

STABILITY, CONCEPT OF

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GLOSSARY

community The collection of all species living together in a given area. Alternatively, some designated subset, such as the avian community or the vascular plant community.

deterministic system A dynamical system whose detailed future behavior can be predicted, in principle, for all time, assuming perfect knowledge of the system at the present.

dynamical system A set of rules defining how certain variables change with time. Ecological models are dynamical systems representing what are believed to be (vastly more complex) dynamical systems in nature.

dynamical variable A quantity in a dynamical system that changes with time according to the rules of the system (contrast with parameter).

ecological model A vastly simplified mathematical representation of an ecological system intended to capture the full system's essence. Qualitatively, ecological models are to natural ecological systems as line drawings are to full-color photographs.

equilibrium A condition of stasis in some dynamical variable.

parameter A quantity in a dynamical system that is fixed as part of the rules of the system (contrast with dynamical variable).

perturbation A temporary change in one or more dynamical variables or parameters of a dynamical system due to external factors.

population A collection of individuals of the same species, often interacting ecologically and genetically.

stochastic system A dynamical system whose detailed future behavior cannot be predicted, even in principle, due to random forces inherent in the system.

STABILITY may be defined broadly as the tendency of a system to return to its former state after some disturbance. In the natural world, the term can be applied to the capacity of an ecosystem to resist environmental disturbances. Given the fact that human activity now produces such disturbances on a vast global scale, the ability of ecosystems to remain stable has become an issue of great significance. Current investigators study the interrelationship of stability and biodiversity; i.e., the effect that the biodiversity of an ecosystem has on its stability, and the corresponding role of stability in maintaining the biodiversity of the system.

Falling down once makes a building unstable.

—GERALD WEINBERG (1975)

I. BACKGROUND

A. The Meaning of Stability

Something is said to be stable if its condition tends to remain unchanged despite external influences. The population sizes of two different species may both be relatively constant in a steady, unchanging environment, but such constancy by itself discloses nothing of the stability of the two populations. If both populations were somehow perturbed—for example, by a spring flood eliminating half of each population—and if the first population subsequently recovered to former levels while the second declined to extinction, then the first population is said to have been stable while the second was unstable. Stability is not mere constancy—it also implies an ability to recover from perturbations.

The condition that recovers from perturbations need not be as simple as a constant population value. Populations of predators and prey, for example, may have an intrinsic tendency to cycle repeatedly through high and low values, but the cycle may be stable. Suppose the populations of a predator and its prey were both maintained at fixed levels by artificial management, such as by hunting. If the cycle returned after management ceased, then the cycle could be said to be stable, even though neither population is constant during the cycle. The cycle would be an abstract condition to which the populations return after a perturbation. In fact, the condition that recovers from perturbations can be any recognizable property of the system. It could be the number of species in the system, the collective biomass of all species together, the length of the food chain, the average quantity of nutrients leached from the soil, the degree of susceptibility to disease, or many others.

In the natural world, the stability of an object is closely tied to our perception of the very existence of that object. Any property that is unstable will not retain its condition after a disturbance, by the definition of stability. Given that the world is filled with continual disturbance, any property that is unstable is therefore likely to soon change to something else and hence not be observed. For example, if food chains beyond a certain length tend to be unstable in diverse communities, then a very long food chain, should it ever appear by chance combination of species in an ecosystem, will eventually collapse to a length that is stable.

As human domination of global biogeochemical systems increases—including eutrophication of habitats, changes in atmospheric gases, fragmentation of habitats, distribution of toxic organic compounds, translocation of species, and a general reduction of biodiver-

sity—the resulting perturbations test the stability of ecosystems. Also, as global changes take effect, induced changes in the systems alter the stability of their parts. Stability in ecosystems is therefore not just an abstract concept but something deeply connected to the persistence of the services on which all living beings, humans included, depend.

B. The Diversity–Stability Question

In the 1950s and 1960s, investigators such as Charles Elton argued that ecosystems containing more species would be more stable—less subject to fluctuations due to the myriad forces acting on them—owing to such factors as the greater number of pathways for energy to flow through them. This is the diversity–stability hypothesis. The hypothesis was generally accepted in the 1960s, although not without controversy.

Theoretical studies on the topic in the 1970s shook this general acceptance. Working with mathematical models of ecological communities, Robert May and others showed that such communities with more species were less stable: Populations of individual species returned to normal after a disturbance less rapidly as the number of species in the community increased. Although May (1974) later pointed out that certain ecosystem properties, such as total biomass of the community, can be more stable than biomasses of the constituent species, and despite objections by McNaughton (1977) and others to rejecting an accepted hypothesis based solely on theory, the acceptance of the diversity–stability hypothesis waned. During the 1970s and 1980s, ecologists generally expected that greater biodiversity would reduce stability, or at least that there was no consistent connection between biodiversity and stability.

By the 1990s, experimental evidence had accumulated that seemed to support both views simultaneously, depending on the level of focus. As the number of species increased, population densities of individual species became more variable from year to year but ecosystem parameters such as total productivity and nutrient leaching became less variable. In other words, the system seemed less stable when viewed in detail, from the perspectives of individual species, but more stable when viewed in total, from the perspective of the ecosystem (Tilman, 1999) (see Section III.A).

At the end of the twentieth century, issues concerning the effect of biodiversity on stability, and of environmental stability on biodiversity, were still being resolved, but greater biodiversity could be seen to stabilize certain important properties of the ecosystem as a

whole. Many of the past controversies and apparent conflicts resulted from the application of different aspects and definitions of stability in different contexts.

C. Aspects of Stability

The seemingly simple idea of whether a system returns to its former condition after a disturbance has several aspects. Which is relevant depends on the ecological question at hand:

1. Does the system return to its former state after a disturbance, given unlimited time without further disturbance? This is the basic idea of stability, and if the system does return from all small disturbances, that state is said to be asymptotically stable or, commonly in the ecological literature, simply stable.

2. How much does the system fluctuate under variable conditions? This is called variability and it is typically measured statistically, for example, by the standard deviation of a time series, by the standard deviation divided by the mean, or by the reciprocal of that quantity. (The standard deviation being the square root of the average squared deviation from the mean.)

3. How small does the disturbance have to be in order that the system return? The set of all possible disturbances that allow the system to return to its former condition is called the domain of attraction. As the domain of attraction becomes vanishingly small, the system becomes unstable. Small domains of attraction correspond to fragile systems, whereas large domains of attraction correspond to robust systems.

4. How much is the system changed by a given disturbance? The more a given condition is changed, the lower the resistance associated with that condition. For example, suppose population values in a given area do not change much when average temperature increases above its normal but may change considerably when rainfall does so. Then the system would be said to be resistant to temperature changes but not to rainfall changes.

5. How fast does a perturbation decay? Resilience is the amount of time needed for a perturbation to be reduced to a specified fraction of its initial size. There has been variation in the use of this term in the ecological literature. Before the 1980s, resilience often simply referred to factors that reduced the chance that one or more species would become extinct (e.g., the size of the domain of attraction and the populations densities in that domain).

6. How long does the system take to return after a given disturbance? This is related to both how far the

system is perturbed by the disturbance (resistance) and how fast the perturbation decays (resilience). The lower the resistance and resilience, the longer it takes to return.

7. How long can the condition be expected to last? The longer on average it lasts, the greater its persistence. The idea of persistence applies to systems subject to random variations, where the chance of encountering dangerously large variations during a time interval increases as the interval grows longer. The longer the time interval, for example, the greater the chance that one or more species will be driven extinct by random events.

8. Does the condition remain intact as the parameters of the system change slightly? If it does, the system is structurally stable with respect to those parameters. For example, if precise birth and death rates of the constituent species change slightly occasionally, does the condition remain?

9. Does the condition remain intact under evolutionary pressures? If it does, the condition is evolutionarily stable. A condition may appear stable over short time, ignoring evolution, but may change on longer timescales. Indeed, over the course of geological time, no ecosystem is invariant.

10. Does the condition depend on spatial scale? What is stable in a small area may be unstable over a larger region and vice versa.

Pimm (1984) enumerated five definitions of stability in the ecological literature at three levels of complexity and three levels of organization—potentially 45 different nuances to the meaning of stability. Hence, care is necessary in defining and applying the concept.

II. BASIC THEORY OF STABILITY

A. Equilibrium

The basic concepts of stability become precise when considered in the abstract. The many complexities in natural ecological communities, including factors that cannot be completely understood, mean that any abstraction of an ecological system is necessarily a vast reduction. To start this reduction, suppose the population increases solely by births and decreases solely by deaths. That is, processes such as immigration are not active. Suppose the rate of birth is highest and death is lowest when conditions are least crowded. As the population increases, resources become more limited—less light, reduced nutrient levels, less food, and so

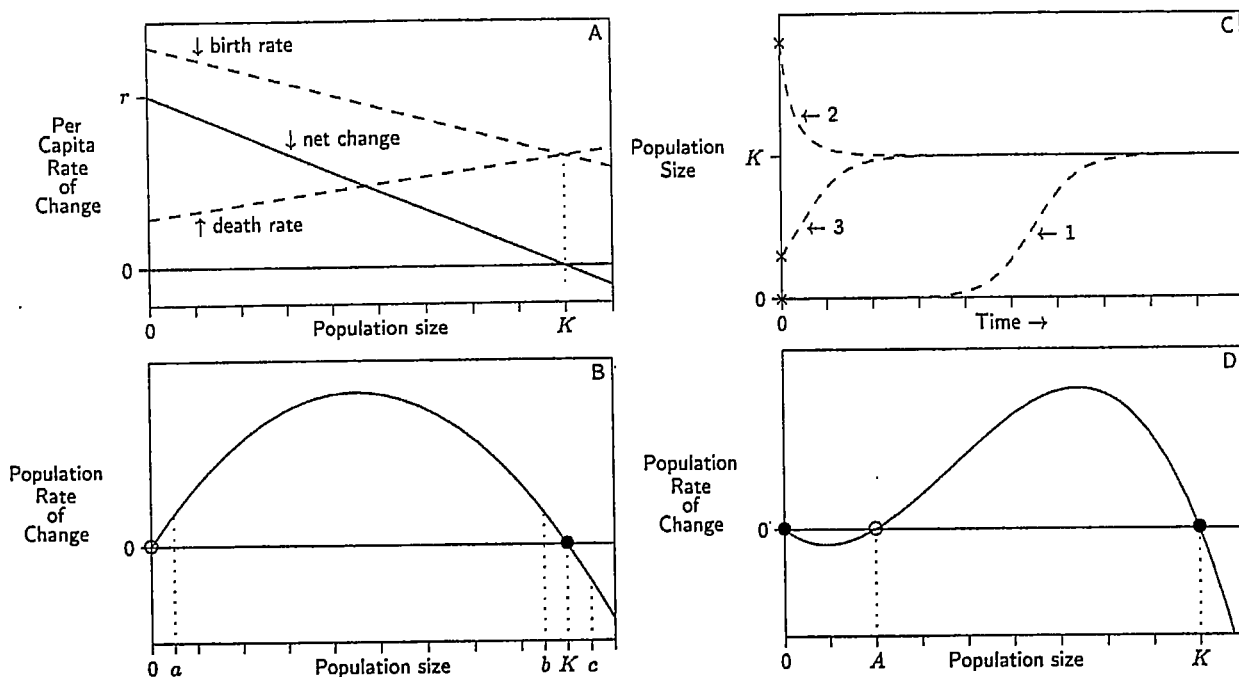


FIGURE 1 Geometric interpretation of stability. Solid and open circles represent stable and unstable equilibria, respectively. (A) Per capita birth and death rates are functions of population size; (B) growth of the entire population as a function of population size; (C) populations approaching carrying capacity with the passage of time, for the functions of A and B. The horizontal axis is time; the vertical axis is the population at the corresponding time. Cross symbols at the far left indicate the starting points. Curve 1 starts from a small population near zero. Curve 2 starts above the carrying capacity. Curve 3 starts below the carrying capacity but well above zero. (D) Growth of a population subject to the Allee effect, where 0 is a stable equilibrium.

forth; the birth rate decreases and the death rate increases. At some point, the population will increase enough so that births just balance deaths. This occurs at the carrying capacity, at which an individual, on average during its lifetime, just replaces itself with a single offspring. Above this carrying capacity, deaths exceed births, so an individual on average does not quite replace itself. In the simplest case, births decrease and deaths increase along straight lines as the population increases (Fig. 1A). The net rate of change per individual (the difference between births and deaths) is largest at the far left in Fig. 1A (r) but decreases to zero when the population size reaches the carrying capacity (K) and becomes negative when the population size is greater than the carrying capacity.

The rate of change of the entire population is simply the rate of change per individual times the number of individuals in the population. This is graphed in Fig. 1B, which shows the growth rate of the entire population (vertical axis) as a function of the population (horizontal axis). If the population is nonexistent (zero), then of course population growth is zero; with no individuals there are no births and can be no deaths. If the

population is at carrying capacity, population growth is also zero; births balance deaths. These are two population equilibria—places where the population remains constant.

Between these two equilibria, the population grows. In this simplest case, in which the birth and death rates are straight lines, the population reaches the greatest rate of growth at half its carrying capacity. (In economic models, this is called the point of maximum yield.)

B. Geometric Interpretation

1. Single Species

To understand the stability of an equilibrium, the properties of the growth rate are first examined in the neighborhood of the equilibrium. Consider the equilibrium at the carrying capacity (solid circle in Fig. 1B at position K). The graph representing population change crosses the horizontal axis precisely at the carrying capacity, which means the population neither grows nor declines there. At that point the growth curve slopes downward to the right (the slope is negative). If the population for any reason falls below the carrying ca-

capacity (e.g., point *b* in Fig. 1C), the growth function is above the axis, meaning that population growth is positive or that births exceed deaths. Thus, the population increases toward the carrying capacity. On the other hand, if the population is above the carrying capacity (e.g., point *c* in Fig. 1B), the growth function is below the axis, meaning that population growth is negative or that deaths exceeds births. Thus, the population decreases toward the carrying capacity. In both cases, an external change moving the population away from its carrying capacity induces population growth or decline in exactly the right way to counteract the external change. The population returns to the carrying capacity. That equilibrium is stable.

Now consider the equilibrium at 0 (open circle in Fig. 1B). As before, the graph representing population growth touches the horizontal axis precisely at 0. However, at this point the curve slopes upward toward the right (the slope is positive). Therefore, if the population ever increases, however slightly, above zero (e.g., point *a* in Fig. 1B)—due, for example, to the arrival of propagules from some outside source—the growth function is above the axis, meaning that population growth is positive or that births exceed deaths. Thus, the population increases away from 0. The zero equilibrium is unstable.

Thus, internal dynamics carry these populations toward their carrying capacity (which is called an attractor) and away from 0 (called a repeller). If the population starts near zero, but not precisely at zero, it may linger a long time at low values and then begin a rapid growth phase before leveling off toward its carrying capacity (Fig. 1C, curve 1). If the population starts above the carrying capacity, it rapidly decays back (Fig. 1C, curve 2). If it starts below the carrying capacity but well above zero, it can increase to the carrying capacity without the long lag period (Fig. 1C, curve 3).

2. Local versus Global Stability

In the previous example, the carrying capacity is said to be a global attractor or globally stable because almost all replicate populations eventually arrive there (all but those starting at zero in this case). Because the equilibrium at 0 is unstable, the population has a level of permanence; if driven to low values, but not completely to zero, it can recover spontaneously.

This contrasts with populations operating under an Allee effect, wherein the equilibrium at 0 is an attractor. Figure 1D depicts the growth function in such a situation. Very low densities inhibit reproduction, for example, by reducing chances of encountering a mate. There are three equilibrium points—at 0, *A*, and *K*. Slopes

both at 0 and at *K* are negative, meaning that these equilibria are stable, whereas the slope at *A* is positive, meaning that equilibrium is unstable. If such populations are driven to a low enough level (below *A*), they will spontaneously become extinct.

In this case, both 0 and *K* are local attractors (locally stable), but neither is a global attractor (neither is globally stable). If the system is pushed a small distance away, it will return to its former state. However, if pushed too far (beyond the domain of attraction of that equilibrium), the system will switch to another state. This is a bistable system. The region between 0 and *A* is the domain of attraction of the 0 equilibrium; the region between *A* and *K* and the entire region above *K* make up the domain of attraction of the carrying capacity. There is no domain of attraction for the equilibrium at *A* because this equilibrium is unstable (it is a repeller).

3. Multiple Species

The geometric example of Fig. 1 represents a single species in isolation. In this case, geometric stability arguments are direct and intuitive. The geometric arguments are similar for more than one species, but instead of curves representing growth rates, surfaces in multidimensional space are used. Each additional species requires another dimension. Unfortunately, such surfaces are difficult to visualize for more than two species.

The growth surface for a single species will in general cut through the plane of zero growth (analogous to the horizontal axis in Figs. 1B and 1D) along a curve. This curve is called the zero net growth isocline, and each species in general will have its own such curve. If the zero net growth isoclines for many species meet at a single point, then this is a multispecies equilibrium point. For this equilibrium to be stable, however, it is not sufficient that the growth surfaces of all species, considered separately, have negative slopes there. Interactions among the species must be accounted for, and this is best done algebraically.

C. Algebraic Methods

The geometric interpretation of stability, as depicted in Fig. 1B, has a direct algebraic interpretation in terms of derivatives and eigenvalues, which correspond geometrically to slopes. Where an algebraic description of the ecological system is available (i.e., in ecological models), the algebraic method is widely used and can be followed as a recipe. The algebraic method is essential for theoretical work in ecology, but the material in

this section is not essential for an intuitive understanding of the concept of stability.

1. Single Species

Consider an ecological system of a single species in which the symbol N represents the population size. This may be measured in individuals, biomass, or other units. The rate of change of this population is represented by dN/dt , which tells how large an increment (dN) occurs in the population during a small increment of time (dt). Assuming that this rate of change is a function of the population size, as in the previous discussion, then the system will be described by $dN/dt = f(N)$. For example, in Fig. 1, $f(N) = rN(1 - N/K)$, which is the well-known logistic equation described in most introductory ecology texts.

Equilibria are commonly designated by symbols like \hat{N} (pronounced "hat N "). They occur at such \hat{N} where $f(\hat{N}) = 0$. If the slope of the function $f(N)$ at any such equilibrium is negative (i.e., if $df/dN|_{N=\hat{N}} < 0$, as shown by the solid circles in Figs. 1B and 1D), then the equilibrium is stable. If the slope is positive (as shown by the open circles in Figs. 1B and 1D), then the equilibrium is unstable. If the slope is zero, then further information is needed to determine stability. In the case of zero slope, the equilibrium may be stable, unstable, or neutrally stable, depending on the exact shape of the function near the equilibrium. In the ecological literature, neutral stability means that if the system is perturbed from equilibrium a small amount, it neither returns nor moves further away but rather maintains its new value. (Note that there is a difference between the way ecologists use the word "stable" and the way mathematicians do, as summarized in (Table I.)

2. Multiple Species

Multiple species are represented by multidimensional dynamics, in general described by m equations of the

form $dN_i/dt = f_i(N_1, N_2, N_3, \dots, N_m)$, one equation for each species. Equilibria are multidimensional points $(\hat{N}_1, \hat{N}_2, \hat{N}_3, \dots, \hat{N}_m)$ that cause all dN_i/dt to be simultaneously zero. Some of the \hat{N}_i may be zero, in which case fewer than m species coexist at that equilibrium.

The slope of a system in one dimension generalizes to eigenvalues of the Jacobian matrix in multiple dimensions. (In one dimension, the slope is a special case of an eigenvalue.) To determine stability of an equilibrium, (1) construct the Jacobian matrix of the system, $J = \{\partial f_i/\partial N_j\}$, (2) substitute the equilibrium value $(\hat{N}_1, \hat{N}_2, \hat{N}_3, \dots, \hat{N}_m)$ into the matrix of step 1, and (3) determine the eigenvalues of the matrix of step 2. Neuhauser (2000) or other mathematical texts may be consulted for full details.

The resulting eigenvalues are complex numbers, and as such may contain both real and imaginary parts. (That is, an eigenvalue has the form $a + bi$, where a is the real part, bi is the imaginary part, and $i = \sqrt{-1}$.) The real part determines the rate of approach to or retreat from equilibrium after perturbation. In one dimension, the imaginary part is always zero, but in higher dimensions it need not be. When it is not zero, the approach to or retreat from equilibrium follows a spiral path.

Only the real parts of the eigenvalues affect stability. If the real parts of all eigenvalues are negative, that equilibrium point is stable. If one or more real parts is positive, that equilibrium point is unstable. If none is positive but one or more real parts are zero, then further information is needed to determine stability. If some eigenvalues have negative real parts but others have positive, then the equilibrium is a saddle point (so called because of its shape in the two-dimensional case). Such saddle equilibria are attracting in some directions and repelling in others; hence, they are unstable.

3. Discrete-Time Systems

Many ecological models are more naturally defined on a discrete time axis. For example, insects may emerge together at a specific time each year or seeds may be set once per year in the fall. In such models, time is better represented not as a continuum but rather as a series of integers (1, 2, 3, . . .), for example, representing a series of years. In simplest form, discrete-time models have the structure $N_i(t + 1) = f_i(N_1(t), N_2(t), N_3(t), \dots, N_m(t))$, where $N_i(t)$ is the population level of species i at time t . To determine stability of an equilibrium in a discrete-time system, the three steps outlined previously are followed, but the resulting eigenvalues must be interpreted differently. Again, the eigenvalues are complex numbers. In the discrete-time case, it is

TABLE I
Common Ecological Usage vs Common Mathematical Usage

Term	Size of perturbation with time	
	Ecological literature	Mathematical literature
Asymptotically stable	Decreases	Decreases
Stable	Decreases	Does not increase
Unstable	Increases	Increases
Neutrally stable	Remains unchanged	(Typically not used)

the absolute values of the eigenvalues that determine stability. That is, it is the positive square root of the sum of the squares of the real and imaginary parts. (For the eigenvalue $\lambda = a + bi$, $|\lambda| = \sqrt{a^2 + b^2}$.) If the absolute value of all eigenvalues is less than 1, then the equilibrium is stable. If the absolute value of one or more eigenvalues is greater than 1, that equilibrium point is unstable. If none is greater than 1 but one or more absolute values are precisely equal to 1, then further information is needed to determine stability, as in the case of zero eigenvalues discussed previously.

4. Strength of Return

The magnitude of the eigenvalues (or, equivalently, the steepness of slope) determines the resilience, or the strength of return to equilibrium. If the eigenvalues are all very negative, the corresponding slopes will be very steep. Small deviations from equilibrium will result in large rates of growth or decline, and the system will return rapidly. On the other hand, if any of the eigenvalues is negative but close to zero, then the corresponding slopes will be shallow. Small deviations from equilibrium will not lead to rapid recovery. Of course, given a sufficiently long time, and given the absence from disturbance, the system will return regardless of the eigenvalue's magnitude, given that it is negative. However, over short times, or with repeated disturbances, the magnitude of the eigenvalues is an important part of stability.

III. STABILITY UNDER CHANGING CONDITIONS

A. Biodiversity and Temporal Stability

If a system is subject to repeated disturbances, variations in a given property of that system over time will be related to the asymptotic stability of that property. Because asymptotic stability is an abstract concept, well defined in ecological models but difficult to determine in natural systems, various measures of fluctuations are often used instead to quantify stability of natural systems.

Suppose two populations are fluctuating through time about their individual mean abundance levels due to stochastic effects in the environment and possibly due to internal dynamics as well. Suppose fluctuations in the first population are on average relatively small compared to the first population's mean abundance, whereas fluctuations in the second population are noticeably larger compared to the second population's

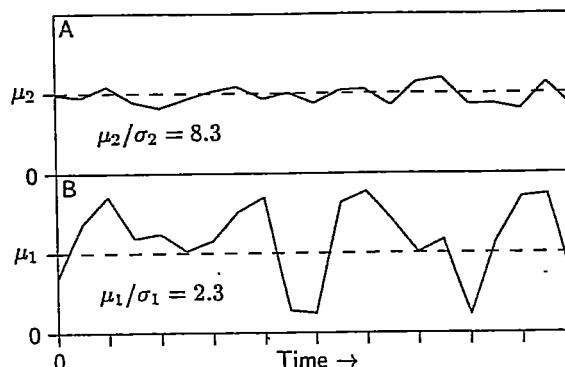


FIGURE 2 Temporal stability. Dashed lines indicate the long-term means, and solid lines indicate fluctuating variables. (A) Relatively small fluctuations about the mean, with a relatively high measure of temporal stability (8.3); (B) larger fluctuation about the mean, indicating lower stability, with a lower measure of temporal stability (2.3).

mean abundance (Fig. 2). Independent of the idea of asymptotic stability, the first system can be defined to be more stable with respect to constancy in abundance. Precisely how this fluctuational stability is related to the concept of asymptotic stability discussed in Section II is a separate theoretical issue.

The average fluctuation can be quantified in alternative ways; for example, as the average absolute value deviation from the mean or as the standard deviation of the mean. In any case, if fluctuations are large relative to the mean, the system is likely to obtain values very far from the mean. Also, if the underlying dynamics have a domain of attraction that is responsible for maintaining the mean, then large fluctuations are more likely, on rare occasions, to combine in the wrong direction and push the system out of that domain, inducing a switch to a new mode of behavior. Thus, the relative amount of fluctuation can carry information on the long-term persistence of the system.

Measures proportional to the coefficient of variation—the standard deviation over a time series divided by the mean of that time series—have been used as a measure of fluctuation. These are actually proportional to instability because larger values in the coefficient of variation correspond to lower stability. The reciprocal of the coefficient of variation (i.e., the mean divided by the standard deviation, μ/σ) has been termed temporal stability (Tilman, 1999). It carries the same information, but larger values of temporal stability correspond to greater stability of the system. In this form (μ/σ), it is reminiscent of signal-to-noise ratio in engineering. Clearly, temporal stability is greater if the mean is greater (μ , the numerator), if the standard deviation is

smaller (σ , the denominator), or both. Therefore, any forces that tend to increase the mean or decrease the variation will increase temporal stability. Temporal stability is maximal (infinite) when the standard deviation is zero—when there is no variation at all.

Evidence from both experiment and theory suggests that the temporal stability of certain community characteristics of competitive plant communities tends to increase as the number of species they comprise increases (Tilman, 1999). Along a long-term nitrogen fertilization gradient, the number of species varied, changing from diverse prairie communities at low nitrogen levels to only a few agricultural grass species at high nitrogen levels. Individual species abundances varied from year to year due to many causes, both environmental and ecological. As the number of species increased, (i) the total biomass of the community tended to increase and (ii) the total biomass of the community became less variable. Simultaneously, the biomass of an individual species tended to become more variable relative to the mean biomass for that species embedded in the community. In other words, increased biodiversity appears to stabilize the community while destabilizing the individual species.

Given this pattern from experimental systems, a theoretical question immediately arises: Do standard ecological models predict similar phenomena? This is a rapidly developing area, but initial results appear to indicate that they do (Tilman, 1999). In a model of competition for a single resource, and in other more general models, temporal stability of total community biomass increased steadily and linearly as the number of species increased (Fig. 3A). Temporal stability of individual species biomass decreased sharply as biodiversity increased from one to about five species, and then it leveled off at higher diversities (Fig. 3B). In other words, simple ecological models appear to predict the effects observed along the nitrogen gradient—increased biodiversity will stabilize the community but destabilize individual species.

The importance of various possible causes of stabilization of community properties remain under discussion. When abundances of individual species are perturbed by complex and effectively random forces, some abundances may be perturbed to higher levels and others to lower levels. On statistical grounds, the variation in the total biomass will likely contain both positive and negative perturbations. Hence, the total is likely to fluctuate less, relative to its mean value. This has been called the portfolio effect (Tilman, 1999) by analogy to economics, wherein a portfolio diversified over many investment instruments will fluctuate less than one con-

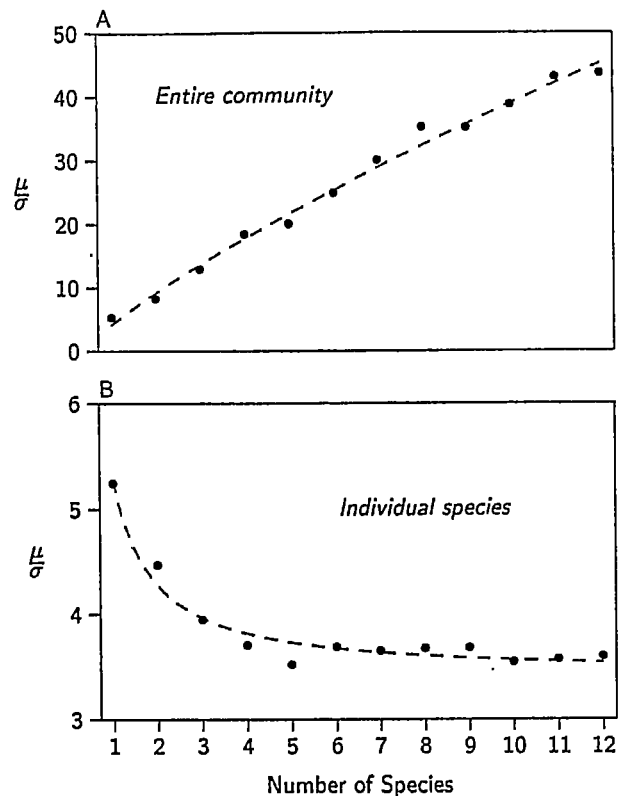


FIGURE 3 Biodiversity affects temporal stability. From a resource model reported by Tilman (1999) showing patterns similar to those observed in nature. Large dots indicate means of 100 replicates. (A) Increasing biodiversity stabilized total biomass; (B) increasing biodiversity destabilized individual species biomass.

taining only a few. It depends on species responding differently to perturbations, if only for statistical reasons. Effects of competition allow species to expand in abundance when a competing species is suppressed by external forces. This expansion, in turn, buffers any change in total biomass. This is called the covariance effect because it is evident when there is strong negative covariance between pairs of species. Finally, increased biodiversity also often leads to increased total abundance, and this increases stability by making any given level of fluctuations smaller in proportion. This is called the overyielding effect.

Regardless of the source of the stabilization, however, it appears that certain composite community properties may be stabilized by increased biodiversity. More direct experiments that will eventually be able to clarify the effects of biodiversity on stability and other ecosystem properties have been established in many countries (Hector *et al.*, 1999; Tilman, 1999). Results of this coordinated set of experiments will emerge during the

first decade of the twenty-first century and bear watching for information they will provide on the diversity-stability question.

B. Temporal Niches

Temporal stability, as defined previously, certainly applies to a system continually perturbed from equilibrium. However, equilibrium was not part of the definition—only the mean and the variation about the mean participated in the measure of temporal stability. Temporal stability therefore applies to cases in which equilibrium, stable or otherwise, may not even exist.

Changing environmental conditions, such as variation in average rainfall from year to year, can favor different species at different times. This, in effect, can partition resources among species, setting up temporal niches and permitting long-term coexistence of species that greatly outnumber the resources they consume (Chesson, 1994). Without changing conditions, biodiversity would be reduced—coexistence would be limited by the number of resources available.

For a given regime of environmental fluctuations, and for a given community, each species will have some pattern of fluctuations in response to the fluctuations in the environment and those of other species in the community. Again, the issue with respect to biodiversity is how the relative size of the fluctuations—the temporal stability—of each species depends on the number of species in the community and how community-level properties such as total productivity or nutrient leaching depend on the number of species.

Coexistence among species in the absence of a multi-species equilibrium can result from stochastic variations in the environment, as explained previously. However, it is not necessary that the variations be stochastic, nor that their source be the external environment. The variations could result from some regular, well-determined periodic changes in the environment, or they could result from population cycles set up by dynamics of the ecological community (Armstrong and McGehee, 1980; Huisman and Weissing, 1999). Whether the effects are external or internal, stable coexistence at increased biodiversity can exist under fluctuating conditions.

C. Emerging Deterministic Stability

Stable deterministic characteristics such as those described in Section II can emerge from stochastic systems. Individuals may live and die, populations may fluctuate in abundance, and some species may become

extinct while others appear; however, amid all this complexity, simple patterns of biodiversity can emerge.

One of the early successful theoretical explanations of biodiversity concerned island biogeography (MacArthur and Wilson, 1967). On islands, simple deterministic characteristics emerge amid complex ecological change. It is a conspicuous fact that oceanic islands have fewer species than adjacent mainlands. This effect can be attributed, to a large extent, to a stable balance between local extinction of resident species and immigration of new species.

A new individual arriving on the island may be a member of a species already resident on the island, or it may represent a novel species. If the island is devoid of life, the new individual is certain to be a member of a novel species. As the island becomes more populated with mainland species, the chance that the individual is a member of a novel species decreases. Similarly, the chance that an existing species vanishes from the island increases as the number of resident species increases.

Such considerations lead to immigration and extinction curves such as those in Fig. 4. Notice the qualitative similarity of the immigration and extinction curves in Fig. 4 to the birth and death curves, respectively, in Fig. 1. The immigration and extinction curves intersect at an equilibrium point, where resident species becoming extinct are balanced by new species arriving. Note that at this equilibrium, neither population values nor

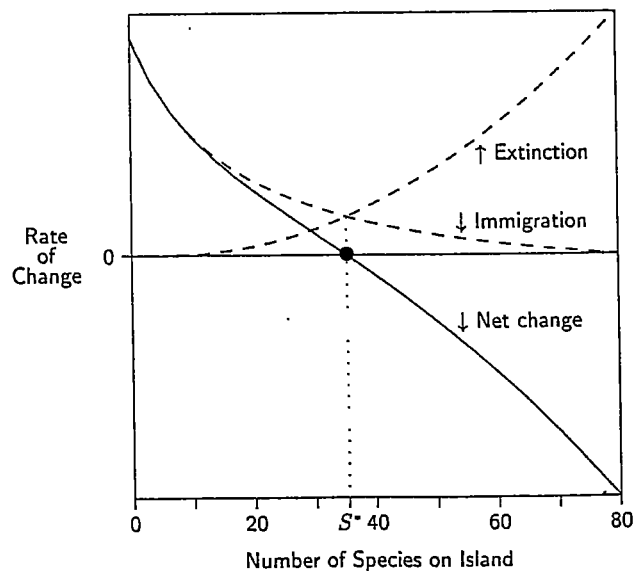


FIGURE 4 Stable island equilibrium. Island biogeographic immigration and extinction curves patterned after observed rates for real islands. Biodiversity reaches a stable equilibrium when immigration balances extinction.

community composition are constant. In fact, the individual species making up the community are constantly in flux. It is simply the biodiversity that remains constant.

Is this biodiversity equilibrium stable? The net rate of increase or decrease in the number of species is simply the difference between the immigration and extinction rates, which is the solid curve in Fig. 4. Unlike the curves of Fig. 1A, this net rate represents the entire island; it is not a per capita or per species rate. Therefore, its slope at the equilibrium directly corresponds to stability—it need not first be multiplied by the number of species on the island. Because the slope is negative, by the arguments of Section II this equilibrium is stable.

D. Stability Amid Chaos

Consider a population that changes deterministically according to the rules of Box 1—a straight-line relative of the logistic equation of Fig. 1. Populations oscillate chaotically between high and low values, but except for certain infinitely rare starting conditions they never return to a previous state (Fig. 5). This system is chaotic in the sense that slight deviations are always magnified. In almost all cases, two slightly different starting populations, no matter how nearly identical, grow increasingly different with time.

However, amid such complete chaos can be stability. After sufficient time, population values fall into a pair of disjoint intervals, shaded in Fig. 5. This pair of intervals is an attractor. The population then alternates regularly between the intervals, though its position within either interval cannot be predicted for very long from measurements of finite precision. This is a deterministic system with dynamics that appear superficially stochastic, but among all its instabilities arises another level of stability.

Box 1

$$N_{t+1} = \begin{cases} 2N_t & \text{if } N_t < a \\ 2a(1 - N_t)/(1 - a) & \text{if } N_t \geq a \end{cases}$$

Piecewise linear discrete-time population growth. If $a < 1/3$, there is a stable equilibrium at $N = 2a/(1 + a)$. If $a > 1/3$, there are no stable equilibria or cycles (see Fig. 5).

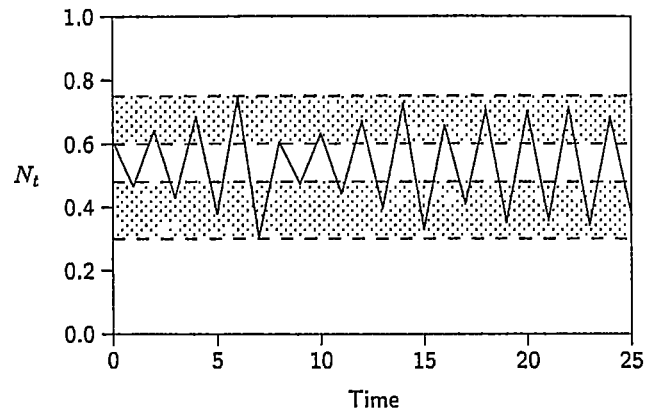


FIGURE 5 Stable attractor enclosing unstable population cycles. The system of Box 1 with $a = 3/8$ is chaotic, but population fluctuations are pulled into the shaded intervals (0.3, 0.48) and (0.6, 0.75). The horizontal axis is time; the vertical axis is the population at the corresponding time.

IV. OTHER KINDS OF STABILITY

A. Structural Stability

In the cases discussed previously, the ecological system did not change. Dynamical variables such as population levels were perturbed, but ecological parameters such as birth rates remained fixed. Ecological parameters, however, constantly change: Global temperatures increase, glaciers retreat, and spruce forests give way to pine and then hardwoods. Rainfall, soil substrates, and a host of environmental conditions alter the parameters and the structure of ecological systems. Hence, not only may the dynamical variables such as population abundances be perturbed but also the very structure of the ecological system may change.

If a given property of a system persists under small changes in the system itself, then the system is said to be structurally stable with respect to that property. The equilibrium carrying capacity in the system of Fig. 1, for example, is structurally stable. Changes in the slopes of the birth and death rates, or small changes that make the birth and death rates curves rather than straight lines, still leave a carrying capacity that all nonzero initial populations eventually reach, provided that the net per capita growth declines smoothly with increasing population. The precise size of the carrying capacity may change, but the fact that it exists and is stable does not.

1. Classical Predator-Prey Systems

Some ecological models are on a razor edge of structural instability. In the simplest form of the classical Lotka-

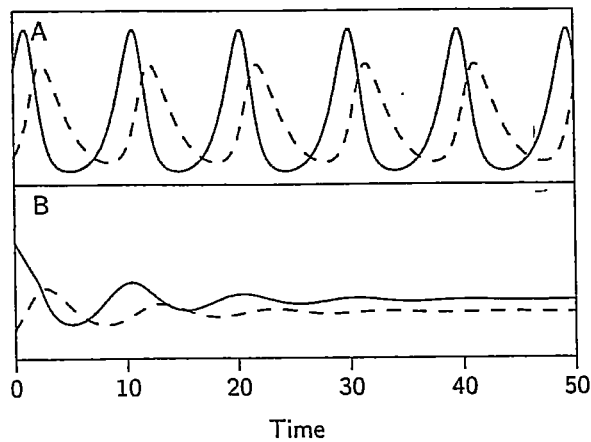


FIGURE 6 Structural instability in Lotka–Volterra predator–prey cycling. Solid curves represent population densities of the prey, and dashed curves represent that of the predator. Here, $r_N = 1$, $r_P = 1/2$, $a = 1$, $b = 1/2$, $K = 5$, $N(0) = 2$, and $P(0) = 1/2$. (A) The prey population is limited only by predation (top two equations in Box 2). The populations oscillate on neutrally stable cycles. This effect is structurally unstable. (B) The same starting conditions when the prey is also limited by its own carrying capacity in the absence of the predator (bottom two equations in Box 2). Initial variations damp out. This effect is structurally stable.

Volterra predator–prey system, included in most introductory ecology texts, the prey population is limited by predation and the predator population is limited by availability of prey (first pair of equations in Box 2). Predator and prey populations oscillate indefinitely about an equilibrium, with the predator population lagging behind that of the prey (Fig. 6A). This is a common

Box 2

$$\frac{dN}{dt} = r_N N - aNP$$

$$\frac{dP}{dt} = r_P NP - bP$$

$$\frac{dN}{dt} = r_N N \left(1 - \frac{N}{K} \right) - aNP$$

$$\frac{dP}{dt} = r_P NP - bP$$

Lotka–Volterra predator–prey system. Top two equations, no carrying capacity for prey; bottom two equations, carrying capacity included (see Fig. 6).

characteristic of predator–prey systems or, more generally, of producer–consumer systems. However, this particular system has a peculiar property for an ecological system: It possesses a “memory” of past events. If something perturbs either population, or both populations, to a new level, that new level will be revisited on each subsequent cycle. This system has no asymptotically stable behavior; instead, everything is neutrally stable.

Such neutral stability would not necessarily be pathological in an idealized physical system, such as a perfect harmonic oscillator, but here it is pathological. All abstractions are simplifications, and here one of the simplifications is the assumption that the prey population is limited only by the predators; in the absence of predators, prey can increase in numbers without bound. Inclusion of any carrying capacity for the prey, no matter how large or small (as in the second pair of equations in Box 2), changes the dynamics completely. The equilibrium becomes stable, oscillations die out, and memory of past perturbations fades with passing time (Fig. 6B). Another simplification is that predators are never satiated: They consume all the prey they encounter. Inclusion of a more realistic predator response can make the equilibrium unstable. The oscillations converge to a stable cycle of fixed amplitude, again with memory of past perturbations fading.

Thus, this simplest Lotka–Volterra formulation is structurally unstable with respect to important ecological factors. Structurally unstable ecological systems do not commonly appear in nature, so conclusions drawn from structurally unstable models must be used with caution.

2. Related Effects of Eutrophication

The change in structure from stable equilibrium to stable limit cycle, as described previously, may be induced by changes to parameters of the ecosystem. Eutrophication is enrichment by high levels of nutrients, such as increased phosphorus in a lake or nitrogen in the soil. Eutrophication is one of the principal effects of human domination of ecosystems, and it may affect both their biodiversity and their stability.

Graphical analysis by Rosenzweig and others in the 1970 (Rosenzweig, 1990) showed that stable equilibria in producer–consumer systems were favored when the carrying capacity of the consumer was relatively small. If the carrying capacity of the consumer were higher, the equilibrium would be less stable (less resilient). At a sufficiently high carrying capacity, the system would pass through a structural instability and the equilibrium would lose its stability entirely. Oscillations in producers and consumers would then occur. At even higher

carrying capacities, the size of the oscillations would increase, driving both producer and consumer periodically to low population levels, thereby increasing the chance of extinction.

Now, carrying capacity is directly related to the level of resources available. Eutrophication increases these resources, thereby increasing the carrying capacity of the producer. Ironically, the act of providing more food or resource to the producer can lead to its destruction as a result of induced instability. This effect has been called the paradox of enrichment. A common result in observed fertilized terrestrial systems is a reduction in the number of species. Although there can be many reasons for this, loss of stability upon enrichment has been suggested as a contributor (Rosenzweig, 1990).

B. Spatial Stability

A property that is stable at one spatial scale need not be stable at larger or smaller scales (Levin and Segel, 1985). This was decisively demonstrated in the mid-twentieth century by the mathematician Alan Turing. Turing's simplest example was a (nonecological) dynamical system operating in two separate cells, optionally with some migration between the cells (Box 3). If the two cells are completely disconnected, then there is an asymptotically stable equilibrium that both cells approach. Thus, if the density in either cell is perturbed, it will return to its equilibrium value (Fig. 7, times 0–4).

Box 3

$$\frac{dx_1}{dt} = ax_1 - by_1 + h - m_x(x_1 - x_2)$$

$$\frac{dy_1}{dt} = bx_1 - cy_1 + h - m_y(y_1 - y_2)$$

$$\frac{dx_2}{dt} = ax_2 - by_2 + h - m_x(x_2 - x_1)$$

$$\frac{dy_2}{dt} = bx_2 - cy_2 + h - m_y(y_2 - y_1)$$

Turing's basic example of diffusive instability. Variables x_i and y_i are densities in cell i . The remaining symbols are constant coefficients, $a = 5$, $b = 6$, $c = 7$, $h = 1$, $m_x = 1/2$, and $m_y = 9/2$ (see Fig. 7).

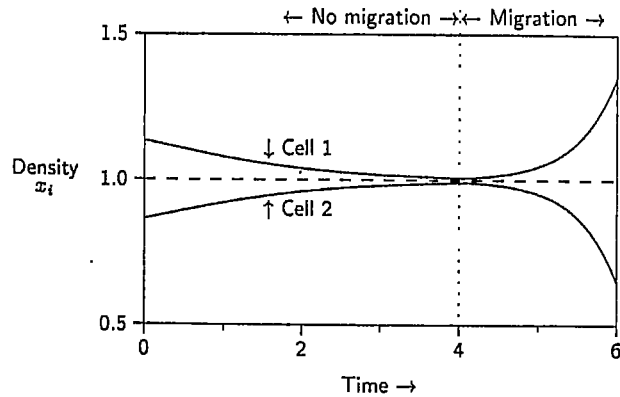


FIGURE 7 Spatial diffusive instability in a two-cell example. The vertical axis is density, or concentration, of two of the variables (x_1 and x_2) for the example shown in Box 3. The two cells are isolated until time 4, when a migration corridor between the cells is opened. Isolated, each cell approaches the same stable equilibrium (times 0–4). Connected, this equilibrium is destabilized by migration and the two cells diverge rapidly (times 4–6). Initial conditions are $x_1(0) = 1.13533$, $y_1(0) = 1.1218$, $x_2(0) = 0.864666$ and $y_2(0) = 0.8782$.

However, if there is sufficient migration between the cells, then the equilibrium, though it still exists, becomes unstable. Any random deviation that causes a difference between cells, however slight, unbalances migration and causes a sustained and accelerating net transport toward the cell with the higher concentration (Fig. 7, times 4–6). This is called a diffusive instability or a Turing instability. An equilibrium that is stable at a point of space can become unstable when its components can diffuse to neighboring parts of the space. This resulting instability can lead to variations and patterns in biodiversity over the landscape, with the resulting patterns being stable.

The opposite can also hold. A system that is unstable in a point of space can become stable, or at least persistent, when extended over a region. Predators clearly coexist with their prey and parasites coexist with their hosts for long periods in nature. However, such coexistence has been difficult to scale down to the size of experiments. Many of the early experiments on predator-prey and host-parasite systems found them to be unstable at small scales. Confined to a small area, the predators captured all the prey, and then themselves disappeared from the experiment for lack of food (or, analogously, the parasites infected all the hosts and then themselves disappeared). However, as the spatial extent of the experiment was increased, persistence of the system increased dramatically. Ecological models of such systems show a similar behavior (Hassel and

Wilson, 1997). Although each individual cell quickly runs to extinction, migration "rescues" empty cells, and the host and the parasite can have a stable average density over a large group of cells. Thus, an equilibrium that does not exist or is unstable in a point of space can be replaced by a stable equilibrium averaged over the entire region.

Something similar happens in ecological systems described by metapopulation dynamics (Hanski, 1997). Individual populations of a species may be separated by distances or barriers that inhibit movement between populations. If movement is strongly inhibited, individual populations may be driven extinct locally by stochastic effects, only to be restored later by propagules from some other population. Despite individual populations going in and out of existence, the portion of local sites occupied at any time can approach a stable equilibrium. This locally nonpersistent system can be both persistent regionally and have a stable regional equilibrium.

C. Evolutionary Stability

On the ecological timescale, ecological parameters such as birth and death rate are considered fixed. They are taken to be immutable characteristics of the species under consideration. However, ecological systems have many layers of complexity beyond our simple abstractions of them. On the evolutionary timescale, the parameters are malleable through the process of mutation and natural selection. Moreover, species formerly isolated may come into contact either as a result of natural causes or, now with great frequency, through the actions of humans. Both invading species and mutant phenotypes present new parameters that test the evolutionary stability of the system. A condition that is stable with ecological parameters fixed need not be stable when these parameters can change.

How the parameters might change can be seen by examining the growth rate of potential invaders, initially at negligible densities, entering the community at equilibrium. If the growth rate of any phenotype is positive, then the system can be invaded by that phenotype. The resident species, and hence the parameters of the system, are evolutionarily stable only if the growth rate of every potential invader is negative. Originally developed for behavioral systems, this idea is being applied to ecological communities (Geritz *et al.*, 1998), and such work promises to shed light on the properties of invasions and ultimately on the evolution of biodiversity.

See Also the Following Articles

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