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Philippe A. Rossignol

Elton (1927) realized that, intuitively at least, nature was complex and stable. And that the last property contributed to the first. This idea was challenged mathematically by Gardner and Ashby (1970) and May (1972), and in the years following various models have attempted to reconcile these opposing views. Unlike previous mathematical approaches that demonstrated that simple stable systems are destabilized through added complexity, the approach presented herein began with a model that was unstable. This perspective provided allows model complexity and at the same time increased likelihood of mathematically stable. This novel observation suggested that ecosystem complication might stabilize a community. Within these models a system may be stable despite the coexistence of several competitors, in direct opposition to the Competitive Exclusion Principle. The hypothesis that the principle may not hold as an absolute generality beyond two competitors is proposed. This paradox may be explained by (1) interactions between competitors, (2) a keystone predator, or (3) a combination of the first two factors.

Stability and Complexity: A Reappraisal of the Competitive Exclusion Principle

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Israel N. Duran

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APPROVED:

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Major Professor, representing Entomology

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Chair of Department of Entomology

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CONTRIBUTION OF AUTHORS

Drs. Philippe A. Rossignol and Hiram W. Li were involved in discussions and in writing the manuscript in chapter 3.

TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

LIST OF FIGURES

LIST OF FIGURES

This thesis is dedicated my parents: Dad, Mom, Tom, Katie, and to my brother, Adam…I love you all.

STABILITY AND COMPLEXITY: A REAPPRAISAL OF THE COMPETITIVE EXCLUSION PRINCIPLE

CHAPTER 1

INTRODUCTION

Observations of nature led ecologists to the conclusion that nature was amazingly complex and at the same time extremely stable. This dogma went unquestioned for many years. In an important turn of events, economic models were introduced into ecology. This led to apparent mathematical incompatibility between complexity and stability of ecosystems that arose following the analysis of simplistic models that yielded quite different results. It was discovered that as an ecosystem becomes more complex, the mathematical stability of the system suffers. The incompatibility of complexity and stability led many ecologists to seek ways of incorporating the intuitive complexity of nature with the stability of simple models. In doing so, some ecologists have also managed to create models in violation of another very important tenet of biology, the competitive exclusion principle, which states that "complete competitors cannot coexist. This intriguing result served as fuel for continuing investigation into the competitive exclusion principle.

Chapter 2 is a review of pertinent literature, exploring various attempts to overcome the problems presented by these theories. In some cases there have been efforts to unite these two biological conundrums. These solutions are examined and discussed in context to these two ideas. While the solutions presented by various authors are not wholly wrong, there are explanations that at first seemingly explain the issues.

Nevertheless, after further review, past studies only skirt or completely dodge the questions of importance. These issues of significance examined are the generality of the competitive exclusion principle and the negative association of stability and complexity.

While making inquiry into the principle and whether it may be generalized to larger systems using theoretical qualitative analysis of simple models, it was found that the competitive exclusion principle holds true only in the situation where two species are competing for a single resource, and that coexistence is possible when a third competitor is present. Although in certain circumstances, the principle is accurate. While the complication of a simplistic, unstable system proved that the competitive exclusion principle has limited applications, the analysis also hinted that stability could result from complexity. Testing whether the confounding factor was in fact complexity and not the types of interactions involved meant the effects had to be separated. The best way to approach this problem was by applying the model that most precisely upholds the competitive exclusion principle. The examination began with a study of how increased complexity can bring stability to a series of models derived from an initially unstable model. The addition of a fourth species to the two competitor-one resource system increases the likelihood of coexistence irrelevant of interaction type.

CHAPTER 2

LITERATURE REVIEW

2.1 THE ELTONIAN BEGINNING

Our understanding of ecosystems has grown slowly from humble beginnings. According to Elton (1927), nature, teleologically speaking, employed complexity to ameliorate 'weak' and simple ecosystems. 'Weak' was Elton's way of describing an ecosystem's tendency to lose species to extinction, to undergo wide population fluctuations, and to suffer invasions from exotic species. Elton (1927) throughout his classic book, *Animal Ecology,* stated that natural ecosystems were complex and hints at their stability versus simple ecosystems.

Although Elton never defined stability, it is assumed by most modern ecologists to be the same kind of stability as applied in recent ecological studies. This view, that the complexity of a natural system leads to stability, is known as 'Eltonian'. From various observations of the natural world, Elton came to the conclusion that a complex ecosystem possessed extensive connectiveness and stability not found in simple ecosystems. Remote islands for example were supposed to be more vulnerable to invasions (Elton 1958; Pimentel 1961). Both Elton and Pimentel also used examples, as well as experiments and mathematical models, of one predator-one prey systems, showing that these simple systems usually crashed quickly. Examples of pest outbreaks in agricultural systems were

used to emphasize their contention. Monocultures were simple ecosystems and frequently had outbreaks of pests. They argued that these simple systems were 'unstable'. Comparisons of complex tropical rainforests, seemingly more stable, with simple arctic communities, with frequent fluctuations, were used to indicate that an ecosystem's complexity apparently led to stability. Observations of the vulnerability of islands to invasions were included as evidence of the superiority of the more complex and, therefore, more stable tropical biota. These arguments helped to bolster their view that, in fact, complexity and stability were positively related. The Eltonian view dominated for some time as a hypothesis of importance, eventually becoming an accepted tenet in ecology.

MacArthur (1955) supported the positive relationship between complexity and stability. Using the Shannon-Weaver formula derived from the theory of information, he believed to have demonstrated that complexity and stability were consistent within trophic webs. When the number of energy pathways to a consumer was increased the failure of any one pathway would not be as devastating as when there were only one pathway. Thus, MacArthur suggested a correlation, however tenuous, between complexity and diversity, "The intuitive requirements seem to be that if each species has just one predator and one prey the stability should be minimum, say zero, and that as the number of links in the food web increases the stability should increase. (p. 534)". He concluded, just as Elton did, that arctic regions were less stable than tropical locales.

Hutchinson (1959) determined, erroneously it turns out, that MacArthur had found an exact mathematical explanation of stability within diverse ecosystems. Goodman (1975) indicated later that MacArthur's formula was descriptive and not explanatory. Additionally, Hutchinson remarked on the evolutionary properties of the aforementioned

findings, such that stable ecosystems would endure longer than less stable ecosystems, and therefore diversity would increase through evolutionary time.

For many years, the intuition of Elton and MacArthur led ecologists to assume that there was a vast complexity to nature. Not until the early 1970's was this Eltonian view challenged. Goodman (1975), and later Pimm (1984), summarized theoretical arguments of Gardner and Ashby (1970), May (1972) and subsequent workers that criticized the original conclusions and observations of Elton and others. These workers explained that the previous arguments in relation to the diversity-stability hypothesis were incomplete, that their criteria, tools and vocabulary were dubious, that recent models suggested just the opposite, and that stability (or instability) was a response of the population. They protested that the single predator-single prey systems were not compared to systems with many predator-prey interactions, which may or may not be more stable than simpler systems.

One of Goodman's arguments against the Eltonian instability of agriculture was that while outbreaks do occur, the continual annual replanting never allows the system to equalize, and that given the chance to do so the system may stabilize. Disputing the claim that tropical locales are more stable than less complex regions such as island or arctic communities, he suggests that islands may be vulnerable to invasions because it is "simply a consequence of accidents of distribution or of islands, for some reason, accumulating species that are especially susceptible to competitive or exploitative displacement." The greater stability of tropical ecosystems could be an artifact of sampling. Samples may poorly and inaccurately represent species, resulting in undetected fluctuations. In fact, the absence of pest outbreaks Elton reports was based on the observations of three foresters.

He investigated MacArthur's study of diversity-stability and because MacArthur did not provide a clear argument for linking stability to trophic diversity, S, in his stability function, and that S is not readily translated biologically. Goodman stated "Clearly, the belief that more diverse communities are more stable is without support", a statement later echoed by Goh (1980).

Pimm (1984) in his review of stability-complexity repeated the thoughts conveyed the different points that had been reproduced throughout various studies. When a community is highly connected, there should be fewer species in order to be stable. Within a highly connected community a loss of one species will tend to increase the chance of losing others, but overall, the ecosystem would be more persistent and resilient (speed of return to equilibrium). Conversely, an ecosystem with many species needs to be less connected and less resilient.

2.2 THE POST-ELTONIAN VIEW

The Eltonian view came under serious fire after ecologists began to apply Quirk and Ruppert's (1965) and Maybee and Quirk's (1969) economic models. Models of Liapunov stability conclude that stability does not arise from complexity; Routh-Hurwitz criteria are sufficient and necessary for mathematical stability. The criteria state that feedback at all levels of interaction must be negative, and interactions at the lower levels (those interactions between one or two variables) must be stronger than interactions involving many species. Thusly, models using Routh-Hurwitz criteria as a rigorous assessment of stability, were introduced in ecological theory. First, Gardner and Ashby

(1970) ran simulations and found that stability decreased with increasingly complex systems. Soon after, May (1972) argued that mathematical stability required simplicity in ecological systems, an argument pursued to an extreme by Pimm (1984). It was realized by the ecological community that the Routh-Hurwitz criteria could be used as a powerful mathematical description of biological systems.

That complexity did not give rise to stability as suggested from earlier work was questioned and essentially negated when May in the early 1970's reached the conclusion that increased complexity is not mathematically stable, and in fact complexity leads to reduced stability. Possible confusion arose because most authors assumed that 'mathematical stability' similar to Elton's concept of ecological stability. When large systems were examined by May (1972) he found that they exhibited a great tendency to become unstable as complexity increased, when a certain critical threshold was reached. Complexity is measured as connectance (probability that any pair of species will interact), as number of variables and as the mean interaction strength between variables. Therefore, any community with too much connectance, too many species or too high of an average interaction strength will be unstable. May found that an increase in any one of these three factors could lead to instability at a critical threshold. This critical threshold was lowered if the number of species increased in conjunction with either of the two other factors; to maximize complexity in systems of three or more species precludes quantitative stability. These results undermined the diversity-stability hypothesis and led to the diversity-stability paradox.

May promoted the idea that within a community the maintenance of stability requires that a species that interacts with many other species should do so weakly, while

any species with strong interactions should interact with only a few species. This quantitative evidence was supported by Margalef (1968) "From empirical evidence it seems that species that interact feebly with others do so with a great number of other species. Conversely, species with strong interactions are often part of a system with a small number of species having strong fluctuations." Another point broached by May (1972) is that communities exhibit greater stability when large communities are separated into distinct blocks (in his work, roughly 35% of blocked communities are stable as compared to "essentially none" of the non-blocked versions).

May (1973) also determined that mutualism and competition add instability (both have positive feedback and are in this sense mathematically identical); no closed loops could exist within the system, and the matrix determinant must be non-singular. Simple systems according to this work and contrary to earlier belief are more, not less stable, than complex systems. This is in direct disagreement with the Eltonian vision.

In his conclusion of these papers and reiterated in *Stability and Complexity in Model Ecosystems*, May (1972, 1973, 1974) asserted that complexity and increased interactions is detrimental to qualitative stability. Workers became aware of this apparent paradox inherent in the mathematical and economic models as applied to biological systems. Namely, that for the sake of stability, complexity will not occur. Yet, the observations of the Eltonian view described complex and stable systems. These observations were in direct conflict with the mathematical models. Several workers tried to reconcile these differences.

2.3 EXPLAINING THE STABILITY-COMPLEXITY PARADOX

Goh (1980) deduced that the size and structure of ecological systems were limited. To deal with this apparent paradox between diversity and stability several workers chose to describe ecosystems as singular similar simple systems connected in elementary and obvious predator-prey relationships. This is the idea of a "straight chain of straight chains" relationships (Jeffries 1974; McMurtrie 1975; Tansky 1978). Later, Pimm and Lawton (1978), Goh (1979), and Yodzis (1980, 1982) each rationalized that complex ecosystems could be broken down into several self-regulated compartmentalized subsystems. Perhaps, they conjectured, these compartmentalized subsystems are linked together through simple predator-prey relationships in a hierarchical fashion, as indicated by the work of Tansky (1978) and O'Neill et al. (1986).

This idea of a straight chain of straight chains relationships was brought forth by Jeffries (1974) who revealed that these simple chains were indeed stable. Jeffries, in his study of qualitative stability, found that stability is dependent upon the existence of self-regulating interactions and upon the location of these interactions, such that asymptotic stability arises with self-regulation. McMurtrie (1975) employed Monte Carlo studies in his investigation of the relationship between system size, connectance and the probability of stability. In randomly generated matrices, McMurtrie noticed a decrease in stability with a concurrent increase in complexity, but noted that 'real life' systems do not act in such a manner. Real life systems have complexity as well as stability. Therefore, he concluded real life ecosystems are not randomly associated. A mechanism is not given for this non-random organization in real life systems. Furthermore, he noted that random

systems with well-developed hierarchical structures are able to maintain much greater connectance than systems without such organization.

Pimm and Lawton (1978) investigated food webs involving omnivory, suggesting that some trophic patterns are more stable than others. As the 'rank' of omnivory increases, stability decreases. Rank describes the number of omnivorous links in the system, such that systems of rank 0 has no omnivores, while rank 1 has one omnivore, and rank 2 has either one omnivore feeding on two additional trophic levels or two omnivores, on up to the higher ranks. Results were broken down into unstable and stable systems, with stable food webs further broken down into those that returned to stability in less than 100 generations and those that did not. They concluded that high ranking omnivory (large numbers of omnivores within a system) will be less common than low ranking omnivory (few or no omnivores in an ecosystem) in real world situations, with the exception of insect host-parasitoid systems. These conclusions were reached by using the criterion of local stability and the idea that a rapid return to equilibrium is stabilizing.

Yodzis (1980) suggested that within a community food web species richness and average interaction strength are inversely related. As one factor is increased the other must be reduced. If not, the systems become more susceptible to perturbations in the least, or unstable at most. However, these results were reached in part by assuming that non-trophic interactions were less usual than trophic interactions.

Goh (1979) and Yodzis (1982) each rationalized that complex ecosystems could be broken down into several self-regulated compartmentalized subsystems (Figure 2.1). The compartments would be composed of the various 'guilds' within the ecosystem. These were the guilds described by Root (1967) as "a group of species that exploit the

same class of ecological resources in a similar way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements." These compartments would be, according to their interpretation, sufficient to describe the food web. Nonetheless, complexity had been misrepresented, by taking apparent complexity for actual complexity. Although the systems contain many species, these species are grouped together as one unit and then the energy flows between units, no longer between the species within the units. This grouping not only fails to take into account interspecific competition, but also intraspecific competition, as well as those non-trophic interactions.
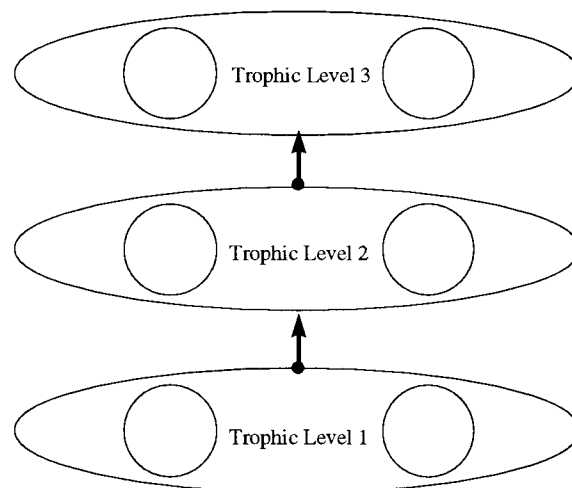
Figure 2.1 Compartmentalized subsystems.

The work of Tansky (1978) and O'Neill *et al.* (1986) indicated that compartmentalized subsystems are linked together (Figure 2.2). This allows for greater overall complexity, even though each subsystem is simple they are linked to each other

through simple predator-prey relationships, resulting in a hierarchical structure. This brings the model to a closer representation of what is observed in natural ecosystems. The approach taken by Tilman (1996) combined the use of guilds and hierarchical structure into the concept of 'functional group' to allow for further complication of a system (Figure 2.3). In doing so, he found that beyond a certain point increased diversity was less stable than having a few dominant species. His work relates almost exclusively to plants.
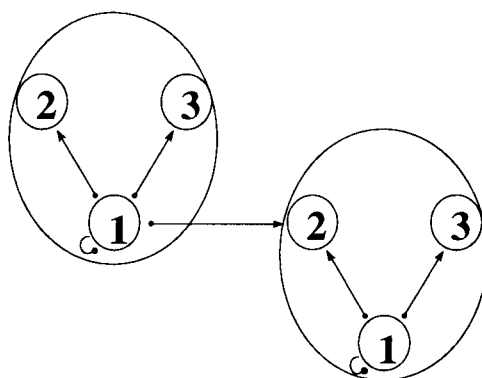
Figure 2.2 Hierarchical subsystems.
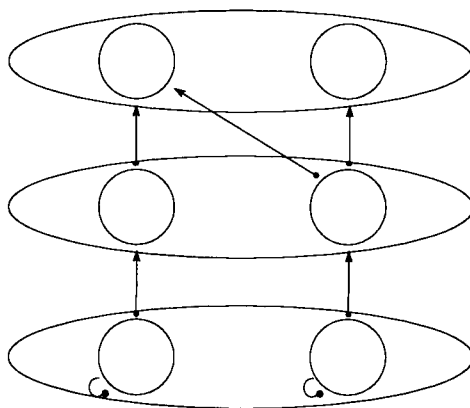
Figure 2.3 Tilman's approach.

Pilette *et al.* (1989) and Lane (1986) used loop analysis to study community models based on a large natural community. They observed that with large systems there was almost no correlation between stability and complexity. Their conclusion was that the relationships within the system may be tempered by other factors. A higher degree of stable relationships occurred when individual entities were less connected to the overall system. Yet, at the population level the relationship between stability and complexity was negative for large systems, while subsystems had increased stability as size increased.

However, as is the case for almost every worker to investigate the effects of complexity on stability the same method has been used. The models used for this aspect were stable to begin with, and in Gardner and Ashby's study (1970) and May's study (1972) complexity was more or less haphazardly added to the system. One result of such a casual increase in complexity was to increase the probability of violating conditions that would stabilize the ecosystem. At least a partial consequence of using initially stable models to study the diversity-stability hypothesis is that the procedure may have led to an exaggerated negative association between complexity and stability.

2.4 OPPOSITION TO THE NEW VIEW

The power of qualitative stability analysis is that the criteria are derived from a community matrix made up exclusively of Malthusian parameters and that the characteristic polynomial is intuitively interpretable as biological loops (Levins 1975). However, the approach has also brought the disturbing consequence that complexity and stability are virtually incompatible (Goh 1979; Goodman 1975).

Ecologists realized that rigorous models could be used to depict ecosystems and found that, contrary to the common notion, there was no direct theoretical relationship between complexity and diversity. In fact, the relationship, if it existed at all was inverse. The conflict between these this view and the Eltonian view was accounted for in several ways. Unfortunately, the findings that complexity led to instability were flawed in that they used simple systems that were already stable and all subsequent studies followed this basic pattern (Figure 2.4). To address this conflict many ecologists have attempted to use complexity, but only in an apparent manner. That is, although the system seems complex, it is broken down so that only a few interactions are present or individual species are grouped together.
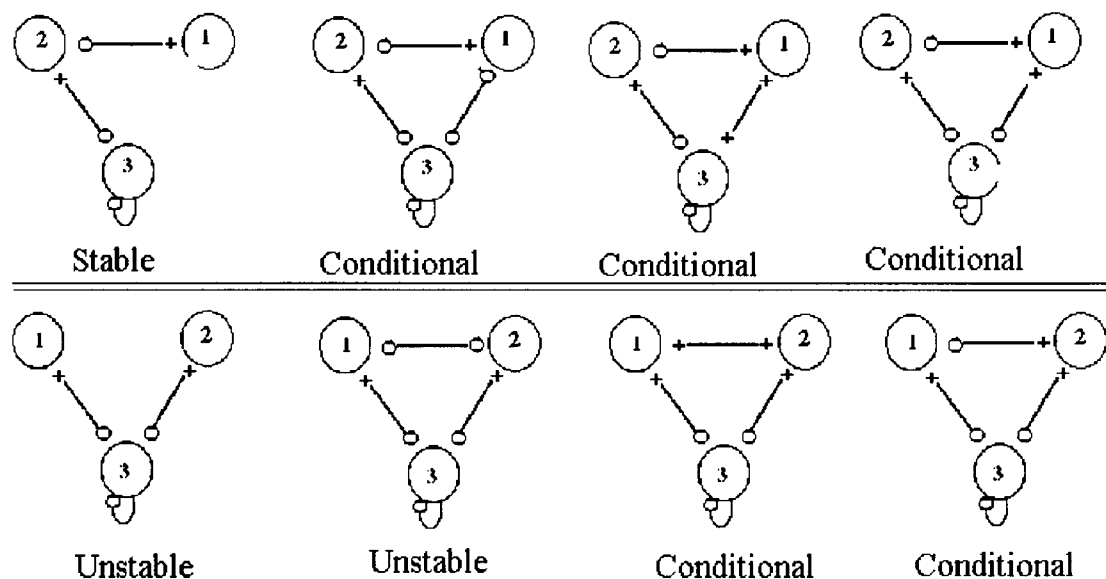
Figure 2.4 Stable vs. unstable starting point.

Lewontin (1969) gave a general warning that although Liapunov functions are the criteria with which many ecologists use to describe their systems of study, the functions may not be adequate to represent biological terms through these functions. Lewontin stated that Liapunov functions represent stability through minima, but asks whether this is appropriate for, or capable of, describing ecological stability. He went on to state that in order to fully understand how ecosystems evolve and transform through non-equilibrium properties, then studies of ecosystems that are not enjoying equilibrium must be studied further.

2.5 CURRENT CONCEPTS

A theoretical challenge to the stability-diversity paradox came when Haydon (1994) demonstrated that stability and complexity are not mutually exclusive. On the contrary, he found that connectance can contribute to stability. His study used simulation analysis of Gershgorin disks (a measure of Eigenvalue distribution) to reach his conclusions. He presented a quantitative (not qualitative) analysis which concluded that, under biologically reasonable conditions, complexity in the form of added links and widened range of interaction strength increased stability.

A recent study of the food web of a tropical rain forest which, supposedly is the largest of its kind, refuted the claims of incompatibility between complexity and stability, and specifically those predictions proposed by the food web theory. Reagan *et al.* (1996) specifically tested the restrictive predictions of food web theory, which arise from Routh-Hurwitz criteria. The predictions of food web theory (short trophic chains, few loops, low

predator-prey ratio, low species-to-link ratio) were all negated, sometimes in an extreme fashion.

One consequence of the loss of the Eltonian view has been the proliferation of definitions of stability. Wissel and Grimm (1997) reviewed the literature and documented over "163 definitions of 70 different stability concepts", which makes it difficult to equate one author's use of stability to another study. They point out that most confusion in the terminology comes from addressing the different properties of stability. They conjectured that stability concepts that arise from mathematics or physics are appropriate solely to describe the behavior of simple dynamic systems. The authors then stated that ecological systems are not simple dynamic systems, but rather may be described by many different variables. Therefore, pigeonholing ecological systems with a certain concept of stability is difficult at best and translating a particular concept of stability between studies is consequently that much more troublesome. They propose a series of questions that are designed to help avoid confusion and use the correct concept of stability in order to introduce some agreement between usage of stability concepts, and to increase viable comparability between literature.

2.6 GAUSE'S PRINCIPLE

Theory and practice have focused on one particular system, yet with no clear conclusion. This classic system is referred to either as Gause's principle or the competitive exclusion principle. Gause (1934), through his experiments, legitimized the concept of competitive exclusion. He used populations of *Paramecium caudatum* and *P.*

aurelia to study the effects of competition and came to the conclusion that two species competing for a unique resource will not be able to coexist indefinitely. In order for two species to coexist there must be a partitioning of the resource, or niche partitioning. Otherwise, the inferior competitor will necessarily go extinct. In 1960, Hardin coined the expression "competitive exclusion principle", previously called Gause's principle or law, and restated it in a different manner, to wit "complete competitors cannot coexist". Hardin credited Gause with strengthening the idea of competitive exclusion which had been under consideration for several years, but claimed that Gause did not clearly state nor realize the full extent of "Gause's principle". Hardin made clear through his statement "complete competitors cannot coexist" that his intent was to explore the limits of the principle. He made the wording of the principle ambiguous to emphasize that it was novel and unexplored. He reviewed the historical beginnings of Gause's principle and associates it with the fields of economics and genetics. Furthermore, Hardin expressed a slight uneasiness, acknowledging that as of that point in time the principle was still in need of either verification or refutation, through fuller models. Paradoxically, his restatement is a negation; it cannot be directly refuted from a strict scientific perspective.

Slobodkin (1961) used a mathematical model to demonstrate that the eventual exclusion of one species could be reversed to some extent and that competitors could coexist. The conclusion of Slobodkin was that over the long run, Gause's principle would still prove correct and exclusion of one species would occur. Based on a previous model used by MacArthur and Levins (1967), Roughgarden and Feldman (1975) advanced the idea that unequal predation pressure allows prey species to occupy niches that overlap. Using Lotka-Volterra equations, the authors found that the niche separation between

competing prey species is determined mutually by predation pressure and the degree of kurtosis of the competition function. Kurtosis is the characteristic of the competition function directly related to the niche utilization curve. A leptokurtic utilization curve has a sharp peak and broad tail, allowing for closer packing of species than if the curve contained broad peaks and a short tail. The sharp peak of a leptokurtic curve indicates a specialized organism. Niche separation distance is determined by predation pressure and kurtosis. Niches can become more closely packed as the predation pressure increases or the leptokursis of the competition function increases.

2.7 DIFFERENCES BETWEEN INTERFERENCE AND COMPETITIVE EXCLUSION

Confusion arose and still exists in the ecological literature about the term 'competition'. There are two types, strictly speaking. One is exploitation, resource, or indirect competition, which is trophic and arises in the parsimonious interpretation of competitive exclusion. In exploitation competition there is no direct competition between the species. Indirectly, one species appropriates resources and those resources then become unavailable for use by any other competing species. The other type of competition is called interference, which is direct and usually non-trophic, involving competing species that directly clash. While Gause's model dealt with competition, it is important to note that in his studies of *Paramecium*, he was looking at exploitation competition and not at interference competition. As was the case with Gause's

Paramecium, there was no direct competition, just one species using the available resources more efficiently and quickly than the other.

Other studies point out that interactions with additional species consequently allow for niche overlap and this has been suggested for interference (Levins 1975; Roughgarden & Feldman 1975; Vance 1978), but not exploitation competition. The studies indicate that the competitors do not compete for food resources. Conclusions concerning niche partitioning found in these studies cannot be utilized to make generalizations about exploitation competitors, since the disputed "dimension" (Pianka 1988) of the resource may be different for interference than for exploitation competition.

Interference between two species is destabilizing, yet unlike resource competition is not necessarily unstable, and conditions for negative feedback are achievable under reasonable conditions (Strobeck 1973). However, workers have confused the two types of competition within the literature and applied conclusions from one to the other. Thus, apparent exceptions to competitive exclusion arose.

Vance (1978) analyzed a one-predator-two-prey model community with the so-called 'keystone' predator, and pointed out that an unstable competitive relationship can be stabilized through the introduction of a generalist predator. Note, however, that the unstable interference relationship is not inherently unstable but is assumed to be so only for the sake of argument. It was suggested from that study that predators bring stability to systems in general. Vance looked at how two competing prey species could be stabilized by adding a predator to the system. In effect, Vance went from an unstable system to a stable system by including a keystone predator. This was a unique way of attacking the problem, because the traditional way of adding complexity to a model began

by using a stable model as a framework for the analysis. Using simple predator-prey systems, Vance varied the number of predators and prey and concluded that the addition of a predator can lead to coexistence between two competing prey species. The competitive exclusion principle asserts that competing species can coexist if they utilize resources in a different manner. Vance revealed that circumstances existed under which competing species can coexist without differential resource utilization. With the addition of a single predator species, he demonstrated that the general stability of the system had increased, and no species went extinct. Vance discussed conditions that make these systems possible. Vance asserted that coexistence of competing prey species due to predation should be commonplace. He concluded, nonetheless, that Gause's principle still held. Although coexistence was the result, there was still resource partitioning between the competing prey species. Both mechanisms worked at varying degrees to allow coexistence of similar species in nature. Still, Vance contended, differences between prey were an important aspect of his investigation. Predation plays a crucial role in coexistence, but frequency-dependent predation was the main force behind the coexistence of the competing prey species.

Vance's (1978) study reflected Paine's (1966) top carnivore field test removal. *Pisaster* was kept from a shoreline, and several months later the space was dominated by just a few species, and species diversity dropped from 15 to 8. Paine found that *Balanus cariosus* had occupied between 60-80% of the available space. He concluded that predation ameliorates competition allowing weaker competitors to coexist, and increased local diversity.

Bodini (1991) further investigated the role of predation on stability. He contended that predation was neither stabilizing nor destabilizing in general. In spite of that result, he stated that specialized predators are likely to stabilize a given ecosystem versus the destabilizing effects of a generalist predator. He suggested further work to be done that specifies the particulars of complex models and the relationship between predator and prey. In many cases, the positive response of the systems is due to the new variable acting as a keystone predator. The addition of a keystone predator is shown to have a stabilizing effect and has been under consideration for several years (Levins 1975; Vance 1978; Gilpin 1979; Levins & Vandermeer 1989).

Other workers (Haig & Maynard Smith 1972; Armstrong & McGehee 1980; Chesson 1982, 1994; Vance 1984; Lavorel & Chesson 1995; Chesson & Huntly 1997) have also been able to construct systems apparently in violation of Gause's principle. Haig and Maynard Smith (1972) used systems with niche partitioning and exploitation competition. One example found in their study is that of two herbivores and one plant. In that case, one herbivore feeds on root tissue, while the other feeds on leaves (Figure 2.5).
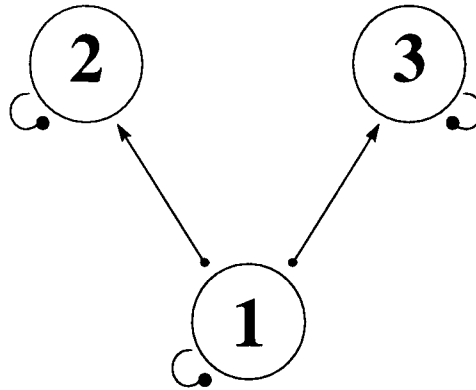
Figure 2.5 Signed digraph of Haig and Maynard Smith's system, showing niche partitioning and exploitation competition.

Armstrong and McGehee (1980) used a functional (Holling type II) response to introduce apparent stability to their system. The functional response results in neutral stability that permits the system to undergo perpetual oscillations, thereby creating a system that violates Gause's principle. It should be noted that without the functional response, the system still has neutral stability. Such oscillating systems had been previously investigated, all demonstrating similar results (Koch 1974; Armstrong & McGehee 1976; Hsu *et al.* 1978; Nitecki 1978; Waltman 1980).

Tilman (1980, 1982) argued that many competitors could coexist given sufficient spatial heterogeneity of resource abundance. The patchiness of the resource effectively creates refugia for the competing species. He provided a biological example of resource partitioning. Vance (1984) found that two species can coexist at a globally stable equilibrium point. He used a mechanistic model in which two species compete for a single, non-accumulating resource. This study used intraspecific competition as a factor that, when greater than interspecific competition, diminishes one species' competitive advantage over the other, thereby allowing coexistence.

Chesson (1982, 1994) and Lavorel and Chesson (1995) used environmental factors to contribute to the stability of ecosystems and dampen the effects of competition. They argued that competitors can coexist when an environment is highly random because it causes niche partitioning. Later arguments developed by Chesson and Huntly (1997) included not only the environment as a factor allowing competitor coexistence, but also that environmental fluctuations themselves can cause spatial and temporal niches.

While these are valid approaches to competitive exclusion, there are problems that can readily be seen. In Haig and Maynard Smith's (1972) study for example, there is partitioning of that resource, although both herbivores are using the plant as a resource. Furthermore, the species are not in direct competition for the resource. Rather, they are competing exploitatively. Armstrong and McGehee (1980) and Vance (1984) utilized an approach that involved self-limiting effects by the competitors. Although this approach allowed coexistence, there is less parsimony to these models than in those presented in subsequent chapters. Chesson's studies involving environmental factors as niche creators goes about solving the problem in a dubious manner. By using the environment to create niches the competitive exclusion principle is not being addressed at all. The principle states that "complete competitors cannot coexist" and species with different niches are not complete competitors. These approaches, therefore, are not parsimonious, and one could argue that some do not directly address the competitive exclusion principle.

Hutchinson (1961) viewed the competitive exclusion principle as useful because he perceived the principle as a statement that is logically true and not subject to empirical falsification. In a classic article, he specifically discussed the problem presented by phytoplankton. Specifically, he reported that a number of species coexist in an

unorganized, homogeneous environment. The phytoplankton species compete for the same resources and at times, there are severe nutrient limitations. Hence, this seemingly violates Gause's principle. Hutchinson suggested that coexistence was due to failure of the system to reach equilibrium, or to a heretofore unrecorded environmental heterogeneity. He dismissed the idea that perhaps a light gradient or condition of the surface film was responsible for the stratification of the environment.

2.8 LOOP ANALYSIS

2.8.1 Historical

The history of mathematical ecology as it relates to the stability-complexity paradox progressed as follows. Before 1970, the fields of mathematical stability and ecology were isolated. Mathematical theory of stability had progressed from late 19th century astronomy and led to Liapunov's contribution that the stability of a complex system could be assessed based on its qualitative properties alone. Its first application was in electrical engineering (Mason 1953).

In the 1960's, a series of influential economically oriented papers were published that laid the foundation of ecological work in the next decade (Quirk & Ruppert 1965; Maybee & Quirk 1969). These rigorous studies demonstrate that Liapunov principles could be applied beyond engineering in order to elucidate complex systems.

In parallel to this development, ecology was striving to explain the link between complexity and stability. Most notably, Elton conjectured on the stability of ecosystems

and as stated before, his thinking helped to define the ecological role of complexity and stability.

In the 1970s, two papers shattered the Eltonian view. The first, by Gardner and Ashby (1970), demonstrated through simulations that mathematical stability rapidly decreases with increasing complexity. The second, by May (1972), further reinforced the idea by introducing to ecology the Q-R rules, as they were called. These rules theoretically demonstrate that stability and complexity are incompatible. These papers laid the foundation for further work, most notably by Pimm and by Levins, who both exploited the new theory to develop the food web theory and loop analysis, respectively.

2.8.2 Qualitative Analysis

Levins (1974) examined the mathematical criteria for stability, the so-called Routh-Hurwitz criteria, and demonstrated that their results could be interpreted in terms of 'loops', that is, paths of links between populations. He also demonstrated that the matrix from which these results were obtained, which he coined a 'community matrix', consisted of Malthusian parameters. Both of these discoveries lent a very persuasive argument in favor of mathematical theory since it tied it directly to Darwinian principles and was very intuitive biologically.

The specific techniques of loop analysis are as follows. First, a signed digraph of a community is drawn. Each link between the variables (populations) is entered directly into a matrix, from which a characteristic polynomial can be derived by assessing its determinant. The elements of the matrix are mathematically obtained from the partial derivatives of the system equations. The criteria for stability are that the coefficients of the polynomial be negative, which biologically means that feedback is 'thermostatic', and that the Hurwitz determinant be positive, which biologically means that feedback at 'lower' levels must be stronger that that at higher levels.

Variables are represented by circles and usually symbolize populations, although they may represent stable complex subsystems (Figure 2.6). The variables are connected through links which designate rates of transfer between variables, usually interpretable as birth and death rates. Links may be either positive or negative between variables, while no link indicates no interaction. A path is a series of links that never crosses the same

variable twice, while a loop is a path that returns to the same variable without crossing a variable twice.
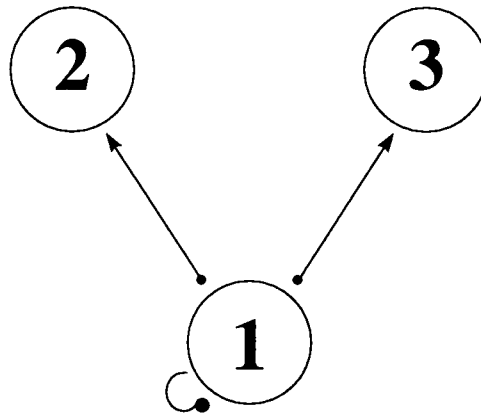
Figure 2.6 Signed digraph of a community, showing two species (2 & 3) utilizing a third species (1).

The three types of relationships used are predation (+ -) which has negative pairwise feedback, while both competition (- -) and mutualism (+ +) have positive pairwise feedback. Negative self-effects, represented by a negative self-feeding arrow, refers to density-dependence or self-regulation (Figure 2.7). Feedback is either positive or negative, depending on the path or loop followed. To get the feedback of a loop or path simply multiply the signs of each link in the loop or path (Figure 2.8). For example, the product of two positive links (+ +) or two negative links (- -) is positive feedback, while a negative link and a positive link makes the path's overall feedback negative (Figure 2.9).
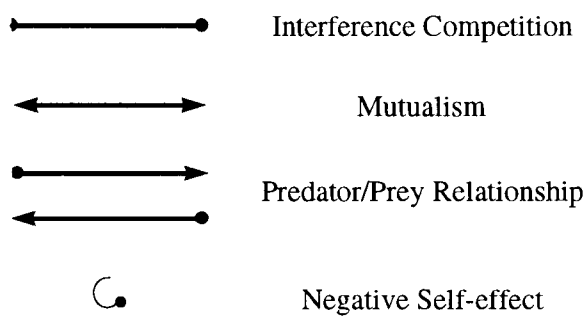
Figure 2.7 Pairwise links.
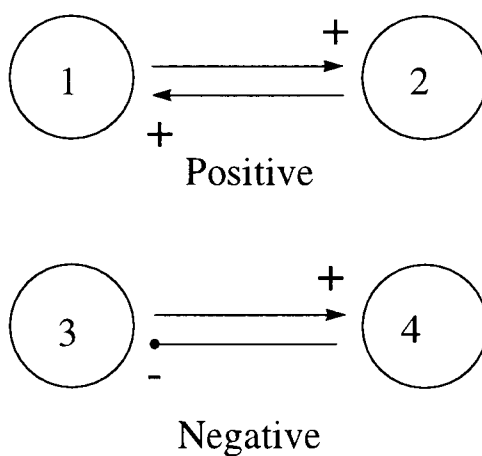
Figure 2.8 Feedback loops of length 2. The positive feedback loop is represented in a community matrix as a12*a21. The negative feedback loop would be -a34*a43.
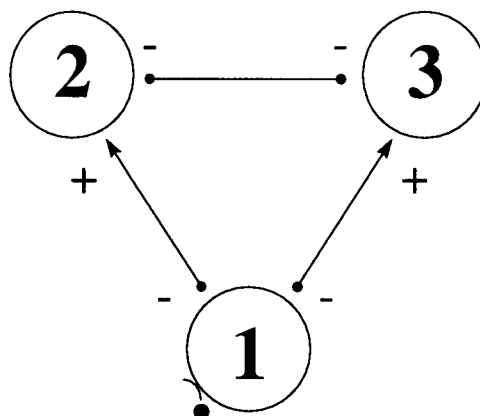
Figure 2.9 Signed digraph showing a loop of length 3 exhibiting positive feedback.

Within an absolutely unstable model, (model 1), a single variable (4) is added and connectiveness within the system is increased through links to the other variables (Figure 2.10). Beginning with one variable the new variable is linked sequentially, cycling through all the possibilities, until finally, the introduced variable is linked to all other variables. That is, the models are broken down to a fourth variable linked pairwise with one other variable, two variables, and, finally, to all three variables. The interactions have previously been described as predator-prey, mutualistic, and competitive.
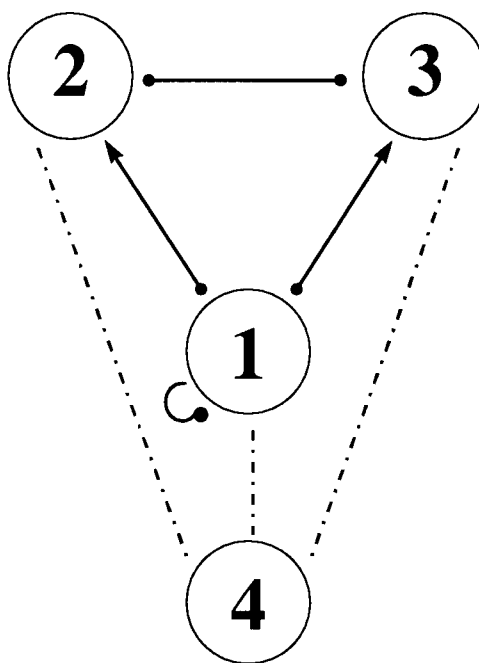
Figure 2.10 Loop model (signed digraph) 1 with a single variable (4) added. Solid lines represent relationships that are constant through the models. Links that are added in the models are denoted as dashed lines and indicates interference, mutualistic, or predator-prey interactions.

The analysis of loop models in this study was performed in Mathcad. The first step is to enter the model into a Jacobian or community matrix. For example, an ecosystem is first represented by a signed digraph (Figure 2.11), then as a community matrix. To assess equilibrium stability criteria the eigenvalues or roots of the equation, λ, must be subtracted from each diagonal element. The determinant of the matrix is then calculated and the results checked against Routh-Hurwitz criteria. For mathematical stability to occur there are two conditions that must be met. The Hurwitz determinant must be >0 such that feedback at lower levels is stronger than the feedback at higher levels. The second criterion states that feedback at all levels must be negative, which is represented by all the

coefficients being of the same sign. In this analysis negative feedback is designated by positive sign at each feedback level. Feedback may also be hand calculated. Feedback at level 0 is always -1, at level 1 feedback is the sum of all loops of length 1. At level 2 the feedback consists of the sum of all loops of length 2 and the subtraction of the products of loops of length 1. Feedback levels higher than two become more difficult to calculate, but for level 3 the feedback is calculated as follows. Addition of all loops of length 3 and subtractions of all combinations of products of loops length 1 with loops of length 2 that are disjunct. Disjunct means that there are variables in common between the loops. Although dated, the text by Puccia and Levins (1985) is still a useful reference.

-a11a23a32-a21a13a32-a31a12a23
-a23a32+a21a12+a31a13
a11
1
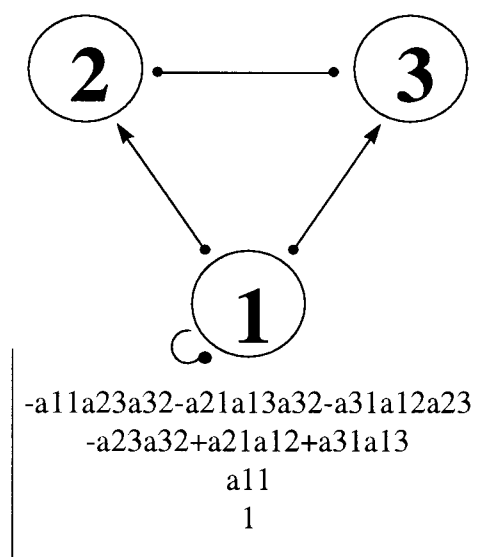
Figure 2.11 Signed digraph showing feedback at three levels. Variables are represented in the community matrix as aij and designate a link, and the term is interpreted as: 'link a to i from j'. The feedback, which are coefficients of the characteristic polynomial, are reproduced in descending order below the figure. Feedback level 3 contains two loops of length 3 and the product of one length 2 loop and a loop of length 1 (a11a23a32) that are disjunct. Feedback level two is the sum of all loops length 2, one positive and two

negative loops and feedback level 1 contains only the negative self-effect. In this example, negative feedback is represented by a negative sign.

From this determination, it is then possible to obtain a 'table of predictions' to assess the direction of change in any variable following change in one of the links. This is obtained from the inverse matrix, by multiplying the community matrix by -1, inverting it and then transposing it. This procedure seems to have been 'discovered' a number of times in ecology (Riebesel 1974; Levins 1974; Bender 1984). This method is the basis for ecological 'PRESS' experiments (Stone 1990; Schmitz 1997).

Bender *et al.* (1984) analyzed perturbation experiments of real and conceptual communities. Using an inverse matrix the authors scrutinized PRESS perturbation experiments. The application of inverse matrices to define interactions within communities was also used by Stone (1990) and Schmitz (1997). The authors claim that an inverse matrix offers up a more realistic look at community process than a community matrix. However, the use of an inverse matrix is mathematically the same as the qualitative analysis that was applied by Levins, and these authors have, essentially, reinvented the wheel.

2.8.3 Applications of Qualitative Analysis

The term loop analysis was coined by Levins, but actually refers to his interpretation of the procedures and not the procedures themselves. We therefore prefer the term qualitative analysis, which dates back to May's original work. A large number of studies have used this approach, and a partial bibliography is included (Table 8.1). Most

notable is the work of Levins's followers, such as Vandermeer, Lane, Bodini, Puccia, Pilette, and Roughgarden. Virtually any modern algebraic analysis of mathematical models in ecology will rely on these principles. The most popular current text in mathematical ecology (Edelstein-Keshet 1988) emphasizes a qualitative approach.

Table 2.1 Partial catalog of refereed studies utilizing qualitative analysis.

Author	Journal/Book	Year
Bodini, A.	BioSystems	1991
Lane, P.A.	Ecology	1986
	ESA Supp. Pub. Ser. Doc. No. ESPS 8525	1986
Levins, R. and Vandermeer, J.H.	Agroecology	1989
Levins, R.	Ann. NY Acad. Sc.	1974
	Ecology and Evolution of Communities	1975
Pilette, R., Sigal R., and Blamire, J.	Biosystems	1989
Puccia, C.J. and Levins, R.	*Qualitative Modeling of Ecosystems*	1985
Roughgarden, J. and Feldman, M.	Ecology	1975
Edelstein-Keshet	*Mathematical Models in Biology*	1988

Loop models are discussed by Puccia and Levins (1985) as models helpful in the analysis of real world ecosystems. The model, or digraph, corresponds to a matrix of interactions and to equations. Loop analysis emphasizes qualitative predictions, and rather than knowing exactly how much change has occurred, the model shows whether change has occurred or not, and whether the change is positive or negative.

Pilette *et al.* (1987) assessed the potential for the use of qualitative (loop) analysis in community evaluations, concluding that loop analysis is indeed a useful tool for evaluating communities, although underused. They present a computer simulation that accurately reproduces the results of Levins' (1975) calculations. Recently, perturbation experiments in ecology have used the inverse matrix.

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CHAPTER 3

A REAPPRAISAL OF THE COMPETITIVE EXCLUSION PRINCIPLE

By
Israel N. Duran, Hiram W. Li, and Philippe A. Rossignol

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3.1 INTRODUCTION

The competitive exclusion principle has had a major impact on ecological theory ever since its introduction (Gause 1934). Although it was, and still is, occasionally called Gause's principle, the expression in current usage was coined by Hardin who stated the principle as an alliterative negation: "Complete competitors cannot coexist" (Hardin 1960). The principle has a rich history of theoretical study (see Chesson & Huntly 1997).

We found that a theoretical analysis of community matrices with linearizable responses that supports the principle in the case where only two competitors exploit a resource, with or without interference competition. Such a result has been known from previous studies (McGehee & Armstrong 1977). However, when the two species interfere with a third one, or when mutualism or omnivory occur, then conditions for a stable equilibrium can be met and niche overlap can occur. To account for the role of complexity, we investigated the impact of the number and type of interactions by adding another species to a two-competitor-one-resource system. We analytically evaluated the feedback levels of the 124 possible systems that can ensue from this addition. Unexpectedly, the likelihood of stability increases not so much with the nature of interactions but with their number.

Recent simulations, using Gershgorin disk analysis of eigenvalue distribution (Haydon 1994), demonstrate that increased connectance can contribute to stability, while field observations of complete ecosystems suggest that food web theory predictions of simplicity are not even closely supported (Reagan *et al.*, 1996). We similarly conclude

that the doctrine that stability and complexity are inversely related is not supported, at least in this particular situation.

3.2 THE COMPETITIVE EXCLUSION PRINCIPLE

Minimally, the competitive exclusion principle applies to a system where two species compete to exploit a single and unique resource, but without direct interaction (Figure 3.1). This system displays zero feedback, which mathematically, although not practically, speaking allows equilibrium to occur. The addition of interference links generates positive feedback and the system is qualitatively unstable, that is, cannot meet criteria for stability (Edelstein-Keshet, 1988) under any condition (Figure 3.2). In both cases, niche overlap is incompatible with coexistence. These model ecosystems alone support the principle, but in our opinion, are not sufficient for generalization.

$$\begin{bmatrix} 0 \\ -a21 \cdot a12 - a31 \cdot a13 \\ -a11 \\ -1 \end{bmatrix}$$
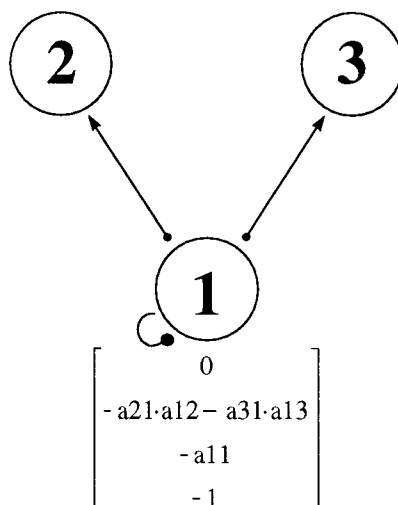
Figure 3.1 System in which two species exploit a single resource, without direct competition. This system has zero feedback at the third level, and therefore allows equilibrium to occur, if only mathematically and not in any practical sense.

$$\begin{bmatrix} a11 \cdot a23 \cdot a32 + a21 \cdot a13 \cdot a32 + a31 \cdot a12 \cdot a23 \\ a23 \cdot a32 - a21 \cdot a12 - a31 \cdot a13 \\ -a11 \\ -1 \end{bmatrix}$$

Figure 3.2 An interference link is added to the previous model, indicating direct interaction between species 2 and 3. The new link causes feedback at the highest level and the system is unstable.

3.3 GENERALIZING THE PRINCIPLE

We therefore addressed whether or not the principle can be generalized to more complex systems. The addition of another competitor without any interference again yields zero feedback (Figure 3.3). This result holds for any number of exploitation competitors. When one or two interference interactions are pre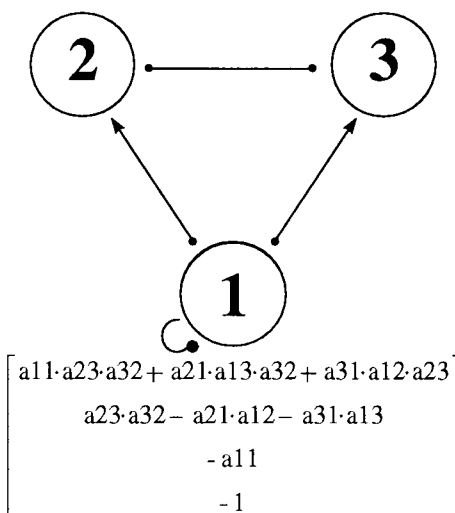sent, the addition of a third competitor gives rise to a system that cannot meet stability criteria under any condition (Figure 3.4, 3.5). However, when all three competitors interfere with each other (Figure 3.6), negative feedback loops are present at all levels and Routh-Hurwitz criteria can be met conditionally, allowing for niche overlap.

$$\begin{bmatrix} 0 \\ 0 \\ -a21 \cdot a12 - a31 \cdot a13 - a41 \cdot a14 \\ -a11 \\ -1 \end{bmatrix}$$
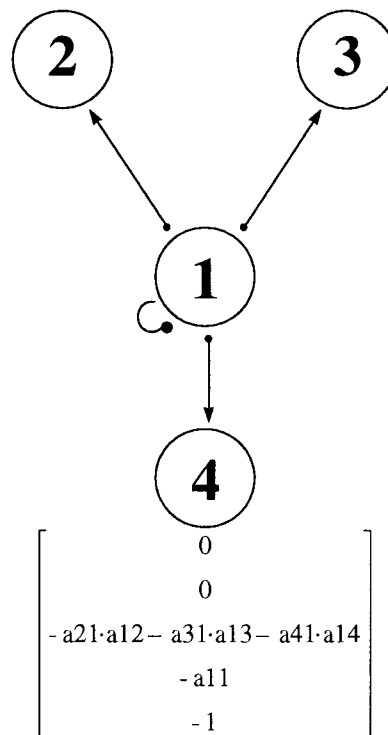
Figure 3.3 A third competitor species (4) is added. As in Figure 3.1 this system has zero feedback.

$$\begin{bmatrix} a41 \cdot a32 \cdot a14 \cdot a23 \\ a11 \cdot a32 \cdot a23 + a21 \cdot a32 \cdot a13 + a31 \cdot a12 \cdot a23 \\ a32 \cdot a23 - a21 \cdot a12 - a31 \cdot a13 - a41 \cdot a14 \\ -a11 \\ -1 \end{bmatrix}$$
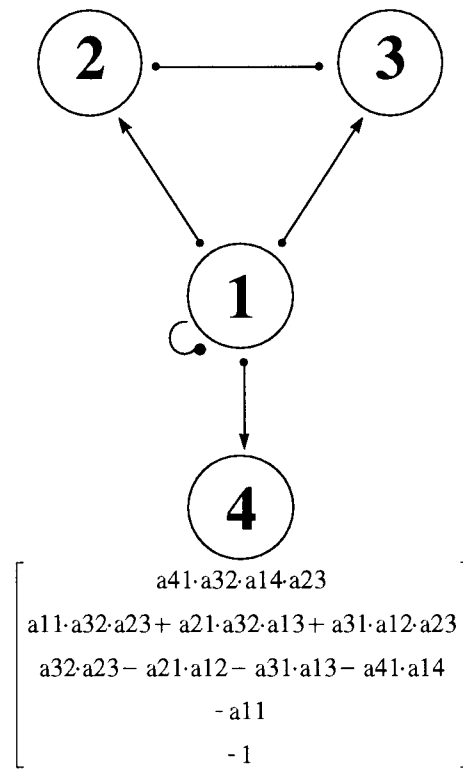
Figure 3.4 Interference competition between species 2 and 3 produces a system that is unstable. Positive feedback at the two highest levels prevent this system from meeting stability criteria.

$$\begin{bmatrix} a21 \cdot a12 \cdot a34 \cdot a43 - a21 \cdot a32 \cdot a14 \cdot a43 - a41 \cdot a12 \cdot a23 \cdot a34 + a41 \cdot a32 \cdot a14 \cdot a23 \\ a11 \cdot a34 \cdot a43 + a11 \cdot a32 \cdot a23 + a21 \cdot a32 \cdot a13 + a31 \cdot a12 \cdot a23 + a31 \cdot a14 \cdot a43 + a41 \cdot a13 \cdot a34 \\ a34 \cdot a43 + a32 \cdot a23 - a21 \cdot a12 - a31 \cdot a13 - a41 \cdot a14 \\ -a11 \\ -1 \end{bmatrix}$$

Figure 3.5 With a second interference link added between species 3 and 4 the result is still unstable, and positive feedback is present.

Figure 3.6 Interference among all three competitors creates a conditionally stable system. The condition for satisfying Hurwitz determinant criterion:
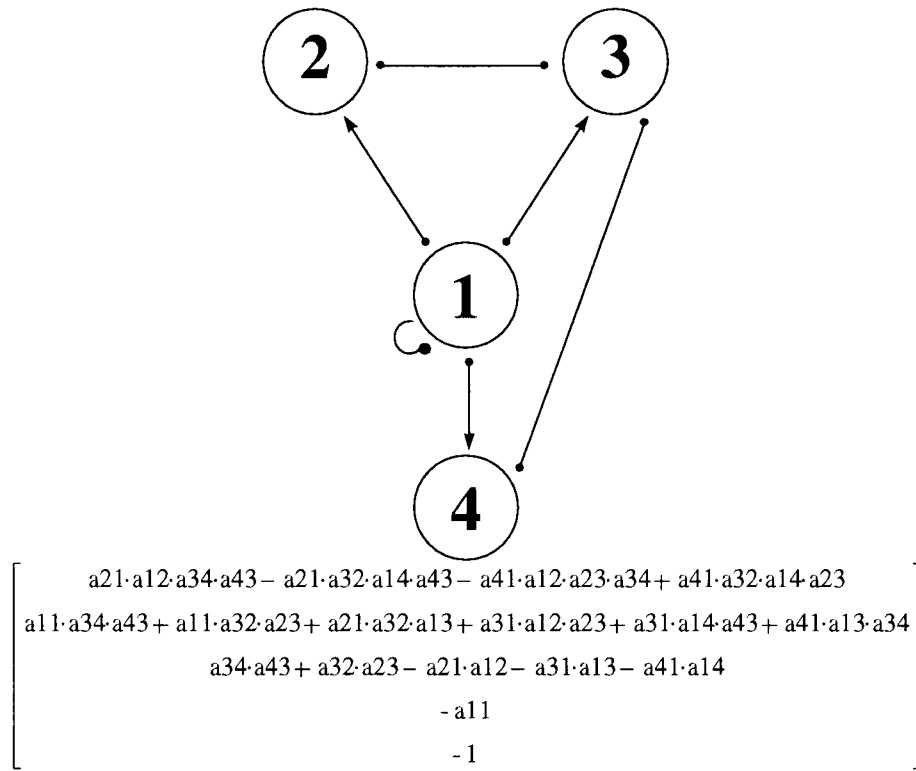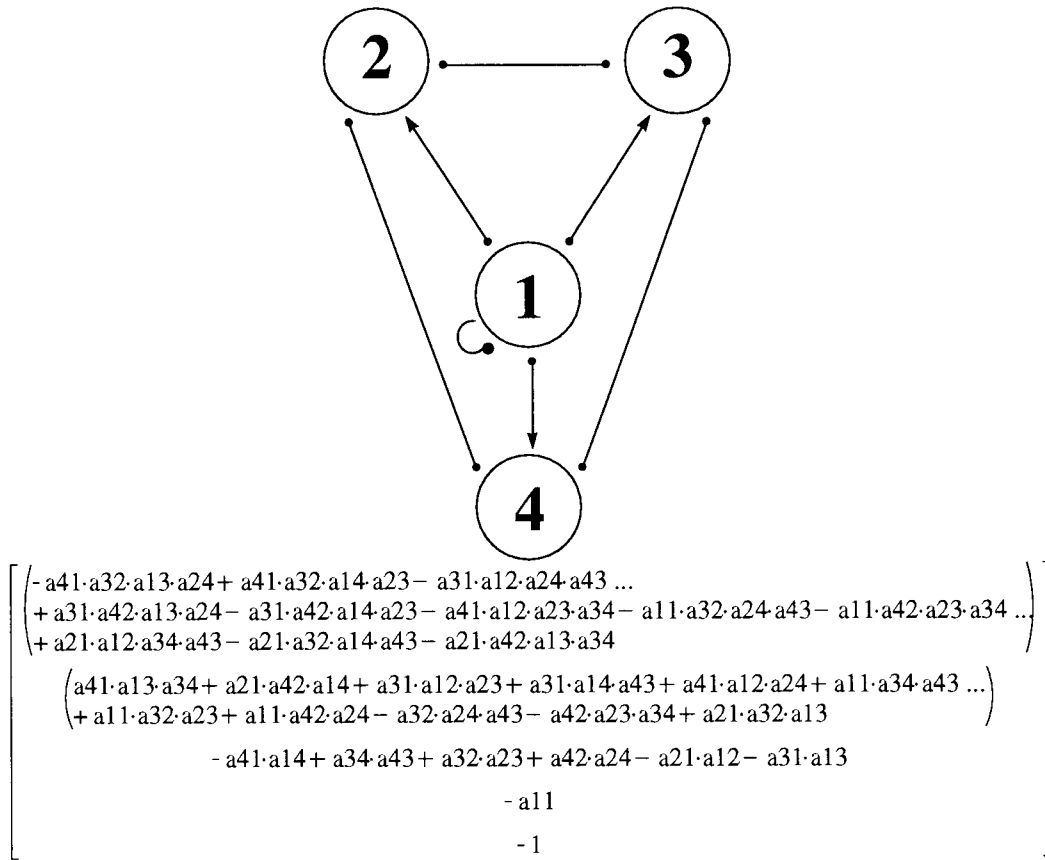
al1·a21·a12+ al1·a31·a13+ al1·a41·a14>

− a41·a12·a24− a41·a13·a34− a21·a42·a14− a31·a12·a23− a31·a14·a43− a21·a32·a13+ a32·a24·a43+ a42·a23·a34

From this analysis, interference competition would appear to introduce conditions that can satisfy the Routh-Hurwitz criteria when species are competing to exploit a resource. We therefore analyzed the effects of other types of interactions between the two exploitation competitors. The addition of either mutualism (Figure 3.7) or omnivory (Figure 3.8) introduces conditions under which stability is also possible and niche overlap can occur. Competitive exclusion occurs only in a restricted set of circumstances.

$$\begin{bmatrix} a11 \cdot a23 \cdot a32 - a21 \cdot a13 \cdot a32 - a31 \cdot a12 \cdot a23 \\ a23 \cdot a32 - a21 \cdot a12 - a31 \cdot a13 \\ -a11 \\ -1 \end{bmatrix}$$
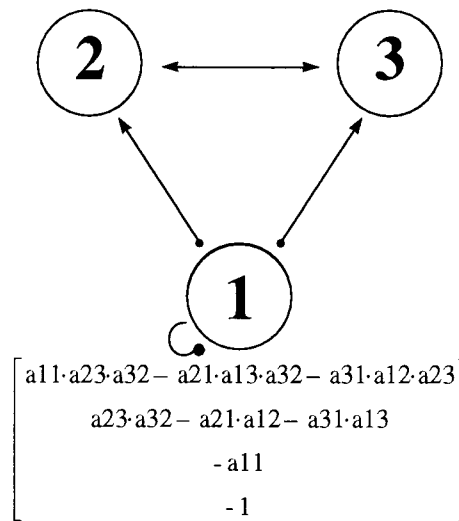
Figure 3.7 The interference link is replaced by a mutualistic link. Conditions arise allowing stability.

$$\begin{bmatrix} -a11 \cdot a23 \cdot a32 - a21 \cdot a13 \cdot a32 + a31 \cdot a12 \cdot a23 \\ -a23 \cdot a32 - a21 \cdot a12 - a31 \cdot a13 \\ -a11 \\ -1 \end{bmatrix}$$
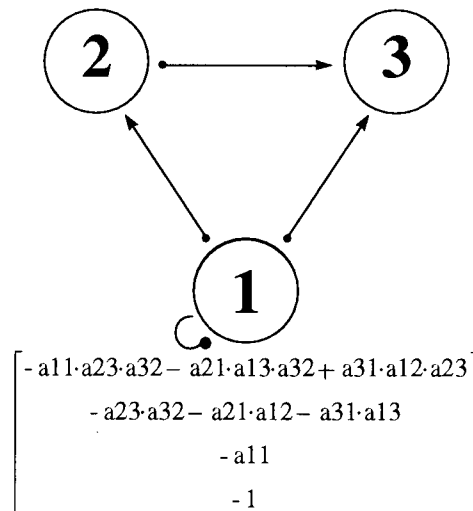
Figure 3.8 Conditions arise allowing stability when omnivory is substituted into the system.

3.4 ADDITION OF COMPLEXITY

A confounding factor is introduced in most of the systems above through increased complexity, manifested by the increased numbers of species and interactions. To isolate connectance from the type of interactions present, we chose the two-competitor-one-resource unstable system (Figure 3.2) that most strictly supports the competitive exclusion principle, and assessed the effect of increasing the number of links to a fourth species on stability criteria. We determined whether or not complexity and conditions for stability are positively correlated. We analyzed all possible model ecosystems arising from this arrangement, for a total of 124 (there are 12 possible systems with one pair of added links, 48 with two pairs and 64 with three pairs). Based on the coefficients of the characteristic polynomial of every system, we observed that the proportion of systems that can achieve conditional stability increases directly with the number of paired links (Figure 3.9). Overall, in 80% of 124 systems, a two-competitor-one-resource system can meet conditions for negative feedback when a fourth species is added. The new system therefore can violate the competitive exclusion principle and species can display complete niche overlap. In particular and notably, at maximum connectance 100% of 64 possible systems can meet such conditions irrelevant of the types of interactions introduced. We conclude that complexity emerges as a more important factor in introducing conditions for stability and niche overlap between competitors than the types of interaction.
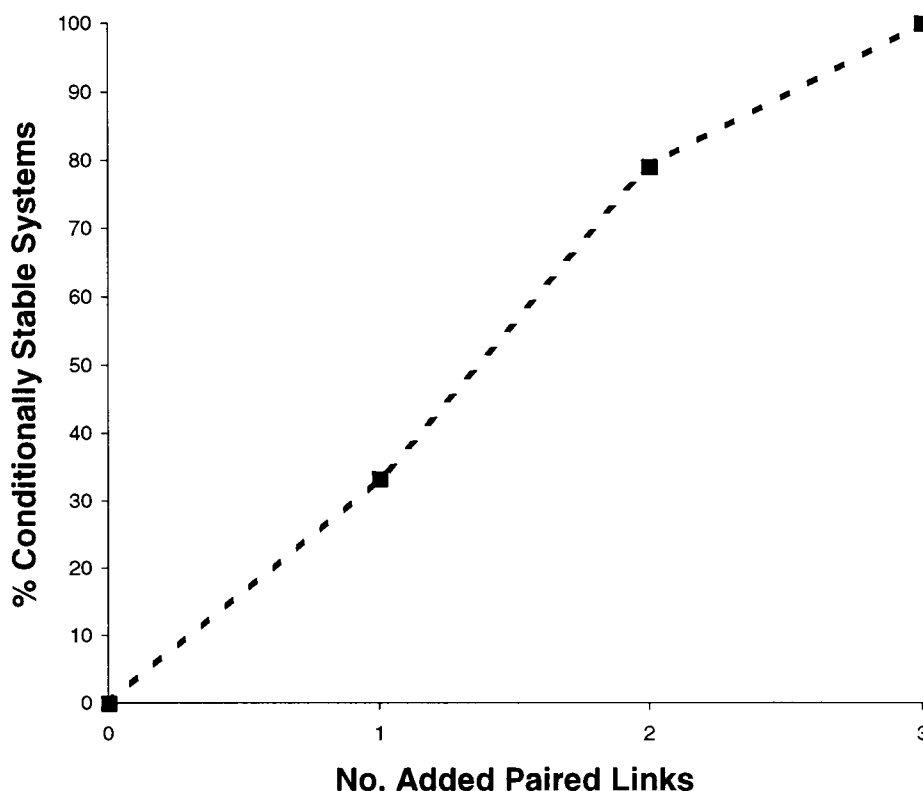
Figure 3.9 Percentage of model ecosystems with conditions satisfying the Routh-Hurwitz criteria as a variable of the number of interactions present when a fourth species is added to the system in Figure 3.2 above. All links were paired, that is, predator-prey, mutualistic or interference competition. There are 12 possible systems with one pair, 48 with two pairs and 64 with three pairs of added links. Coefficients of the characteristic polynomial, that is, the values of feedback at the different levels, were calculated analytically on a PC-based symbolic processor (Mathcad Plus 6.0, MathSoft, Cambridge, MA) according to procedures in Li *et al.* (1998). The complete analysis is available upon request.

3.5 DISCUSSION

Based on our analysis, we conclude that the competitive exclusion principle unambiguously applies only to particular cases resulting from a combination of 1) absence of interactions between exploitation competitors and of 2) extreme simplicity of a system.

Although counter-intuitive, when numerous competitors exploiting a single trophic resource also interact with each other, negative feedback interference loops can be introduced which allow the competitors to 'group self-damp', so to speak, their interactions. For example, in the case of Figure 3.6, one competitor cannot benefit or lose from resource exploitation without counteracting negative feedback from the three-species interference loop (species 2-3-4) and *vice versa*.

Two main objections may be raised against our conclusion. First, our analysis is qualitative, and the quantitative requirements in practice may negate the reasonable possibility of equilibrium of systems in Figure 3.9. A recent study using simulation analysis of Gershgorin disks (a measure of eigenvalue distribution) concluded that under biologically reasonable conditions, complexity in the form of added links and widened range of interaction strength in fact increased stability (Haydon 1994), contrary to previous assertions. Our analysis applies the strictest equilibrium criteria. Were we to apply negative overall feedback as the sole criterion, as is sometimes suggested (Haydon 1994; Pimm & Lawton 1978), our qualitative analysis indicating an increase in the likelihood of stability also would be supported quantitatively, since stability can increase with connectance (Haydon 1994).

Second, it may be argued that field studies do not support the coexistence of complexity and stability. A long-term and extensive study of a tropical rain forest food web, claimed to be the largest such quantitative study, specifically testing the restrictive predictions (namely, short trophic chains, few loops, low predator-prey species ratio, low species to link ratio) of food web theory arising from the Routh-Hurwitz criteria found all these predictions negated, often in an extreme fashion (Reagan *et al.*, 1996). We suggest

that one reason for the failure of food web theory is its bypassing of non-trophic links, thus underestimating true connectance.

We do not identify specific field situations that correspond to each of our models, but at least some of the systems correspond to actual situations in nature. Thus, Figure 3.8 corresponds to the extensively studied situation of omnivory (Pimm & Lawton 1978), while Figure 3.7 was derived from an interpretation (Rossignol, unpubl.) of fungus-conifer mutualism in mature forests (Perry *et al.*, 1989).

Another approach that has yielded coexistence between the two resource competitors comes from the addition of negative elements to these competitors in the diagonal of the community matrix. In essence, two non-interfering predators have access to another resource(s) (Haig & Maynard Smith 1972). However, competitive exclusion is defined as systems where the number of resource species are less than the number of competitors and the above work therefore falls outside the principle. Alternatively, by introducing a Holling type 2 (non-linearizable) functional response in a system of non-interfering competitors (our Figure 3.1), a special case of neutral stability and coexistence is possible at non-constant densities (Armstrong & McGehee 1980). The reason for this coexistence arises from complication to the system, as we have also concluded. However, complication in the Armstrong and McGehee model arises from the non-linearity. Indeed, in a fluctuating system, a non-linearity acts as an input to the system. Changes in statistical descriptors, such as variance, will affect then the level of the species where the input is occurring and in essence become variables themselves (Puccia & Levins 1985 pp. 226ff). That approach allows then for the coexistence of two non-interfering competitors which cannot occur in linearizable relationships except at neutral stability. However, it

can hardly be argued that this approach is parsimonious because, as we demonstrate above, when three consumers are present, coexistence is possible under standard assumptions of linearizability. The approach of Armstrong and McGehee need be invoked only when two consumers are involved or where interference does not occur.

The concept that interactions with additional species allow for niche overlap has been suggested for interference competitors not sharing a trophic resource (Strobeck 1973; Levins 1975; Roughgarden & Feldman 1975; Vance 1978) but not, to our knowledge, for exploitation competitors. In those studies of interference competitors, model equations clearly indicate that the competitors do not share a trophic resource in any. Some studies concluded that predation could further stabilize a system of competitors and allow for niche overlap (Levins 1975; Roughgarden & Feldman 1975; Vance 1978). Conclusions regarding niche partitioning based strictly on interference competition probably should not be generalized to resource competition. The contested "dimension" (Pianka 1988) of the niche may be different for interference than for exploitation competitors, for example space rather than food.

A broad suggestion that emerges from our study is that complexity can increase proportionately the likelihood of stability in an initially unstable system. In the particular system of competitive exclusion that we studied, a species introduction will increase the likelihood of conditional stability from zero to the point that if the added species interacts in any way with all species present, conditions are always theoretically present. Although we cannot project this conclusion to all situations, a project that will require extensive simulation, we can conservatively assert that, from this perspective, stability and complexity are not always inversely related. We caution that the presence of conditions

for stability does not mean that these will necessarily be met. Mostly, it means that it is difficult to prove instability and that ambiguity has increased.

Our somewhat reverse outlook, that is, of studying the impact of species addition on an unstable system, while still using a community matrix, bears review. It was concluded in similar studies (Levins 1975; Roughgarden & Feldman 1975; Vance 1978) that species interfering with each other, but not exploiting a common trophic resource, could be stabilized by the addition of a generalist predator. Those landmark studies formalized the concepts of the keystone species and of niche separation distance as well as the hypothesis that predation increases the likelihood of stability and narrows niche separation distance between the prey. We suggest that complexity may have been the principle that unwittingly was being addressed in those studies since the generality of the conclusion regarding predation has not been supported theoretically in later studies (Bodini 1991).

As to more practical aspects, the competitive exclusion principle as worded by Hardin (1960) is strictly speaking not refutable since it is a negative statement. Sidestepping this semantic hurdle, we are still faced with the limitation that, for Hardin's definition to hold beyond two competitors, "complete competitors" would have to mean organisms that do not compete directly. Competitors would scramble for a single niche dimension, namely food, but not contest space or interact significantly with any other species in the system, which hardly seems "complete" or even likely to occur. Hardin's own comments however seem to indicate that he assumed that interference competition was also present (Hardin 1960).

Two possibilities therefore seem to exist for the coexistence of two resource competitors. They can coexist because of niche partitioning as classically proposed, and complete competition is only an appearance. Since partitioning can take very subtle forms and arise from unexpected sources, such as from a random environment (Chesson & Huntly 1997), the possibility of cryptic partitioning always looms large. Alternatively, coexistence exists because the system is regulated through complication, either through interactions with other species within the whole system as we propose or through non-linearities (Armstrong & McGehee 1980), and complete competition is a reality.

Many types of interactions that we introduce, specifically interference and mutualism, are often non-trophic and usually not documented in food webs (Hall & Raffaelli 1993). If one were to extract exploitation competitors from any complex system by relying exclusively on trophic relationships, the only model seemingly possible would be as in Figure 3.3. One might conclude erroneously that the principle is refuted even in its narrowest sense. This situation may have occurred in a classic refutation of the theory behind competitive exclusion wherein many similar species of plankton were shown to have essentially total niche overlap (Hutchinson 1961). In that study, non-trophic relationships which could have accounted for coexistence may not have been documented. In contrast to Hutchinson, we suggest that the principle need not be abandoned entirely, but only its general application to complex systems. Structure is a crucial aspect of community behavior.

The societal impacts of the competitive exclusion principle and of the stability-diversity paradox have been tremendous and we trust that policies arising from them will be re-examined. Both theoretical economists (Quirk & Ruppert 1965) and human

ecologists (Hardin 1960) have made influential and sometimes very specific conclusions or

recommendations regarding competition that may not be valid in the context of

complexity. Furthermore, conservation of biodiversity and management of ecosystems are

currently global economic considerations of modern society. The extreme interpretation

of theory that led to the stability-diversity paradox and the possibly ill advised

management approach that we rely on (Holling & Meffe 1996) may not be suitable for

systems where complexity is characteristic.

3.6 ACKNOWLEDGMENTS

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CHAPTER 4

SUMMARY

The popular view in ecology is that stability and complexity are incompatible. That is, with an increase in complexity, there is a loss of mathematical stability within any given system. Most previous studies (with few exceptions) that examined the link between complexity and stability began with model ecosystems that were stable to begin with. In these cases it has generally been shown that an increase in complexity causes a loss of stability and *vice versa*. Unlike those studies which were based on stable models and found that complexity causes instability, complicating an unstable model only serves to increase the stability. Understanding that complexity can add stability to unstable systems shows that the stability-complexity paradox may only be the result of how the system under investigation is perceived.

These models, although simplistic (not simple), have shown to some extent that increasing complexity of the model does lead in the direction of conditional stability, even if it is not complete stability. Simply adding a variable can help stability, but additional links within this particular unstable system have a stabilizing effect. Investigation, of the stability-diversity hypothesis leads me to believe that it is complexity, rather than types of interaction that is the more significant factor allowing stability and niche overlap to occur.

I analytically and parsimoniously, that is, using Routh-Hurwitz criteria, demonstrate that the competitive exclusion principle holds as an absolute generality only

when no more than two species are competing for a single resource, either with or without interference. The competitive exclusion principle explicitly pertains only to those particular cases that are both extremely simple and lack interference interactions. Therefore, the principle has limited applications even under the parsimonious assumption of equilibrium. I demonstrate that the principle may fail, that is, coexistence is possible, when a third competitor is present, depending on the number of interference links. With the addition of a fourth species in the system, the likelihood of coexistence increases with connectance to the point that at maximum connectance conditions for niche overlap are always possible, irrelevant of the type of interactions.. When applied to larger systems the principle is not applicable due to the introduction of thermostatic loops into the system.

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