Volterra, V. (1926). Variations and fluctuations of the numbers of individuals in animal species living together. (Reprinted in 1931. In R. N. Chapman, *Animal Ecology*. New York: McGraw Hill.)

Wimsatt, W. C. (1987). False models as means to truer theories. In M. Nitecki & A. Hoffmann (Eds). *Neutral models in biology* (pp. 23–55). Oxford: Oxford University Press.

Further Reading

Kingsland, S. E. (1985). *Modelling nature: episodes in the history of population ecology*. Chicago: University of Chicago Press.

Mikkelson, G. (2003). Ecological kinds and ecological laws. *Philosophy of Science*, 70(5, December), 1390–400.

Odenbaugh, J. (2001). Ecology, stability, model building and environmental policy: a reply to some of the pessimism. *Philosophy of Science*, 68:Supp (September), S493–S505.

Odenbaugh, J. (2005). Ecology. In S. Sarkar & J. Pfeifer (Eds). *The Philosophy of Science: an encyclopedia*. New York: Routledge.

Peters, R. (1991). *A critique for ecology*. Cambridge: Cambridge University Press.

Sarkar, S. (2007). Ecology. In E. N. Zalta (Ed.). *Stanford encyclopedia of philosophy (Fall 2007 Edition)*. URL=<http://plato.stanford.edu/archives/fall2007/entries/ecology/>.

Schrader-Frechette, K., & McCoy, E. (1993). *Method in ecology*. Cambridge: Cambridge University Press.

Chapter 18

Complexity, Diversity, and Stability

JAMES JUSTUS

1. Introduction

The stability–diversity–complexity (SDC) debate has persisted as a central focus of theoretical ecology for half a century. The debate concerns the deceptively simple question of whether there is a relationship between the complexity and/or diversity of a biological community and its stability. From 1955, when Robert MacArthur initiated the debate, to the early 1970s, the predominant view among ecologists was that diversity and complexity were important if not the principal causes of community stability. Robert May, a physicist turned mathematical ecologist, confounded this view with analyses of mathematical models of communities that seemed to confirm the opposite, that increased complexity jeopardizes stability. The praise May's work received for its mathematical rigor and the criticisms it received for its seeming biological irrelevance thrust the SDC debate into the ecological limelight, but subsequent analyses have failed to resolve it. Different analyses seem to support conflicting claims and indicate an underlying lack of conceptual clarity about ecological stability, diversity, and complexity.

At a coarse level of description, ecologists disagree little about the concepts of diversity and complexity. A biological community is a set of interacting populations of different species. Its diversity is commonly understood to be positively correlated with the number of species it contains (richness), and how evenly individuals are distributed among these species (evenness) (Pielou, 1975; Margurran, 1988), though other possible components of diversity have been considered. Complexity of a community is positively correlated with its richness, how many of its species interact (connectance), and how strongly they interact. Diversity and complexity are similar properties and may be strongly positively correlated, but they are not identical. Species of a highly diverse community may interact little and therefore exhibit low complexity, and vice versa.

Beyond these relatively uncontested claims, disagreement arises over how the two concepts should be operationalized. Ecologists have proposed several mathematical functions that differ about what properties (richness, evenness, connectance, etc.) are given priority over others in assessing diversity or complexity, and which differ in functional form. Currently, there is little agreement about what operationalizations, especially of diversity, are ultimately defensible (Ricotta, 2005).

Another problematic aspect of the SDC debate is the lack of consensus about how ecological stability should be defined. This reflects uncertainty about what features of a community's dynamics should be considered its stability, and has resulted in studies that suggest conflicting conclusions about the debate based on different senses of ecological stability (e.g., May, 1974; Tilman, 1999; Pfisterer & Schmid, 2002). Ecological stability is not, however, unique in this regard. As McIntosh (1985, p.80) has quipped: "A traditional problem of ecology has been that ecologists, like Humpty Dumpty, often used a word to mean just what they chose it to mean with little regard for what others said it meant." Disagreements about how to define concepts arise in other sciences as well. Careful analysis of the concept of ecological stability (and diversity and complexity) would thus help resolve the SDC debate, as well as illuminate the general problem of finding adequate definitions for concepts in science. Besides providing insights about how problematic scientific concepts should be defined, the SDC debate also has a potential bearing on biodiversity conservation. For most senses of stability, more stable communities are better able to withstand environmental disturbances, thereby decreasing the risk of species extinction. Positive feedback between diversity/complexity and stability would therefore support conservation efforts to preserve biodiversity, assuming biodiversity and ecological diversity/complexity are closely related (see Goodman, 1975; Norton, 1987, chs. 3 and 4).

To better understand the SDC debate, Sections 2–4 trace its history. Section 2 discusses the seminal works that initiated the debate in its current form, and Section 3 examines Lewontin's (1969) analysis of the relationship between mathematical concepts of stability and ecological stability. Section 4 considers May's influential work, which brought greater mathematical rigor and sophistication to the debate and upended the popular slogan among ecologists that "diversity begets stability."

Section 5 presents a comprehensive classification of different senses of ecological stability; argues that the concepts of resistance, resilience, and tolerance jointly define ecological stability adequately; and defends the concept against the charge that it is "conceptually confused" or "inconsistent." Section 6 surveys some common measures of diversity and complexity, and adequacy criteria proposed for them. Section 7 concludes by describing some methodological challenges the evaluation of stability–diversity and stability–complexity relationships confronts.

2. Emergence of the Stability–Diversity–Complexity Debate

Robert MacArthur (1955) published the first precise definition of ecological stability while still a graduate student of Yale ecologist G. E. Hutchinson. To clarify the concept, MacArthur (1955, p.534) first noted that ecologists tended to call communities with relatively constant population sizes stable, and those with fluctuating populations unstable. Stability in this sense denotes *constancy*. He thought, however, that this confused stability with its effects, and offered another account:

> Suppose, for some reason, that one species has an abnormal abundance. Then we shall say the community is unstable if the other species change markedly in abundance as a result of the first. The less effect this abnormal abundance has on the other species, the more stable the community. (1955, p.534)

This account identifies the underlying dynamic responsible for constancy, not constancy itself, as the proper defining property of stability. Stability in this sense depends on how communities respond to disturbance, in this case the abnormal abundance. The smaller the changes in other species abundances, the more stable the community. Although MacArthur did not use the term, this type of stability is a form of *resistance* to disturbance because its attribution to a community is based on the degree that one abnormal abundance changes other species abundances – specifically, the degree the other abundances resist changing – rather than on whether the community returns to equilibrium. For a community at equilibrium, i.e., its populations remain constant if the community is undisturbed, high resistance will ensure relative constancy is retained even if the community is disturbed. Highly resistant communities will therefore usually exhibit approximately constant species abundances through time, which MacArthur believed led many to call them stable. For MacArthur, however, constancy is a consequence of resistance, not equivalent to it.

MacArthur recognized that two properties could account for high resistance: (i) interspecific species interactions, such as predation and competition; and (ii) "intrinsic" properties of species, specifically their physiologies. Focusing on (i), MacArthur (1955, p.534) suggested a "qualitative condition" for stability: "The amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community." "Measure" in this condition is used in the standard statistical sense to represent the type of relationship exhibited between positively correlated properties, in the same sense that IQ is claimed to measure intelligence, for instance. Thus, the qualitative condition assumes rather than supports the claim that there is a positive correlation between community stability (understood as resistance) and food web structure.

MacArthur justified this assumption with an intuitive argument that a large number of links in a community's food web should make it highly resistant. In a food web where species S is atypically abundant, other species abundances are affected less the more widely S's "excess energy" is distributed among different predators. Similarly, a wide variety of alternative prey for S's predators would minimize the effects an abnormally low abundance of S would have on them. In either case, the number of links in a food web is positively correlated with community resistance. If correct, it is important to note that this argument only establishes a positive correlation. It does not justify conflating the properties MacArthur used to define ecological stability and those that may be positively correlated with them. Margalef (1958, p.61), for instance, misinterpreted MacArthur's analysis in this way: "In [MacArthur's (1955)] sense, stability *means*, basically, complexity" (emphasis added).

After noting that resistance can be quantified in several ways, MacArthur (1955, p.534) proposed two "intuitive" adequacy conditions for doing so:

(i) resistance should be minimal (e.g., 0) for food webs with exactly one species at each trophic level (food chains); and,

(ii) resistance should increase with the number of food web links.

Conditions (i) and (ii) refer to properties of food webs, not, as MacArthur *defined* resistance, to how communities change after one species becomes abnormally abundant.

What do (i) and (ii) have to do with quantifying how communities change after one species becomes abnormally abundant? What MacArthur was in fact doing was proposing adequacy conditions for quantifying the *measure* of resistance he had just argued for: "the amount of choice which the energy has in following the paths up through the food web." Conditions (i) and (ii) were not intended to help quantify the concept of resistance as MacArthur *defined* it.

This explains how MacArthur could quantify resistance with the Shannon index:

$$-\sum_i p_i \ln p_i; \qquad (1)$$

where p_i is the proportion of the community's "food energy" passing through path i in the food web, which does not represent anything about how species abundances in a community are affected by the abnormal abundance of one species. The decision to use this index, which he called "arbitrary," was intended to specify a mathematical function satisfying (i) and (ii), although MacArthur (1955, p.534) noted that it "may be significant" that (1) has the same form as standard measures of entropy and information (cf. Shannon & Weaver, 1949).

With this quantification of resistance, MacArthur described what properties of food webs would maximize it. For m-species communities, (1) is maximized when the species are at m different trophic levels and each level-k species ($k \leq m$) consumes all species at all lower levels. It is minimized when one species consumes the remaining $m-1$ species, which are all at the same trophic level. If the species consumed per consumer is held constant, moreover, (1) increases with species richness. This fact and the fact that (1) increases with the number of food web links entail either that large numbers of species with restricted diets, or small numbers that consume many different species can produce a particular value of (1). On this basis, MacArthur hypothesized that since species-poor communities only have high values of (1) when consumers eat a wide variety of species, but consumer diets in species-rich communities need not be similarly restricted to attain the same (1) value, species-rich communities will usually be more resistant. This prediction may explain, MacArthur (1955, p.535) suggested, why Arctic communities, which usually contain fewer species than temperate and tropical ones, seemed to exhibit greater population fluctuations.

Compared with other ecological research of the time, MacArthur's analysis was one of the most mathematically sophisticated. Instead of focusing on empirical evidence, his primary concern was to formulate intuitive ideas about food web structure with mathematical precision and explore their implications. Unlike his predominantly data-driven contemporaries, Hutchinson encouraged this approach to ecological questions among his students (Kingsland, 1995). Hutchinson believed that speculative but mathematically rigorous analyses were crucial to stimulating novel approaches to recalcitrant problems. By challenging ecologists to pinpoint their shortcomings, which mathematical clarity helped facilitate, even those later found wanting would stimulate development of improved successors.

Sometimes, however, this kind of speculative research is uncritically accepted and treated as definitive. This was especially true of such work in post-WWII ecology. At that time, many ecologists thought their discipline suffered from a general lack of mathematical precision and the absence of a theoretical basis (Slobodkin, 1953;

Margalef, 1958). It was for this reason that another Hutchinson student, Lawrence Slobodkin, originally encouraged MacArthur to pursue graduate work in biology with Hutchinson after MacArthur finished his master's degree in mathematics in 1953 (Kingsland, 1995). Five years later Slobodkin praised MacArthur's (1955) analysis because he believed that it provided a general method for ranking the stability of different communities based on their qualitative food web structure, and that this would in turn improve ecological theory by helping classify and conceptualize specific mathematical models (Slobodkin, 1958). Slobodkin thought the development of a "unified theory of ecology" required analyses like MacArthur's, and that they would remedy a troubling "trend in theoretical ecology towards each investigator developing his own equations and systems as if he were alone in the field" (1958, p.551). But Slobodkin (1958) also accepted MacArthur's explanation of a positive relationship between ecological stability and food web structure without scrutiny. Hutchinson (1959, p.149) similarly exaggerated and mischaracterized MacArthur's explanation as a "formal proof" based on information theory.

Unfamiliar with MacArthur's work and more wary of ecological theory that was not closely tethered to data, British ecologist Charles Elton (1958) took a more empirical approach to the issue. He was motivated by a cautious skepticism of the biological relevance of Lotka and Volterra's mathematical models of biological communities, and similar approaches to ecological theory. Specifically, for Elton (1958, p.131), "there does not seem much doubt that theories that use the food-chain for an explanation of the regulation of numbers are oversimplified." Elton focused instead on empirical evidence that seemed to show that some communities were more resistant to invasion by exotic species than others, and experienced more population fluctuations than others. Several documented cases of biological invasions and pest outbreaks on islands and in ecosystems "simplified by man" were the main support for his analysis.

Elton's concept of ecological stability had two components: resistance to invasion and constancy of populations (1958, p.145). This differed from MacArthur (1955) in two ways. First, constancy was explicitly part of stability whereas MacArthur thought constancy was a byproduct of stability, and not an appropriate part of its definition. Second, Elton's and MacArthur's concepts of resistance depend upon different types of disturbance. MacArthur's refers to a community's reaction to an abnormal abundance of one species. Elton did not explicitly define his concept of resistance, but it presumably refers to the ability to suppress the establishment, reproduction, and spatial spread of invasive species, i.e., to resist invasion. Ecological stability therefore involves resistance to disturbance for both Elton and MacArthur, but each focuses on different types of disturbance. Consequently, although Elton (1958) and MacArthur (1955) are commonly cited as analyzing the same relationship between stability and diversity (Pimm, 1984; Lehman & Tilman, 2000; McCann, 2000), their analyses presuppose different stability concepts.

Their analyses also study different properties of a community's structure. Elton (1958, p.145) did not define "rich" and "simple" in his claim that "simple communities ... [rather than] richer ones ... [are] more subject to destructive oscillations in populations, especially of animals, and more vulnerable to invasions," but species richness, not food web structure as in MacArthur's analysis, was the primary focus of the six kinds of evidence he presented in its support (1958, pp.146–50):

(i) despite his skepticism about their ecological relevance, Elton noted that simple mathematical models of one-predator, one-prey communities predicted fluctuations of population sizes and often mutual extinction, even in the absence of external disturbances;

(ii) experiments on microscopic one-predator, one-prey communities exhibited the same behavior as these mathematical models. Elton (1958) cited Gause (1934), who showed that population fluctuations to the point of extinction were typical in simple protozoan communities;

(iii) small oceanic islands with few species seemed to be more vulnerable to invasion than similar continental areas of the same size and, Elton assumed, more species;

(iv) successful invasions and population explosions of invasive species occurred more often in communities "simplified by man." Elton suggested four types of simplification as potential causes: (a) cultivation of exotic plants without introduction of the fauna normally accompanying them; (b) cultivation of these exotics in partial or complete monocultures; (c) eradication of species that reputedly harm the cultivated plants; and (d) selection of only a few genetic strains for cultivation;

(v) tropical communities, which contain more species and more complicated intra and interspecific dynamics than temperate communities, experienced fewer population explosions, especially of insects; and,

(vi) orchards, which are relatively simple ecological systems, were frequently successfully invaded. Elton suggested that pesticides usually decrease species richness in orchards and eradicate predators of herbivorous insects, which in turn facilitates invasions by exotic species and explosions in natural pest populations.

Since Elton included both constancy and invasion resistance in his concept of ecological stability, (i)–(vi) address different aspects of the SDC debate. (i) and (ii) focus on the lack of constancy, rather than invasibility, of microscopic communities and mathematical models of communities that contain few species. The lack of constancy, not invasibility, of temperate vs. tropical communities is also the focus of (v). Points (iii), (iv), and (vi), on the other hand, concern the greater invasibility of artificially simple or simplified communities – agricultural monocultures like orchards, for instance – and islands which contain relatively few species compared with continental regions of equivalent size.

Along with MacArthur (1955), Elton (1958) has frequently been cited in support of a positive stability–diversity relationship. Elton (1958, p.146) was careful to emphasize, however, the exploratory nature of his analysis, and he explicitly stressed the need for further data collection and study of the issue. An extensive review almost twenty years later (Goodman, 1975), in fact, revealed some of the ways in which subsequent ecological work had failed to support Elton's predictions.

Goodman (1975) first pointed out that (i) and (ii) are only compelling if community models and microscopic communities with higher species richness exhibit less population fluctuation and fewer extinctions than those with fewer species, which was (and remains) unestablished. Second, (iv) and (vi) were not based on controlled experiments and, Goodman further suggested, the simplified ecological systems in question may have achieved highly stable equilibria with their invasive pests were they not continu-

ally disturbed by cultivation. Third, (iii) is only compelling if the possibility that island communities are more susceptible to invasion than continental communities, irrespective of species richness, can be excluded as the cause of the pattern. Elton (1958) had not eliminated this possibility and Goodman noted that Preston's (1968) work on the evolution of island species might provide a better explanation of the greater invasibility of island communities than their supposed lower species richness. Fourth, the observations of population fluctuations in temperate regions and relative constancy of tropical populations that constituted Elton's support for (v) had not been borne out by subsequent studies. By the early 1970s, population fluctuations and insect outbreaks in the tropics that rivaled those in temperate regions had been observed (Leigh, 1975). Their apparent preponderance in temperate compared to tropical regions was probably an artifact of the greater attention and resources devoted to the former.

While Elton's (1958) monograph was in press, Cornell entomologist David Pimentel (1961) conducted the first experimental test of a stability–diversity relationship in fallow fields outside Ithaca, New York. During the summers of 1957 and 1958, Pimentel planted wild cabbage (*Brassica oleracea*) in two fields, one containing approximately 300 plant species and another in which he removed all other plants. He then observed differences in the insect and arachnid communities that developed on individual *B. oleracea* plants in the two fields, and found that the densities of a few pest insects increased dramatically in the monoculture and that more herbivores resided on the monoculture plants than on those in the multi-species community. Although Pimentel did not analyze the statistical significance of his results, he and other ecologists (e.g., Connell & Orias, 1964) believed they showed that the insect outbreaks were more severe in the monoculture and thereby confirmed a positive relationship between ecological diversity and stability.

One shortcoming of Pimentel's study is that diversity was narrowly measured as species richness in his experimental design and data analysis. Changes in species richness are relatively easy to measure, but they show nothing about changes in the proportions of individual organisms in each species of a community, i.e., changes in evenness. Evenness is an important component of ecological diversity (see Section 6), so measuring diversity as species richness limits what Pimentel's study, and any other study using this diversity measure, can show about stability–diversity relationships.

Even with this narrow measure, furthermore, it is unclear that the results of the experiment justify Pimentel's (1961, p.84) claim that, "The lack of diversity in . . . [the] single-species [monoculture] planting allowed outbreaks to occur." The problem is that there are two types of diversity in the monoculture field: plant and faunal diversity. In fact, the low plant diversity of the monoculture was accompanied by *increases* in insect and arachnid richness on the monoculture plants (higher than those on *Brassica* plants in the other field) and the latter may have been a more important determinant of the outbreaks. Thus, while Pimentel interpreted his data as evidence of a positive relationship between diversity (measured as plant richness) and stability (absence of pest outbreaks), it could also be interpreted as evidence of a positive relationship between diversity (measured as insect/arachnid richness) and *instability* (indicated by the outbreaks). Without separating the effects of plant species richness from insect/arachnid richness on outbreak likelihood, Pimentel's results do not provide unequivocal support of a positive stability–diversity relationship.

Another problem is that Pimentel created the monoculture by removing the extant plant community of one field, whereas *Brassica* individuals were comparatively unobtrusively added to the 300 species plant community of the other field. Removing the extant plants undoubtedly initially eliminated the predators of *Brassica* herbivores so that the herbivores already on the *Brassica* that were planted or that immigrated to the monoculture could reproduce unchecked, while herbivores in the other field faced their usual set of predators and did not increase. In other words, the creation of the *Brassica* monoculture eliminated an important component of the extant animal community in that field, whereas the animal community of the other field was relatively undisturbed. The outbreaks may therefore be a consequence of the disturbance that eliminated the predators of *Brassica* herbivores, rather than the low plant-species richness of the monoculture. Pimentel (1961, p.84) recognized this potential confounding effect, and responded:

> the investigator doubts that the time-lag factor [i.e., that fauna had to immigrate to the plants in the monoculture] played a major role in the outbreaks, because wild *Cruciferae* were flourishing adjacent to all plots and provided ample sources of taxa for invasion of the single-species plots.

Whether this response is sound or not, the problem could have been avoided if Pimentel had eliminated all the plants from both fields and then planted a monoculture and a multi-plant-species community.

In discussing his results, Pimentel (1961) proposed an important hypothesis about possible causes of a positive relationship between species richness and constancy of populations. Pimentel may have been the first biologist to recognize that a "portfolio effect" might produce a positive relationship in the same way a diversity of investments usually reduces financial risk (1961, p.84):

> Each host or prey species reacts differently to the same environmental conditions. One host population may decline as another host population increases. This tends to dampen the oscillations of the interacting host and parasite populations and provides greater stability to the system as a whole.

Although isolated one-predator, one-prey communities may fluctuate, this behavior is collectively averaged out in interactions between multiple predator and prey species so that these systems exhibit more constant population sizes overall.

3. Mathematization of Ecological Stability

Although it was probably the first experimental study of the SDC debate, Pimentel's (1961) work received much less attention than the first theoretical analysis of the debate by MacArthur (1955). This likely reflected the transformation of ecology into a more mathematical and theoretical discipline occurring at the time. Largely through the work of Hutchinson and his students (most importantly, MacArthur), mathematical modeling became more sophisticated and prevalent within ecology in the 1960s.

Ecologists became increasingly concerned with formalization and theoretical systematization of ecological concepts (Kingsland, 1995). Hutchinson's (1957) highly abstract set-theoretic definition of the niche as an n-dimensional hypervolume is one example, as were attempts to develop precise definitions and measures of ecological stability, diversity, and complexity by mathematically oriented ecologists around the same time. Lewontin (1969, p.13) captured the intellectual shift within ecology: "To many ecologists their science has seemed to undergo a major transformation in the last 10 years, from a qualitative and descriptive science to a quantitative and theoretical one."

In the context of this transformation, the stability theory of linearized differential equations might have seemed to provide an adequate framework for evaluating stability–diversity–complexity relationships. For instance, the dynamics of a biological community near equilibrium could be represented mathematically with such equations, and formal stability criteria developed for them could be used to assess whether the community was ecologically stable. This was one of the methods utilized by Lotka and Volterra, for example, to analyze the stability of biological communities.

A problem with this specific modeling strategy, however, revealed a general difficulty with the new theoretical orientation of ecology: achieving mathematical precision and rigor often made empirical measurement more difficult. For this reason, Patten (1961) criticized the ecological relevance of the stability theory of linear differential equations. He pointed out that representing ecological systems with these equations requires extensive quantitative data about numerous parameters, which are practically impossible to obtain in the field. To illustrate the problem, consider a community represented by:

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{A}\mathbf{x}(t); \tag{2}$$

where $\mathbf{x}(t)$ is a vector $\langle x_1, x_2, \ldots, x_i, \ldots, x_n \rangle$ $(i = 1, \ldots, n)$ representing the densities of n species, and $\mathbf{A}$ is an $n \times n$ matrix of constant real coefficients $[a_{ij}]$ representing (linear) relationships between species near equilibrium, such as competition, predation, mutualism, etc. (see Justus, 2005). The problem Patten recognized is that the a_{ij} are extremely difficult to measure for complex, natural communities. Thus, "[s]ince it is usually not possible to obtain sufficient data to represent natural ecosystems canonically [as in (2)] and since they are probably not linear, formal stability criteria are not generally available for ecological applications" (Patten, 1961, p.1011).

Challenges like this and the plurality of distinct senses of stability in the ecological literature by the mid-1960s – resistance, resilience, tolerance, and constancy (see Section 5) – convinced many ecologists that a critical assessment of the concept was needed. Ecological stability was not unique in this regard. Many fundamental but problematically unclear ecological concepts were being examined at that time to determine whether they could be reformulated within mathematical frameworks used in other sciences, especially physics (e.g., Kerner, 1957, 1959; Lewontin, 1969). Doing so would specify their meaning clearly and possibly integrate them into a common mathematical framework. Theoretical unification of this kind had proved fruitful in physics, and ecologists had similar aspirations for their discipline. The existence of a well-developed mathematical theory of stability made such a rethinking of ecological

stability seem especially promising and in May a symposium at Brookhaven National Laboratory was ostensibly devoted to examining the meaning of stability and diversity (Woodwell & Smith, 1969, p.v). Only one paper seriously addressed this task (Lewontin, 1969), but it profoundly impacted the subsequent development of the SDC debate.

Lewontin (1969) surveyed various mathematical notions of stability and their relation to ecological stability. He began by representing a biological community of n species as a vector $\mathbf{x}(t) = \langle x_1(t), x_2(t), \ldots, x_n(t) \rangle$ in an n-dimensional vector space H where t represents time. Different coordinates of $\mathbf{x}$ were intended to represent different abundances or densities of the n species in the community. A deterministic vector function $\mathbf{T}$ over H, $\mathbf{T}: H \to H$, represents the mechanisms responsible for the dynamics of the community. $\mathbf{T}$ represents, therefore, density-dependencies, interspecific interactions, gene flow, etc. between the n species and the effects environmental parameters have on these species. $\mathbf{T}$ is often specified, for instance, in matrix form by a mathematical model of the community (e.g., [2] from above). Application of $\mathbf{T}$ to $\mathbf{x}$ usually induces a change in the vector's coordinates. Points in H for which $\mathbf{T} = \mathbf{I}$ where $\mathbf{I}$ is the identity matrix, induce no change in $\mathbf{x}$ and are called equilibrium points. A vector at such a point will not move from it.

Within this framework, Lewontin distinguished "neighborhood" stability (also called local stability) from global stability. Let $\mathbf{x}_q$ be the position vector for some equilibrium point. Following the mathematical theory of stability pioneered by Lyapunov (1892 [1992]), $\mathbf{x}_q$ is neighborhood stable if and only if for any $\mathbf{x}$ *arbitrarily close* to $\mathbf{x}_q$:

$$\lim_{n \to \infty} \mathbf{T}^n(\mathbf{x}) = \mathbf{x}_q; \tag{3}$$

where $\mathbf{T}^n(\mathbf{x})$ designates n applications of $\mathbf{T}$ to $\mathbf{x}$. The subset of H within which vectors satisfy (3) defines the *domain of attraction* of $\mathbf{x}_q$. Restricting attention to vectors arbitrarily close to $\mathbf{x}_q$ allows approximation of $\mathbf{T}$ by a linear vector function $\mathbf{L}$. In effect, $\mathbf{T}$ behaves as a linear vector function arbitrarily close to $\mathbf{x}_q$. This linearization of $\mathbf{T}$, in turn, allows evaluation of (3) with well-known mathematical techniques (see Hirsch & Smale, 1974). If (3) holds for all of H and not just arbitrarily close to $\mathbf{x}_q$, $\mathbf{x}_q$ is called globally stable.

By representing the perturbation of a biological community as a displacement from $\mathbf{x}_q$ to $\mathbf{x}$, the community's stability can be represented by local and global stability. The set of perturbations (represented by the displaced vectors $\mathbf{x}$) for which the community returns to equilibrium (represented by $\mathbf{x}_q$) determines its attraction domain. In ecological terms, locally and globally stable communities are often informally characterized as those that return to equilibrium after "very small" perturbations – such as slight climatic disturbances perhaps – and those that return after *any* perturbation.

Lewontin (1969, p.16) argued that local stability inadequately defines ecological stability because it only describes system behavior arbitrarily close to a particular point in H. Strictly speaking, therefore, local stability only describes system behavior for *infinitesimal* displacements from $\mathbf{x}_q$. Real-world perturbations, however, are obviously not of infinitesimal magnitude. Any real perturbation will expel a system at a strictly locally stable equilibrium from its infinitesimal stability domain. Besides this, Preston (1969) pointed out in the same Brookhaven symposium that it is fundamentally unclear how infinitesimal displacement can be biologically interpreted (or empirically mea-

sured). Local stability therefore says nothing about system response to real-world perturbation. In contrast, Lewontin suggested that the stability of an ecological system depends upon the (non-infinitesimal) size of its attraction domain. If the formally precise notion of "arbitrarily close" is informally construed as "very close," moreover, local stability still only describes system behavior for very small perturbations and thus provides little or no information about attraction domain size. For this reason, local stability poorly defines ecological stability.

Local and global stability also poorly define ecological stability, Lewontin added, because they are dichotomous concepts, whereas biological communities seem to exhibit different degrees of stability. Elton and MacArthur's concepts of ecological stability confirm Lewontin's claim: Elton believed monocultures were *less* stable than "natural" communities, and the Shannon index MacArthur used to operationalize stability obviously takes values other than 1 and 0. Other stability concepts discussed in Section 5, such as resilience and tolerance, are all matters of degree also.

Lewontin drew an important distinction between stability as a perturbation-based concept, which resistance, resilience, and tolerance are, and non-perturbation-based concepts, such as constancy. Constancy, Lewontin (1969, p.21) suggested, "is a property of the actual system of state variables. If the point representing the system is at a fixed position, the system is constant. Stability, on the other hand, is a property of the dynamical space in which the system is evolving." The two concepts are therefore different and not necessarily coextensive. A system in a large, steep domain of attraction, for instance, may be in constant flux due to frequent external perturbations. Conversely, an unperturbed system may be constant at an unstable equilibrium. Partly for this reason, Section 5 argues that ecological stability should not be defined in terms of constancy.

4. The End of the Consensus

By the time of Lewontin's analysis, a strong consensus had emerged that ecological stability is positively associated with diversity and/or complexity (May, 1974; De Angelis, 1975; Pimm, 1991). In a textbook on environmental science, for instance, Watt (1973) deemed the claim that biological diversity promotes population stability a core principle of the discipline. A half-decade later, the consensus had evaporated. The main reason for its demise was the publication of rigorous analyses of mathematical models of communities that seemed to show increased complexity actually decreased stability.

In a one-page *Nature* paper, Gardner and Ashby (1970) initiated the first doubts with an analysis of the relationship between complexity and asymptotic Lyapunov stability in linear models such as (2) from above. Understood as a model of a biological community, the coefficient a_{ij} from (2) represents the effect of species j on species i. Its quantitative value represents the effect's magnitude and its sign represents whether the effect is positive or negative. For these models, complexity was defined in terms of the number of variables (n) and connectance (C). Gardner and Ashby defined connectance as the percentage of nonzero coefficients in $\mathbf{A}$.

Values of the diagonal elements of $\mathbf{A}$ were randomly chosen from the interval $[-1, -0.1]$ to ensure each variable was "intrinsically stable", i.e., self-damped. For given

values of n and C, Gardner and Ashby then randomly distributed an equal number of -1 and $+1$ values within the off-diagonal parts of $\mathbf{A}$ in accord with the C value. Whether systems represented by (2) are stable depends upon the eigenvalues of $\mathbf{A}$. These are scalar value roots λ_i of the characteristic polynomial of $\mathbf{A}$, $|\mathbf{A} - \lambda\mathbf{I}| = 0$, where $\mathbf{I}$ is the identity matrix. Lyapunov ([1892] 1992) proved an equilibrium of a system represented by (2) is asymptotically stable iff:

$$\mathrm{Re}\lambda_i(\mathbf{A}) < 0 \text{ for } i = 1, \ldots, n; \tag{4}$$

where $\mathrm{Re}\lambda_i(\mathbf{A})$ designates the real part of λ_i, the i-th eigenvalue of $\mathbf{A}$. Whether (4) holds depends on the pattern of nonzero values within $\mathbf{A}$. Different randomizations specify different patterns, which may produce different stability results as evaluated by (4). The probability of stability for given values of n and C can therefore be approximated with the results from a sufficiently large number of randomizations. Contrary to most expectations, Gardner and Ashby found the probability of local stability was negatively correlated with n, and with C. Interpreted ecologically, their analysis seemed to show that the more species (greater n) and the higher the frequency of species interaction in a biological community (greater C), the less likely it is (locally) stable.

The study that inverted the opinion of most ecologists, however, was published by Robert May three years later (May, 1974). One reason for its influence was that May generalized Gardner and Ashby's analysis by randomly assigning non-diagonal elements values from a distribution with a zero mean and mean square value of s^2 for different values of s. s represents the interaction strength between variables, which had been restricted to $+1$ and -1 by Gardner and Ashby. May then analyzed how the probability of stability changed with different values of n, C, and s; Gardner and Ashby had not analyzed how s affects the probability of stability. The main result was that for systems in which $n \gg 1$, there is a sharp transition from high to low probability of stability as s or C exceeds some threshold. He found, for instance, that the probability of stability for these systems is approximately 1 if $s\sqrt{nC} < 1$ and approximately 0 if $s\sqrt{nC} > 1$. His analysis also confirmed Gardner and Ashby's finding that for fixed C and s the probability of local stability decreases with increasing n. In general, these results seemed to demonstrate that high connectance, species richness, or strong species interactions preclude communities from being stable. May defined complexity in terms of connectance, richness, and interaction strength, so the results seemed to confirm a negative stability–complexity relationship.

One compelling feature of May's result was its generality. Besides requiring the entries of the diagonal be -1, no assumption was made about the coefficients of $\mathbf{A}$ from (2). In the parameter space representing all possible linear systems, therefore, May's results seemed to demonstrate that stability is exceedingly rare. It remained possible, May (1974, p.173) recognized, that actual biological communities primarily inhabit a rare stable realm of parameter space:

> Natural ecosystems, whether structurally complex or simple, are the product of a long history of coevolution of their constituent plants and animals. It is at least plausible that such intricate evolutionary processes have, in effect, sought out those relatively tiny and

mathematically atypical regions of parameter space which endow the system with long-term stability.

To address this possibility, May analyzed several common mathematical models of communities. Two patterns emerged. First, generalizations of simple models representing few species, such as one-predator, one-prey Lotka-Volterra models, to more complicated n-species models were generally less likely to be stable than the simple models. This underscored Goodman's (1975) criticism of the first type of evidence Elton (1958) cited in favor of a positive stability-diversity relationship (see Section 2) because it showed that multi-species predator–prey models are less, rather than more, stable than predator–prey models of fewer species.

Second, many modifications that made models more realistic also made them less stable. For instance, community models often unrealistically assume an unvarying deterministic environment and thereby set parameters to constant values. May showed that if some or all parameters are allowed to vary stochastically to represent environmental fluctuation, the resulting model is generally less likely to be stable. Similarly, most community models represent birth and death as continuous processes, even though their occurrences are discrete events in nature. May (1974, p.29) found that that more realistic models with discrete variables are likely to be less stable than their continuous counterparts. The disparity between models with discrete and continuous variables also becomes more pronounced as the number of variables increases.

The upshot of May's work was that stability is rare both in the "parameter space" of possible models and for more realistic community models, and that its probability decreases with model complexity. What it showed about actual biological communities, as opposed to models of them, remained unclear. Lewontin (1969) had argued, for instance, that the relationship between local stability and ecological stability is tenuous at best (see Section 3). The worry was that May's analysis may be an interesting mathematical exercise with little or no biological application. For this reason, in fact, May (1974, p.75–6) hedged about the proper interpretation of his results: "the balance of evidence would seem to suggest that, in the real world, increased complexity *is* usually associated with greater stability." Thus, for May, the results "suggest that theoretical effort should concentrate on elucidating the very special and mathematically atypical sorts of complexity which could enhance stability, rather than seeking some (false) 'complexity implies stability' general theorem" (1974, p.77). May recognized that most natural biological communities may have evolved a specific structure (the "atypical complexity") that generates stability. For May, what this structure is should be the focus of ecological modeling.

Despite May's (1974) qualifications and these criticisms, his work was widely accepted (Lawlor, 1978) and taken to overturn the consensus about a positive correlation between community complexity and stability in favor of a negative one (De Angelis, 1975). Earlier work on the SDC debate, however, did not concern the relationship between local stability and complexity, which was May's main focus. MacArthur (1955), Elton (1958), and Pimentel (1961), for instance, whose work set most ecologists' initial expectations about the debate, were concerned with resistance and constancy, not local stability, and focused primarily on species richness rather than complexity. May's analysis only provides insights into the stability–diversity relationship, therefore, if local stability and

ecological stability (despite Lewontin's [1969] objections) and ecological diversity and complexity are closely related. Diversity and complexity are related in the weak sense that species richness is a component of both, but this relationship is too weak to guarantee even that a positive correlation between them exists.

5. Contextualization and Classification of Ecological Stability

As the history above indicates, one fundamental obstacle to resolving the SDC debate is finding an adequate definition of ecological stability. Numerous definitions and categorizations of the concept have been proposed (Lewontin, 1969; Orians, 1975; Pimm, 1979, 1984, 1991; Grimm & Wissel, 1997; Lehman & Tilman, 2000) and this plurality is responsible for much of the confusion and lack of progress in resolving the debate. As part of their argument that ecological theory has failed to provide a sound basis for environmental policy – they believe the SDC debate provides a clear example of this failure – Shrader-Frechette and McCoy (1993) have also argued that several proposed definitions of ecological stability are incompatible and that the concept is itself "conceptually confused" or "inconsistent."

A plurality of distinct senses of stability have been used within ecology: resistance, resilience, tolerance, constancy, local and global Lyapunov stability. Before considering these concepts in more detail, it should first be noted that their attribution must be made with respect to two evaluative benchmarks. The first is a system description (M) that specifies how the system and its dynamics are represented. The second is a specified reference state or dynamic (R) of that system against which stability is assessed. In most ecological modeling, M is a mathematical model in which:

(i)   variables represent system parts, such as species of a community;
(ii) parameters represent factors that influence variables but are (usually) uninfluenced by them, such as solar radiation input into a community; and,
(iii) model equations describe system dynamics, such as interactions among species and the effect environmental factors have on them.

M therefore delineates the boundary between what constitutes the system, and what is external to it. Relativizing stability evaluations to M is a generalization of Pimm's (1984) relativization of stability to a "variable of interest."

The specification of M partially dictates how R should be characterized. A biological community, for instance, is usually described as a composition of populations of different species. Consequently, R is often characterized in terms of the "normal" population sizes of each species. Since ecological modeling in the late 1960s and 1970s was dominated by the development of mathematically tractable equilibrium models (Chesson & Case, 1986; Pimm, 1991), the "normal" population sizes were often assumed to be those at equilibrium, i.e., constant population sizes the community exhibits unless perturbed. This is not the only possible reference state, however. A community may be judged stable, for instance, with respect to a reference *dynamic* the models exhibit. Common examples are a limit cycle – a closed path C that corresponds to a periodic solution of a set of differential equations and toward which other paths asymptotically approach – or a more complicated attractor dynamic (Hastings et al.,

1993). Ecological stability can also be assessed with respect to some specified range of tolerated fluctuation (Grimm & Wissel, 1997). R may also be characterized solely in terms of the presence of certain species. Only extinction would constitute departure from this reference state.

The details of M and R are crucial because different system descriptions – e.g., representing systems with different variables or representing their dynamics with different functions – may exhibit different stability properties or exhibit them to varying degrees relative to different specifications of R. Specifying R as a particular species composition vs. as an equilibrium, for instance, can yield different stability results. Similarly, different M can produce different assessments of a system's stability properties. Describing a system with difference vs. differential equations is one example (May, 1974a).

The details of M and R are also important because they may specify the spatial and temporal scales at which the system is being analyzed, which can affect stability assessments. Systems with low resistance but high resilience, for example, fluctuate dramatically in response to perturbation but return rapidly to their reference state R (see below). Low resistance is detectable at fine-grained temporal scales, but systems may appear highly resistant at coarser scales because their quick return to R prevents detection of fluctuation. Similarly, significant fluctuations in spatially small areas may contribute to relatively constant total population sizes maintained through immigration and emigration in larger regions.

Once (and only once) M and R are specified, the stability properties of a system can be determined. These properties fall into two general categories, depending on whether they refer to how systems respond to perturbation (relative to R) or refer to system properties independent of perturbation response. A perturbation of an ecological system is any discrete event that disrupts system structure, changes available resources, or changes the physical environment (Krebs, 2001). Typical examples are flood, fire, and drought. Perturbations are represented in mathematical models of communities by externally induced temporary changes to variables that represent populations, to parameters that represent environmental factors, and/or to model structure. Many, perhaps most, real-world perturbations of communities should be represented by changes to both variables and parameters. A severe flood, for instance, eradicates individual organisms and changes several environmental factors affecting populations. In the following, let P_v, P_p, and P_{vp} designate perturbations that change only variables, change only parameters, and those that change both, respectively.

There are four plausible adequacy conditions for a definition of ecological stability:

(A1) the ecological stability of a biological community depends upon how it responds to perturbation ([A2]–[A4] specify the form of the required dependency);
(A2) of two communities A and B, the more ecologically stable community is the one that would exhibit less change if subject to a given perturbation P;
(A3) if A and B are in a pre-perturbation reference state or dynamic R, the more ecologically stable community is the one that would most rapidly return to R if subject to P; and,
(A4) if A and B are in R, the more ecologically stable community is the one that can withstand stronger perturbations and still return to R.

(A1) captures the idea that the behavior of a community is a reliable indicator of its ecological stability only if the behavior reflects how perturbation changes the community. If unperturbed, a community may exhibit great constancy throughout some period. It may be, however, that if it had been even weakly perturbed, it would have changed dramatically. Constancy of this community surely does not indicate ecological stability when it would have changed substantially if perturbed slightly. Similarly, variability of a community does not necessarily indicate lack of ecological stability if it is the result of severe perturbations. perturbations that would cause greater fluctuations or even extinctions in less stable communities.

The reason for (A2) is that more stable communities should be less affected by perturbations than less stable ones. Communities that can withstand severe drought, for instance, with little change are intuitively more stable than those modified dramatically. This was the idea, for example, underlying MacArthur's (1955) definition of community stability. The justification for (A3) is that more stable communities should more rapidly return to R following perturbations than less stable ones. This adequacy condition captures the idea that lake communities that return to R quickly after an incident of thermal pollution, for instance, are more stable than those with slower return rates following similar incidents. The ground for the last condition is that communities that can sustain stronger perturbations than others and still return to R should be judged more stable.

Three concepts – resistance, resilience, and tolerance – represent the properties required of ecological stability by (A2)–(A4). Resistance is inversely correlated with the degree a system changes relative to R following perturbation (P_v, P_p, or P_{vp}). Since perturbations vary in magnitude, resistance must be assessed against perturbation strength. Large changes after weak perturbations indicate low resistance; small changes after strong perturbations indicate high resistance. Resistance is thus inversely proportional to perturbation sensitivity.

Depending on M and R, changes in communities can be evaluated in different ways, each of which corresponds to a different measure of resistance. Community resistance is typically measured by the changes in species *abundances* following perturbation. It could, however, be measured by changes in species *composition* following perturbation, or in some other way. Pimm's (1979) concept of species deletion stability, for instance, measures resistance by the number of subsequent extinctions in a community after one species is eradicated.

Different types of perturbations, moreover, yield different measures of resistance. Since evaluating resistance requires considering perturbation strength, strengths of different types of perturbations must be comparable for there to be a single measure of resistance for a system. Such comparisons are sometimes straightforward. If one perturbation eradicates half of species x in a community, for instance, another that eradicates 75 percent of x is certainly stronger. If another perturbation eradicates 25 percent of 3 species or 5 percent of 15 species in the community, however, it is unclear how its strength should be ranked against the perturbation that eradicates 75 percent of x. What criteria could be used to compare strengths of P_v, P_p, or P_{vp} perturbations, to which systems may show differential sensitivity, is even less clear. Systems that are highly resistant to P_v perturbations may be extremely sensitive to even slight P_p. Comparing

the resistance of communities is therefore only unproblematic with respect to perturbations of comparable kind.

Resilience is the rate a system returns to R following perturbation (P_v, P_p, or P_{vp}). Like resistance, resilience must be assessed against perturbation strength unless, although unlikely for most types of perturbation, return rate is independent of perturbation strength. Slow return rates after weak perturbations indicate low resilience and rapid rates following strong perturbations indicate high resilience. Systems may not return to R after perturbation, especially following severe perturbation, so, unlike resistance, resilience is only assessable for perturbations that do not prevent return to R. Note that resilience and resistance are independent concepts: systems may be drastically changed by weak perturbations (low resistance) but rapidly return to R (high resilience), and vice versa.

Resilience is commonly measured as the inverse of the time taken for the effects of perturbation to decay relative to R. For a specific mathematical model, this can be determined analytically or by simulation. For the community described by equation (2) above, for instance, resilience to a P_v perturbation that eradicates half of one species could be simply measured by, $|t_{eq} - t_p|$, where t_p is the time at which the community is initially perturbed and t_{eq} is the time at which the community reestablishes equilibrium. Resilience to P_v perturbation is determined by the largest real eigenvalue part for systems modeled by linear differential equations, and analytic methods have been developed to assess resilience to P_v perturbation for nonlinear models. Empirical measurement of resilience for communities in nature, however, is often thwarted by subsequent perturbations that disrupt return to R. This difficulty can be avoided if subsequent perturbations can be evaded with controlled experiments. If the return rate is independent of perturbation strength, estimation of resilience is also more feasible because only the decay rate of the perturbation effects need be measured before the system is further perturbed; measurement of perturbation strength is not required (Pimm, 1984). Like resistance, furthermore, different types of perturbations yield different measures of resilience since return rate to R may depend upon the way in which systems are perturbed. A system may be highly resilient to P_v perturbation and poorly resistant to P_p perturbation, for instance, or more resilience to some P_v or P_p perturbations than others.

Tolerance, or "domain of attraction" stability, is the ability of a system to be perturbed and return to R, regardless of how much it may change and how long its return takes. More precisely, tolerance is positively correlated with the range and strength of perturbations a system can sustain and still return to R. The magnitudes of the strongest perturbations it can sustain determine the contours of this range. Note that tolerance is conceptually independent of resistance and resilience: a system may be severely perturbed and still return to R (high tolerance), even if it changes considerably (low resistance) and its return rate is slow (low resilience), and vice versa.

Similar to resistance and resilience, different kinds of perturbations yield different measures of tolerance. Tolerance to P_v perturbations, for instance, is determined by the maximal changes variables can bear and not jeopardize the system's return to R. With respect to P_v perturbations that affect only one species of a community, for instance, tolerance can be simply measured by the proportion of that species that can be eradicated without precluding the community's return to R. If a nontrivial equilibrium of

equation (2) from above is globally stable, for instance, the community described by the equation is maximally tolerant to P_v perturbations relative to this reference state because the community will return to it after any P_v perturbation that does not eradicate one of the species. Variables of a system may be perturbed, however, in other ways. A P_v perturbation may change all the variables, several, or only one; it may change them to the same degree, some variables more severely than others, and so on. How exactly variables are perturbed may affect whether the system returns to R. System tolerance must therefore be evaluated with respect to different types of perturbation. The same goes for assessing tolerance to P_p or P_{vp} perturbations. Note that local asymptotic Lyapunov stability corresponds to tolerance to P_v perturbation in the infinitesimal neighborhood of an equilibrium, and global asymptotic Lyapunov stability corresponds to tolerance to any P_v perturbation (see Section 3).

Although resistance, resilience, and tolerance do not adequately explicate ecological stability individually, they do so collectively. In fact, they constitute jointly sufficient and separately necessary conditions for ecological stability, notwithstanding Shrader-Freschette and McCoy's (1993, p.58) claim that such conditions do not exist. Consider sufficiency first. Since these three concepts represent the properties underlying conditions (A2)–(A4), communities exhibiting them to a high degree would change little after strong perturbations ([A2]), return to R rapidly if perturbed from it ([A3]), and return to R following almost any perturbation ([A4]). As such, these three properties certainly capture ecologists' early conceptions of ecological stability (see Sections 2 and 3), and there does not seem to be any further requirement of ecological stability that a community exhibiting these properties would lack.

Each concept is also necessary. Highly tolerant and resistant communities, for instance, change little and return to R after most perturbations. In regularly perturbing environments, however, even a highly resistant and tolerant community may be iteratively perturbed to the boundary of its tolerance range and "linger" there if its return rate to R is too slow. Subsequent perturbations may then displace it from this range, thereby precluding return to R. If this community rapidly returned to R after most perturbations (high resilience), it would rarely reach and would not linger at its tolerance boundary. In general, low resilience preserves the effects perturbations have on communities for extended, perhaps indefinite durations, which seems incompatible with ecological stability.

Similar considerations show that tolerance and resistance are necessary for ecological stability. A highly resilient and tolerant but weakly resistant community rapidly returns to R following almost any perturbation, but changes significantly after even the slightest perturbation, which seems contrary to ecological stability. The dramatic fluctuation such communities would exhibit in negligibly variable environments is the basis for according them low ecological stability. A highly resilient and resistant but weakly tolerant community changes little and rapidly returns to R when perturbed within its tolerance range, but even weak perturbations displace it from this range and thereby preclude its return to R, which also seems contrary to ecological stability.

Compared with resistance, resilience, and tolerance, constancy is a fundamentally different kind of concept. Unlike them, it is not defined in terms of response to perturbation, and thus violates adequacy condition (A1). Rather, constancy of a biological community is typically defined as a function of the variances and/or covariances in

species biomasses. Tilman (1996, 1999; Lehman & Tilman, 2000), for instance, defined ecological stability as "temporal stability" (S_t):

$$S_t(C) = \frac{\sum_{i=1}^{n} \overline{B_i}}{\sqrt{\sum_{i=1}^{n} Var(B_i) + \sum_{\substack{i=1; j=1 \\ i \neq j}}^{n} Cov(B_i, B_j)}}; \qquad (5)$$

where C designates an n-species communities; B_i is a random variable designating the biomass of species i in an n-species community C assayed during some time period, and let $\overline{B_i}$ designate the expected value of B_i for the time period it is assayed; Var designates variance; and Cov designates covariance. The motivating intuition for this definition is the idea that if two series of abundances are plotted across time, the more stable one exhibits less fluctuation (Lehman & Tilman, 2000). In particular, if a community becomes more variable as judged by variances and covariances between its biomasses, regardless of what causes the variability, the denominator of (5) increases and its temporal stability decreases. One counterintuitive feature of this definition is that a community could become more stable solely because mean biomasses increase. This problem is easily avoided by measuring constancy strictly in terms of biomass variability [e.g., reformulating (5) with a numerator of 1], but this does not circumvent the fundamental difficulty that defining ecological stability as constancy does not satisfy (A1), irrespective of how constancy is measured. Contrary to the intuition motivating this definition, however, constancy is neither necessary nor sufficient for ecological stability. It is insufficient because a community may exhibit great constancy if unperturbed, but change dramatically if it were even weakly perturbed. Unless constancy is a result of how a community responds to perturbation, it can mask extreme sensitivity to perturbation, which is incompatible with ecological stability. By itself, therefore, constancy is not a reliable indicator of ecological stability.

Constancy is not necessary for ecological stability for two reasons. First, although a highly stable community at equilibrium remains relatively constant, it may fluctuate if subject to severe perturbations, perturbations that would drastically modify or eradicate weakly stable communities. It would be unjustifiable to regard these fluctuations as evidence of low ecological stability. The problem is that because constancy is not defined relative to perturbation response, it cannot distinguish between fluctuations that are a consequence of strong perturbation, which are consistent with ecological stability, and those that reveal susceptibility to weak or moderate perturbations, which are incompatible with ecological stability.

The second reason constancy is not necessary is that a highly stable system will not be constant if R is not an equilibrium reference state. Communities may be highly resistant, resilient, and tolerant with respect to regular limit cycles or more complicated attractor dynamics. In this case, the community changes little relative to the limit cycle or attractor after strong perturbation, rapidly returns to the limit cycle or attractor after strong perturbation, and returns to the limit cycle or attractor even after severe perturbation. Lack of constancy of such a community does not detract from the fact that any adequate conception of ecological stability should judge it highly stable relative to R.

Table 18.1 Different concepts of ecological stability. R designates a reference state or dynamic. P_v designates perturbations to system variables; P_p designates perturbations to parameters; and P_{vp} designates perturbations that affect both variables and parameters

	Type	Definition	Properties
Perturbation-based stability types	Resilience	Rate a system returns to R following P_v, P_p, or P_{vp}	Comparative concept
	Resistance	Inverse of the magnitude a system changes relative to R following P_v, P_p, or P_{vp}	Comparative concept
	Tolerance	Range of P_v, P_p, or P_{vp} a system can sustain and still return to R	Comparative concept
	Local asymptotic stability	A system returns to R following "small" P_v	(i) Dichotomous concept (ii) Special case of tolerance to p_v
	Global asymptotic stability	A system returns to R following any P_v	(i) Dichotomous concept (ii) Special case of tolerance to p_v
Perturbation-independent stability types	Constancy	Inverse of the variability of a system	Comparative concept

Most classifications of ecological stability include an additional non-perturbation-based stability concept, persistence: the time a community remains in R irrespective of whether or not it is perturbed. Retaining a particular species composition or biomasses within delimited ranges are typical reference states for gauging persistence. Persistence is usually measured by how long they do, or are predicted to, exhibit these states. It could, for instance, be measured by the time minimum population levels have been sustained (e.g., nonzero levels), or will be sustained based on predictions from mathematical models (Orians, 1975). As such, persistence is in fact only a special case of constancy measured in terms of the time R has been or will be exhibited, rather than variability with respect to R.

Table 18.1 presents a taxonomy of the stability concepts: resistance, resilience, tolerance, constancy, and local and global Lyapunov stability. The taxonomy classifies these concepts into two general categories, defines each, and lists some of their properties.

It is worth pausing over what the framework for ecological stability presented above shows about the general concept. It certainly shows that ecologists have used the term "stability" to describe several distinct features of community dynamics, although only resistance, resilience, and tolerance adequately define ecological stability. This plurality does not manifest, however, an underlying vagueness, "conceptual incoherence," or

"inconsistency" of the concept, as Shrader-Frechette and McCoy (1993, p.57) suggest in their general critique of basic ecological concepts and ecological theories based on them. Two claims seem to ground their criticism. First, that if "stability" is used to designate distinct properties, as it has been in the ecological literature, this indicates the concept is itself conceptually vague and thereby flawed. Although terminological ambiguity is certainly undesirable, most ecologists unambiguously used the term to refer to a specific property of a community and accompanied the term with a precise mathematical or empirical operationalization (see Sections 2–4). Since these were in no sense vague, in no sense was ecological stability "vaguely defined" (Shrader-Frechette & McCoy, 1993, p.40). Ecologists quickly appreciated this terminological ambiguity, moreover, and began explicitly distinguishing different senses of ecological stability with different terms (Odenbaugh, 2001). Lewontin's (1969) review was the first example, and subsequent analyses of the concept did not jettison this insight.

Shrader-Frechette and McCoy's second claim is that, "There is no homogeneous class of processes or relationships that exhibit stability" (1993, p.58). The assumption underlying this claim seems to be that concepts in general, ecological stability in particular, must refer to a homogeneous class to be conceptually unproblematic. That ecological stability does not, and worse, that ecologists have supposedly attributed inconsistent meanings to it, shows that the concept is incoherent, they believe, much like the vexed species concept (1993, p.57).

Shrader-Freschette and McCoy do not offer an argument for this assumption, and it is indefensible as a general claim about what concepts must refer to. Common concepts provide clear counterexamples. The concepts "sibling," "crystal," and "field," for instance, refer to heterogeneous classes, but there is nothing conceptually problematic about them. There is debate about the idea of disjunctive *properties* in work on multiple realization (Fodor, 1974; Kim, 1998; Batterman, 2000), but the criticisms raised there against disjunctive properties do not necessarily apply to disjunctive *concepts*, nor were they intended to. Kim (1998, p.110) emphasizes this point:

> Qua property, dormativity is heterogeneous and disjunctive, and it lacks the kind of causal homogeneity and projectability that we demand from kinds and properties useful in formulating laws and explanations. But [the concept of] dormativity may well serve important conceptual and epistemic needs, by grouping properties that share features of interest to us in a given context of inquiry.

Even if criticisms of disjunctive properties were sound, it therefore would not follow that the disjunctive concepts such as ecological stability are also problematic. The conceptual and epistemic utility of a concept is enhanced, furthermore, if there are clear guidelines for its application. The preceding analysis attempts to provide such guidelines.

Moreover, the definitional statuses of the concepts of ecological stability and species are not analogous. Biologists have proposed plausible, but incompatible competing definitions for the species concept because it is problematically ambiguous (Ereshefsky, 2001). That resistance, resilience, and tolerance have been referred to under the rubric "stability," however, does not show that ecological stability is similarly problematically ambiguous because they are conceptually independent and therefore compatible, as different senses of "species" are not. As classifications of different stability concepts attest (e.g., Lewontin, 1969; Orians, 1975; Pimm, 1984), most ecologists recognized that

there are several senses of ecological stability, and individual stability concepts were rarely proposed as *the* uniquely correct definition of ecological stability. Rather, they were and should be understood as distinct features of ecological stability, not competing definitional candidates. Like many scientific concepts, ecological stability is multifaceted, and the distinct referents ecologists attributed to it accurately reflect this. Conceptual multifacetedness alone does not entail conceptual incoherence or inconsistency.

6. Measures of Ecological Diversity and Complexity

Compared to the concept of ecological stability, little attention was devoted to clarifying the concept of ecological diversity or complexity in the early SDC debate. Significant disagreement about how the concept of diversity should be measured, however, emerged during this period (Magurran, 1988). By the early 1970s, moreover, enough attention was being devoted to common indices of diversity to spark criticism, perhaps the most incisive from Hurlbert (1971) (see below).

Conceptually, there was wide agreement among ecologists at the time that diversity has two main components: species richness and evenness (see Section 1). Distinct quantitative diversity indices result from different ways of quantifying and integrating these two notions. For a clearer understanding of these concepts, consider two simple communities, A and B, both composed of two species s_1 and s_2. A and B have the same species richness. If the percentages of individuals distributed among the two species are 0.02 percent and 99.98 percent for A and 50 percent and 50 percent for B, respectively, B seems more diverse than A. This can be represented by a higher evenness value for B. Besides that a diversity index should increase with species richness, therefore, another reasonable adequacy condition seems to be that it should increase with evenness. Many distinct quantitative indices, however, satisfy these two adequacy conditions.

Probably the most popular index of community diversity, then and now, is the Shannon index (H) (see equation [1], Section 2). The index was originally intended to quantify the amount of information in a communicated message (Shannon & Weaver, 1949). Good (1953) and Margalef (1958) were the first to use it as an index of diversity. In the ecological context, p_i designates the proportion of individuals in the i-th species of a community, so that H is at its maximal value for a given species richness n ($H = \ln(n)$) when the individuals are equally distributed among the species.

Another common diversity index (D) is the complement of Simpson's (1949) "measure of concentration":

$$1 - \sum_{i=1}^{n} p_i^2. \tag{6}$$

Simpson (1949) explained that his concentration index represents the probability that two individuals chosen at random (with replacement) from a community will belong to the same species, so D represents the probability the two individuals will belong to different species. This probability, like Shannon's index, is at its maximal value for a given species richness n ($D = 1 - \frac{1}{n}$) when individuals are equally distributed among the species. D is more sensitive to the abundances of species and less sensitive to species

richness than Shannon's index (May, 1975; Magurran, 1988). Hurlbert (1971) later proposed, furthermore, that if D is multiplied by $\frac{N}{N-1}$, the resulting index represents the probability of interspecific encounter in the community.

By the late 1960s, a large number of diversity indices had been developed, and numerous empirical studies of different ecological systems were being conducted to estimate diversity using these indices (Pielou, 1975; Magurran, 1988; Sarkar, 2007). In an influential critique of this research agenda, Hurlbert (1971, p.577) argued that, "the term 'species diversity' has been defined in such various and disparate ways that it now conveys no information other than 'something to do with community structure'," and that this indicated a fundamental vagueness of the underlying concept. He thought ecologists had further exacerbated this problem by appropriating statistical measures of diversity developed in nonbiological contexts with dubious ecological relevance. Rather than attempt to rehabilitate the concept by proposing adequacy conditions by which to evaluate the relative merits and weaknesses of different indices, Hurlbert suggested that the search for stability–diversity relationships should be refocused on the relationship between community stability and indices that reflect biologically meaningful properties that might influence community dynamics. His index of the probability of interspecific encounter is one example. Species richness seems to fail this test since it is generally unlikely that extremely rare species (e.g., s_1 in community A above) play an important role in community dynamics. Species richness was and remains, however, the predominant surrogate for diversity in analyses of stability–diversity relationships (e.g., Tilman, 1996, 1999).

Since Hurlbert's critique, ecologists have proposed a multitude of new diversity indices to satisfy plausible adequacy conditions besides those about species richness and evenness (see Ricotta, 2005 for a short review). Diversity indices should increase, for instance, as interspecific taxonomic and functional differences in a community increase. Besides properties of species, spatial properties of their geographical distribution could also be included in a diversity index. Since species distributions are significantly influenced by regional geology and environmental gradients, however, including these properties would expand the scope of diversity indices beyond measuring just the biological properties of communities. Expanded in this way, the "diversity" of the physical environment in which a community resided would also contribute to the value of such indices.

How compatible these additional adequacy conditions are with one another, or with the other conditions is not yet clear. Some conditions appear to be conceptually independent, but some formal diversity indices suggest that others are not. Rao's (1982) "quadratic entropy" diversity index, for instance, which generalizes the Simpson index (Ricotta & Avena, 2003), incorporates interspecific taxonomic and functional differences as well as evenness and species richness into a single quantitative measure. Unlike the Shannon and Simpson indices, however, quadratic entropy violates the adequacy condition that diversity should be maximal for a given species richness when individuals are equally distributed among species (Ricotta, 2005). This is as it should be. If functional or taxonomic information is included in assessments of diversity, then

high functional or taxonomic diversity may make a less even community more diverse overall than a more even one. In effect, functional or taxonomic diversity can trump evenness. As new indices are devised, similar incompatibilities between other adequacy conditions may be revealed. Absent a general proof that the conditions themselves are incompatible, however, it remains possible there is a diversity index that satisfies all defensible adequacy conditions.

In evaluating what properties of communities may make them stable, focusing solely on diversity is unjustifiable because intra- and inter-specific dynamics largely determine a community's stability properties. As a function of properties of individual organisms in a community, such as their taxonomic classes, how they are distributed among these classes, etc., even biologically meaningful diversity indices may reveal little about community dynamics. Individuals in species-rich communities with high evenness and taxonomic variety may interact rarely and weakly (intra- and inter-specifically); the former entails nothing about the latter. Hurlbert's (1971) claim that the modified complement of Simpson's index measures the probability of interspecific encounter, for instance, is true only if individuals of different species meet in proportion to their relative abundances. The likelihood may be higher, of course, that species in more even communities will interact more frequently, but the latter cannot be inferred from the former alone. A high or low diversity does not reveal, moreover, anything about how strongly species interact. May (1974) may have focused on complexity rather than diversity for precisely these reasons.

Unlike diversity, complexity is defined in terms of community dynamics. The more species, the more frequently they interact, and the stronger they do, the more complex the community. As a function of intra- and inter-specific dynamics, complexity can only be assessed against a description of these dynamics, usually in the form of a mathematical model (see Section 5). With respect to the simple linear models analyzed by May (1974), for instance, complexity is a function of species richness (n), connectance (C), and mean linear interaction strength (s) (see Section 4). How complexity should be assessed for more complicated nonlinear models, however, is unclear. Determining species richness is obviously unproblematic, and connectance can be determined from functional dependencies between variables in the model. The problem is assessing mean interaction strength. For linear models, the growth rate of each species is a linear function of the abundances of species with which they interact, so s is simply the average of the interaction coefficients. Variables in nonlinear models, however, may interact in disparate ways, and that they may exhibit different functional relationships precludes simply averaging to determine s. Different methods of integrating strengths of distinct types of relationships into a single quantitative complexity value, assuming there is a defensible way of doing this, would beget different measures of complexity.

Restricting complexity to just n, C, and s is also unduly restrictive. The variety of relationships exhibited between variables, the number of parameters, how complicated their relations are with variables, and other properties of community models that represent important features of community dynamics should be part of any defensible measure of ecological complexity. Whether they can be codified into a general complexity index remains to be seen. Without such a codification, however, the question of whether there is a relationship between ecological stability and complexity is poorly formed.

7. Evaluating Stability–Diversity–Complexity Relationships

Given the multitude of ways a biological community can be represented (M), its reference state specified (R), the variety of ecological stability concepts (see Section 5), and the numerous potential operationalizations of ecological diversity and complexity (see Section 6), it is unsurprising that the SDC debate remains unresolved after half a century of ecological research. As might be expected, only a few of the total possible relationships between stability, complexity, and diversity have been analyzed. Specifically, relationships between local stability and complexity of linear models, and between species richness and constancy have been the predominant focus thus far. The tractability of these concepts compared with the general concepts of stability, diversity, and complexity accounts for the selective scrutiny.

Empirically and theoretically oriented ecologists have taken disparate approaches to the debate (e.g., Elton, MacArthur, and May). Theoreticians focus on mathematical models of biological communities, and since these models describe the dynamics of communities, their research has been primarily concerned with the role complexity, rather than diversity, may have in generating or prohibiting stability. Food web models are perhaps the most common type of community model. They usually represent interspecific species interactions by linear relationships between variables, which has two advantages. First, assessing the complexity of these models is straightforward (see Section 6). Second, a well-developed mathematical theory of Lyapunov stability applies to these models, so evaluating their stability seems to be similarly straightforward. A large body of work on food webs since May's (1974) influential monograph has subsequently exploited these facts to uncover properties of community structure that might produce Lyapunov stability (see McCann, 2005 for a short review).

These facts obviously encourage this approach, but at the expense of ecological applicability. The problem is that actual species interactions probably rarely take a linear form, which means food webs poorly represent the dynamics of real-world communities. Species interactions can be treated as linear in the infinitesimal neighborhood of an equilibrium, but this severe restriction precludes inference about how actual communities respond to perturbation (see Section 3). What structural properties of food webs generate or jeopardize Lyapunov stability therefore indicate little about the relation between stability and complexity in actual biological communities. For this reason, Hastings (1988, p.1665) warned, "food web theory is not an adequate approach for understanding questions of stability in nature." It certainly tempers claims that recent advances in food web theory suggest a resolution of the SDC debate (e.g., McCann, 2000).

Evaluating stability–complexity relationships for nonlinear models that more accurately represent community dynamics presents different difficulties. One is the challenge of integrating different types of model properties into a general measure of complexity discussed in Section 6. Another is evaluating the stability of these models. If, as commonly assumed, Lyapunov stability adequately defines ecological stability, the ecological stability of nonlinear community models can be assessed with standard analytic techniques (Hirsh & Smale, 1974). An unequivocal relationship between Lyapunov stability and model complexity (gauged informally), however, has not emerged. Realistic increases in model complexity sometimes decrease the likelihood of stability, but sometimes they increase it. May (1974), for instance, found that including environmental

stochasticity and realistic time delays in Lotka–Volterra models of predator–prey communities destabilized them, while incorporating spatial heterogeneity and more realistic predator response to prey were stabilizing (see Section 4). The more realistic and complex the community model, moreover, the less mathematically tractable it and the assessment of its stability properties become. Since no general method for evaluating the Lyapunov stability of nonlinear systems is known, the ultimate verdict on the relationship between Lyapunov stability and complexity remains unclear.

The assumption that ecological stability is adequately defined as Lyapunov stability, however, should be rejected. The reasons it should not are technically involved (see Justus [in press] for details), but the general idea is that Lyapunov stability only considers response to P_p perturbations, whereas ecological stability also concerns response to P_p and P_{vp} perturbations. As such, Lyapunov stability provides only a partial account of the kind of perturbation response ecological stability requires. Unfortunately, a mathematical theory of stability for this more general class of perturbations has not yet been developed within ecology.

Besides these difficulties, estimating parameters of community models with empirical data, especially of more complicated realistic models, is often practically impossible. It is even less likely, furthermore, that the dynamics of a community can be easily discerned from the limited data usually available (see Connell & Sousa, 1983 for a review of methodological problems). For these reasons, some ecologists have decided to focus instead on evaluating stability–diversity–complexity relationships with statistical measures derived from data. This strategy also faces difficulties. The most daunting is the lack of adequate data. Its absence explains why species richness, which is a poor surrogate for ecological diversity, is used in almost all studies of stability–diversity relationships: data on relative species abundances required to estimate the evenness of a community can rarely be collected, whereas the numbers of species often can. For instance, most of David Tilman's analyses of Minnesota grasslands (e.g., Tilman, 1996, 1999; Lehman & Tilman, 2000), which are probably the most spatially and temporally extensive empirical studies of stability–diversity relationships, measure diversity as species richness (a recent study by Tilman et al. [2006] uses the Shannon index to measure the diversity of a Minnesota grassland). His finding of a positive correlation between grass species richness and temporal stability [see (5) above] therefore shows little about the relationship between diversity and ecological stability, because species richness is a poor surrogate for diversity.

Absence of adequate data also explains the prevalence of constancy as the measure of ecological stability in most empirical studies of the SDC debate, temporal stability being the most prominent example. Lehman and Tilman (2000, p.535) suggest that temporal stability is "readily observable in nature," as one reason for using it to measure ecological stability. It only requires, specifically, data on species biomasses. This contrasts, they suggest, with the infeasibility of empirical evaluation of the stability concepts common in mathematical modeling in ecology.

Facile measurability, however, does little to overcome the shortcomings of *defining* ecological stability as constancy (see Section 5). If, alternatively, temporal stability were merely proposed as a *measure* of ecological stability, its suitability depends upon: (i) whether (and how variously) the community is perturbed during the period temporal stability is assessed, so that the measure indicates how the community responds to perturbation; and (ii) whether the reference state (R) is an equilibrium, so that species

biomasses will remain constant if unperturbed. Communities exhibiting limit cycles and "strange attractors," for instance, violate (ii); a community that resides in a relatively unvarying, unperturbing environment over the period it is assayed violates (i). Since data are usually collected over short periods given the limited monetary and temporal constraints of ecological research, (i) is rarely satisfied, and it has been suggested that complex dynamics violating (ii) may be widespread. For this and the reasons discussed above, Tilman's (1996, 1999) careful analysis of how species richness can increase temporal stability should probably not be considered as even, "a partial resolution of the long-standing diversity–stability debate" (Lehman & Tilman, 2000, p.548).

This survey of the SDC debate helps explain why it remains unresolved. The concepts of ecological stability, diversity, and complexity are multifaceted and difficult to evaluate, theoretically and empirically, and there is significant disagreement among ecologists about how they should be defined. Consequently, only a few of the total possible stability–diversity and stability–complexity relationships have been analyzed. These analyses, moreover, have focused on relations between tractable, but poor surrogates for the three concepts. The debate's broad scope and potential implications for applied biological fields such as conservation, pest control, and resource management ensure its continued scientific scrutiny. The conceptual and methodological issues it raises merit more philosophical scrutiny than thus far devoted to it.

Acknowledgments

References

Batterman, R. W. (2000). Multiple realizability and universality. *British Journal for the Philosophy of Science*, 51, 115–145.

Chesson, P. L., & Case, T. J. (1986). Overview: nonequilibrium community theories: chance, variability, history, and coexistence. In J. Diamond & T. J. Case (Eds). *Community ecology* (pp. 229–239). New York: Harper & Row.

Connell, J. H., & Orias, E. (1964). The ecological regulation of species diversity. *American Naturalist*, 98, 399–414.

Connell, J. H., & Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. *American Naturalist*, 121, 789–833.

De Angelis, D. L. (1975). Stability and connectance in food web models. *Ecology*, 56, 238–43.

Elton, C. (1958). *The ecology of invasions by animals and plants*. London: Methuen.

Ereshefsky, M. (2001). *The poverty of the Linnaean hierarchy*. Cambridge: Cambridge University Press.

Fodor, J. (1974). Special sciences, or the disunity of science as a working hypothesis. *Synthese*, 28, 77–115.

Gardner, M. R., & Ashby, W. R. (1970). Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature*, 228, 784.

Gause, G. F. (1934). *The struggle for existence*. Baltimore: Williams & Wilkins.

Good, I. J. (1953). The population frequencies of species and the estimation of population parameters. *Biometrika*, 40, 237–64.

Goodman, D. (1975). The theory of diversity–stability relationships in ecology. *Quarterly Review of Biology*, 50, 237–66.

Grimm, V., & Wissel, C. (1997). Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecolgia*, 109, 323–34.

Hastings, A. (1988). Food web theory and stability. *Ecology*, 69, 1665–8.

Hastings, A., Hom, C. L., Ellner, S., Turchin, P., & Godfray, H. C. J. (1993). Chaos in ecology: is Mother Nature a strange attractor? *Annual Review of Ecology and Systematics*, 24, 1–33.

Hirsh, M., & Smale, S. (1974). *Differential equations, dynamical systems, and linear algebra*. San Diego, CA: Academic Press Inc.

Hurlbert, S. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, 52, 577–86.

Hutchinson, G. E. (1959). Homage to Santa Rosalina or why are there so many kinds of animals? *American Naturalist*, 93, 145–59.

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–27.

Justus, J. (in press). Ecological and Lyapunov stability. *Philosophy of Science*.

Kerner, E. H. (1957). A statistical mechanics of interacting biological species. *Bulletin of Mathematical Biophysics*, 19, 121–46.

Kerner, E. H. (1959). Further considerations on the statistical mechanics of biological associations. *Bulletin of Mathematical Biophysics*, 21, 217–55.

Kim, J. (1998). *Mind in a physical world: an essay on the mind–body problem and mental causation*. Cambridge, MA: MIT Press.

Kingsland, S. (1995). *Modeling nature*. Chicago: University of Chicago Press.

Krebs, C. (2001). *Ecology*. New York: Benjamin Cummings.

Lawlor, L. R. (1978). A comment on randomly constructed model ecosystems. *American Naturalist*, 112, 445–7.

Lehman, C. L., & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *American Naturalist*, 156, 534–52.

Leigh, E. G. (1975). Population fluctuations, community stability, and environmental variability. In M. L. Cody & J. M. Diamond (Eds). *Ecology and evolution of communities* (pp. 52–73). Cambridge, MA: Harvard University Press.

Lewontin, R. (1969). The meaning of stability. In G. Woodwell & H. Smith (Eds). *Diversity and stability in ecological systems* (pp. 13–24). Brookhaven, NY: Brookhaven Laboratory Publication No. 22.

Lyapunov, A. ([1892], 1992). *The general problem of the stability of motion*. London: Taylor & Francis.

MacArthur, R. (1955). Fluctuations of animal populations, and a measure of community stability. *Ecology*, 36, 533–6.

Margalef, R. (1958). Information theory in ecology. *General Systems*, 3, 36 –71.

Magurran, A. E. (1988). *Ecological diversity and its measurement*. Princeton, NJ: Princeton University Press.

McCann, K. (2000). The diversity–stability debate. *Nature*, 405, 228–33.

McCann, K. (2005). Perspectives on diversity, structure, and stability. In K. Cuddington & B. Beisner (Eds). *Ecological paradigms lost* (pp. 183–200). New York: Elsevier Academic Press.

McIntosh, R. P. (1985). *The background of ecology: concept and theory*. Cambridge, UK: Cambridge University Press.

May, R. M. (1974). *Stability and complexity in model ecosystems* (2nd edn). Princeton, NJ: Princeton University Press.

Norton, B. G. (1987). *Why preserve natural variety?* Princeton, NJ: Princeton University Press.

Odenbaugh, J. (2001). Ecological stability, model building, and environmental policy: a reply to some of the pessimism. *Philosophy of Science* (Proceedings), 68, S493–S505.

Orians, G. H. (1975). Diversity, stability, and maturity in natural ecosystems. In W. H. van Dobben & R. H. Lowe-McConnell (Eds). *Unifying concepts in ecology* (pp. 139–50). The Hague: W. Junk.

Patten, B. C. (1961). Preliminary method for estimating stability in plankton. *Science*, 134, 1010–11.

Pfisterer, A. B., & Schmid, B. (2002). Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, 416, 84–6.

Pielou, E. C. (1975). *Ecological diversity*. New York: John Wiley & Sons.

Pimentel, D. (1961). Species diversity and insect population outbreaks. *Annals of the Entomological Society of America*, 54, 76–86.

Pimm, S. L. (1979). Complexity and stability: another look at MacArthur's original hypothesis. *Oikos*, 33, 351–7.

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Ecology*, 61, 219–25.

Pimm, S. L. (1991). *The balance of nature?* Chicago: University of Chicago Press.

Preston, F. W. (1968). On modeling islands. *Ecology*, 49, 592–4.

Preston, F. W. (1969). Diversity and stability in the biological world. In G. Woodwell & H. Smith (Eds). *Diversity and stability in ecological systems* (pp. 1–12). Brookhaven, NY: Brookhaven Laboratory Publication No. 22.

Rao, C. R. (1982). Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology*, 21, 24–43.

Ricotta, C. (2005). Through the jungle of biological diversity. *Acta Biotheoretica*, 53, 29–38.

Ricotta, C., & Avena, G. C. (2003). An information-theoretical measure of taxonomic diversity. *Acta Biotheoretica*, 51, 35–41.

Sarkar, S. (2007). From ecological diversity to biodiversity. In D. Hull & M. Ruse (Eds). *Cambridge companion to the philosophy of biology*. Cambridge, MA: Cambridge University Press.

Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communication*. Urbana: University of Illinois Press.

Shrader-Frechette, K. S., & McCoy, E. D. (1993). *Method in ecology*. Cambridge: Cambridge University Press.

Simpson, E. H. (1949). Measurement of diversity. *Nature*, 163, 688.

Slobodkin, L. B. (1953). An algebra of population growth. *Ecology*, 34, 513–19.

Slobodkin, L. B. (1958). Meta-models in theoretical ecology. *Ecology*, 39, 550–1.

Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350–63.

Tilman, D. (1999). The ecological consequences of biodiversity: a search for general principles. *Ecology*, 80, 1455–74.

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–32.

Watt, K. E. F. (1973). *Principles of environmental science*. New York: McGraw-Hill.

Woodwell, G., & Smith, H. (Eds). (1969). *Diversity and stability in ecological systems*. Brookhaven, NY: Brookhaven Laboratory Publication No. 22.

Further Reading

Cooper, G. (2001). Must there be a balance of nature? *Biology and Philosophy*, 16, 481–506.

Egerton, F. N. (1973). Changing concepts of the balance of nature. *Quarterly Review of Biology*, 48, 322–50.

Ives, A. R. (2005). Community diversity and stability: changing perspectives and changing definitions. In K. Cuddington & B. Beisner (Eds). *Ecological paradigms lost* (pp. 159–182). New York: Elsevier Academic Press.

King, A., & Pimm, S. (1983). Complexity and stability: a reconciliation of theoretical and experimental results. *American Naturalist*, 122, 229–39.

May, R. M. (1985). The search for patterns in the balance of nature: advances and retreats. *Ecology*, 67, 1115–26.

McNaughton, S. J. (1977). Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist*, 111, 515–25.

Sarkar, S. (2005). Ecology. In E. N. Zalta (Ed.). *Stanford encyclopedia of philosophy*. URL=<http://plato.stanford.edu>.

Tilman, D., Lehman, C. L., & Bristow, C. (1998). Diversity–stability relationships: statistical inevitability or ecological consequence? *American Naturalist*, 151, 277–82.

Chapter 19

Ecosystems

KENT A. PEACOCK

The *ecosystem* is the central unifying concept in many versions of the science of ecology, but the meaning of the term remains controversial, and a few authors (e.g., Sagoff, 2003) question whether it marks any clear or non-arbitrary distinction at all. The following definitions will do as a fairly uncontroversial starting point: The terms "ecology" and "economics" themselves come from the Greek root *oikos*, meaning "household." *Ecology* is the branch of biology that deals with the ways in which living organisms organize themselves into dynamic structures that facilitate the exchange of energy, materials, and information between themselves and the larger physical and biological environments in which such structures are situated; while *ecosystems* themselves are, loosely speaking, the structures in question.

This chapter will begin with observations on the meaning and scope of ecology itself. It will then outline the ways in which ecosystems can be understood from a number of perspectives: the ecosystem as the *descriptive unit* of the working field biologist; the *history* of the concept of the ecosystem; the ecosystem as a *dissipative structure*; the ecosystem as *symbiotic association*; the ecosystem in evolutionary theory; and skeptical views according to which the ecosystem is little more than a *descriptive convenience*. The applications of these conceptions to environmental ethics and the problems of ecosystem health and sustainability will then be reviewed. Ecosystems are not merely of theoretical interest, for understanding them may make a critical difference to how successful we humans are in responding to the ecological crisis precipitated by the unprecedented impact we are currently having on the environment. In the end, the practical perspective must serve as our touchstone; the observations of field ecologists, working agronomists, foresters, soil scientists, and conservationists should temper our flights of theoretical fancy.

1. The Scope of Ecology

K. de Laplante (2004) argues that in recent years there have been two major ways to think about ecology itself, a narrowly orthodox approach and what de Laplante calls the "expansive" approach. The orthodox approach holds that ecology should concern itself largely or entirely with nonhuman communities of species, and that the value of

Blackwell Companions to Philosophy

This outstanding student reference series offers a comprehensive and authoritative survey of philosophy as a whole. Written by today's leading philosophers, each volume provides lucid and engaging coverage of the key figures, terms, topics, and problems of the field. Taken together, the volumes provide the ideal basis for course use, representing an unparalleled work of reference for students and specialists alike.

A Companion to the Philosophy of Biology

Edited by

Sahotra Sarkar

and

Anya Plutynski

Contents