a higher value of b leads to an equilibrium with much lower w as shown in figure 2.8. Now, if b increases with time, the system will first have high w , then lower w as it ages. Fires decrease the average age of trees as well as their density. Hence, the system gets reset to a state analogous to that shown in figure 2.7 after a fire. The cycling of w with time in the full system, with b changing, is shown in figure 2.9.

If one were to observe this system over a time of five to twenty years, it would appear that woody plants would eventually dominate grasses because of the combination of competition and grazing. Over the next thirty years, however, the effect of fire and aging of trees leads to a collapse of the trees, making way for the next cycle. This example illustrates how the time scale over which we observe the system may have a decisive influence upon our classification of its

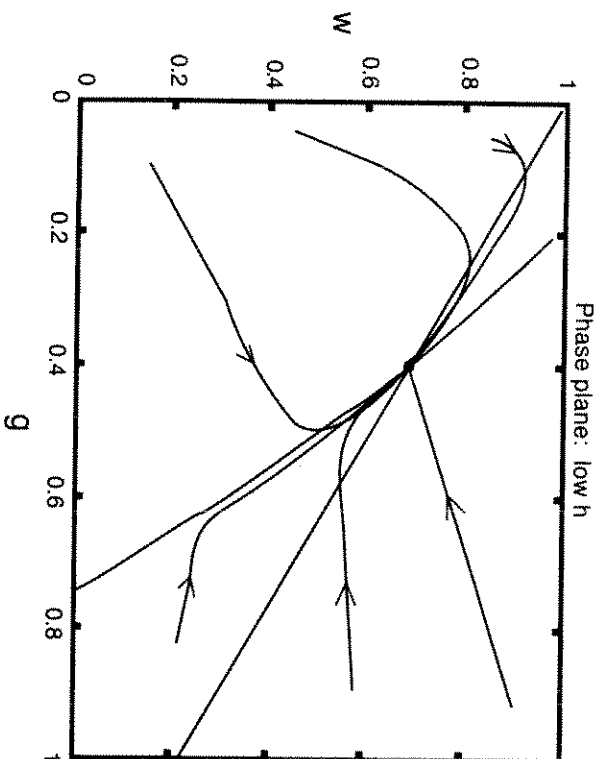


Figure 2.7. The phase plane for grass and trees for the system described in equations (2.21)–(2.28), neglecting the dynamics of the age variable h with a low value of h .

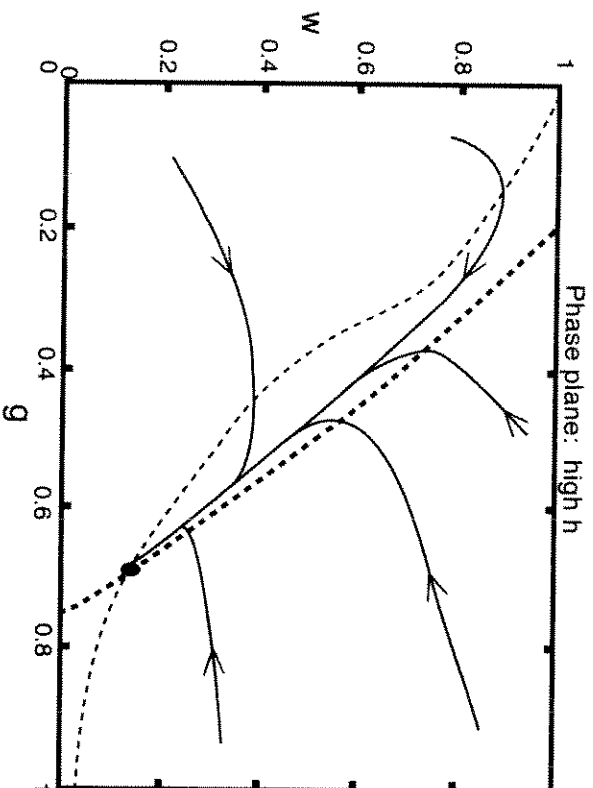


Figure 2.8. The phase plane for grass and trees for the system described in equations (2.21)–(2.28) neglecting the dynamics of the age variable h with a high value of h .

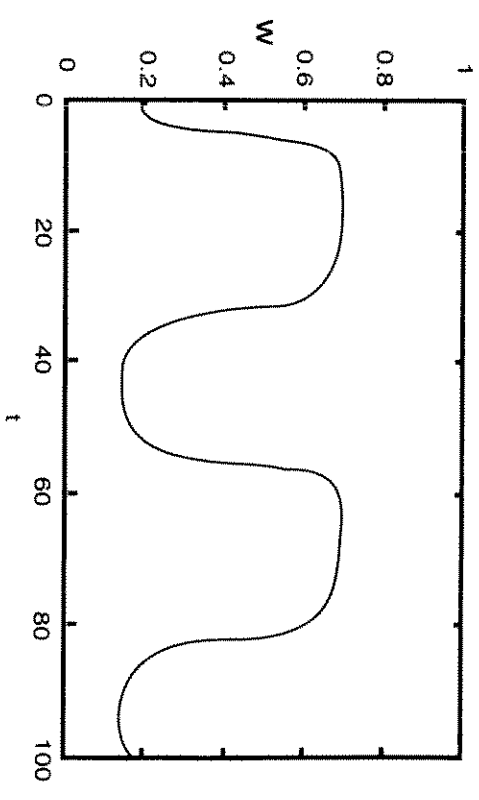


Figure 2.9. Tree density (w) versus time (t , in years) for the system described in equations (2.21)–(2.28), including dynamics for the age variable.

behavior. Unfortunately, the scale over which we are able to observe the system is often much shorter than the scale over which it exhibits its characteristic behavior.

Concluding Remarks

The examples presented here illustrate the complexity of the task facing us as we attempt to clarify the concepts of sustainability and resilience for natural systems. Mathematical theory presents a wealth of possibilities, but the limitations of our understanding and the data available make it difficult to distinguish among them.

Here, we have proceeded from simple conceptual models, such as the raft analogy, to simple but abstract mathematical models, to ecosystem analogues, and finally to a fairly detailed model of a savanna system. In no case can these analogies be considered to be complete, nor is our knowledge of the systems detailed enough to support a full-blown model with statistical justification. Perhaps one might conclude that all this is merely speculation, unworthy of serious attention. On the other hand, prudent decision making requires that we take account of a variety of plausible hypotheses about the responses to our actions. The examples presented here do not encourage complacency about the ability of natural systems to support us and our habits in the lavish fashion we have

enjoyed in the past. If we refuse to contemplate possibilities that are only dimly perceived, we may miss the opportunity to learn about the world and adapt our behavior accordingly. If we insist that the simplest and most convenient hypotheses have priority when choosing actions, we run the risk of allowing sloth and pride to bring us to disaster.

Acknowledgments

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Appendix Return Times and Resilience

It is important to distinguish between behavior near a stable equilibrium and behavior near the boundary of a domain of attraction, which is an unstable equilibrium or separatrix. As discussed in the second section of the chapter, the long return times associated with a loss of resilience are caused by slow dynamics near the unstable equilibrium, not by slow dynamics near the stable equilibrium point. Unfortunately, there are two conflicting definitions of resilience and consequent confusion about the connection between resilience and return times.

Pimm (1991 p. 13) defines resilience as "how fast a variable that has been displaced from equilibrium returns to it. Resilience could be estimated by a return time, the amount of time taken for the displacement to decay to some specified fraction of its initial value." Pimm (1991 p. 33) describes return to equilibrium by the equation (A2.1).

$$X_t - X^* = (X_0 - X^*)e^{-kt} \quad (\text{A2.1})$$

In equation (A2.1), X_t is the population density at time t , X_0 is the initial population density, and X^* is the equilibrium density. The differential equation for X_t that corresponds to this formula is given in equation (A2.2).

$$\frac{dX_t}{dt} = -k(X_t - X^*) \quad (\text{A2.2})$$

A similar model with discrete time could be given instead, but that would not alter the following argument. If we measure displacement from X^* by x , then x satisfies equation (A2.3), which is equivalent to equation (2.1) if $h(\alpha) = x$ is replaced by x .

$$\frac{dx}{dt} = -kx \quad (\text{A2.3})$$

Strictly speaking, Pimm's definition depends upon this simplicity, because the amount of time required for x to decay to some specified fraction of its initial value is only constant if the model (A2.1) is used. In fact, if the initial displacement is x_0 and the fraction is $p < 1$, then (A2.1) implies the relationships in (A2.4).

$$x_1 = px_0 = x_0 \exp(-kt_1) \quad (\text{A2.4})$$

From (A2.4), we conclude that the return time t_1 is given by equation (A2.5).

$$t_1 = \frac{1}{k} \log \frac{1}{p} \quad (\text{A2.5})$$

The remarkable feature is that the magnitude x_0 does not appear in this formula. This is a feature of this model only, as we shall see below. In more general circumstances, such a result can be expected to hold only in the limit as x_0 approaches 0. Such results are called "local." As pointed in this chapter, a common error is to extrapolate local results to global ones. In the present context, it amounts to replacing a complicated function by a linear approximation. Such approximations are certainly easy to work with, but they may miss essential features of the dynamics. In fact, failure to recognize the distinction between local stability and global stability can lead to unwarranted optimism about the likely consequences of interventions in natural systems. If we think that stability to small perturbations necessarily implies stability to large perturbations, then precautions are never required.

In order to distinguish behavior near the equilibrium at $x = 0$ from behavior near an unstable equilibrium, we must use a model with more parameters than those of (2.2), such as equation (A2.6).

$$\frac{dx}{dt} = f_1(x) = \frac{x(x^2 - \alpha)}{x^2 \left[\frac{2}{k_1} - \frac{1}{k} \right] + \frac{\alpha}{k}} \quad (\text{A2.6})$$

Equation (A2.6) leads to an especially simple equation for the return time: the time to reach a position x_1 starting at x_0 is given by equation (A2.7).

$$\tau_r = \int_{x_0}^{\infty} dt = \int_{x_0}^{\infty} \frac{dx}{f_1(x)} \quad (\text{A2.7})$$

The form for $f_1(x)$ was chosen so that equation (A2.8) can be verified algebraically:

$$\frac{1}{f_1(x)} = \frac{-1}{kx} + \frac{1}{k_1(x-\sqrt{\alpha})} + \frac{1}{k_1(x+\sqrt{\alpha})} \quad (\text{A2.8})$$

In view of (A2.7) and (A2.8), equation (A2.9) emerges.

$$\tau_r = \frac{1}{k} \log \frac{x_0}{x_1} + \frac{1}{k_1} \log \frac{x_1 - \sqrt{\alpha}}{x_0 - \sqrt{\alpha}} + \frac{1}{k_1} \log \frac{x_1 + \sqrt{\alpha}}{x_0 + \sqrt{\alpha}} \quad (\text{A2.9})$$

Now, if we replace x_1 by ρx_0 , (A2.9) becomes equation (A2.10).

$$\tau_r = \frac{1}{k} \log \frac{1}{\rho} + \frac{1}{k_1} \log \frac{1}{\rho_1} + \frac{1}{k_1} \log \frac{1}{\rho_2} \quad (\text{A2.10})$$

Here ρ_1 and ρ_2 are given in equations (A2.11) and (A2.12), respectively.

$$\rho_1 = \frac{x_0 - \sqrt{\alpha}}{\rho x_0 - \sqrt{\alpha}} \quad (\text{A2.11})$$

$$\rho_2 = \frac{x_0 + \sqrt{\alpha}}{\rho x_0 + \sqrt{\alpha}} \quad (\text{A2.12})$$

If the last two terms in equation (A2.10) are omitted, this result is identical to Pimm's assumption (A2.1). Our more complicated dynamical assumption (A2.6) is the analogue of Pimm's assumption if there are three equilibria. Under what conditions does (A.10) imply large return times? The first term, which corresponds to Pimm's model, implies a long return time if the ratio $\rho = x_1/x_0$ is small or if k is small. In Pimm's discussion, ρ is a parameter that describes a probe or observation of the system. Ordinarily, ρ is fixed, and the return time provides an estimate for k .

The second term in (A2.10) implies a long return time if ρ_1 is small or k_1 is small. Our previous discussion was concerned with a possibly variable α and disturbances that might take the system near an unstable equilibrium. That corresponds to x_0 near $\sqrt{\alpha}$ or x_0 near $-\sqrt{\alpha}$. In such a case, τ_r will be large even if the parameter k is large. That is, return times may be long, even for systems that show very rapid return when close to the stable equilibrium. According to this point of view, long return times may be diagnostic for a small α or for disturbances that are large enough to take the system near an unstable equilibrium.

They may also correspond to weak repulsion from the unstable equilibrium, or, in other words, small k_1 . If a disturbance takes the system beyond the unstable equilibrium, there is no return at all.

In summary, according to Pimm (1991) and according to us, long return times may be diagnostic for a loss of resilience, but the meanings of the terms are quite different in the two cases. Pimm is concerned with behavior near a stable equilibrium. In that case, a long return time for a given displacement from the equilibrium indicates a small coefficient k or, equivalently, a small derivative of $\log x$. We are concerned with behavior of a system with two or three equilibria, one of which is stable. Resilience describes the tendency of the system to return to its stable equilibrium. A long return time is due to disturbances that bring the system near an unstable equilibrium, or possibly to a weak repulsion from an unstable equilibrium.

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PART II

Resilience in Large-Scale Systems