Some Problems of Community Ecology:

Processes, Patterns and Species Persistence in Ecosystems

A Thesis submitted for the Degree of

Doctor of Philosophy.

by

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May, 1988.

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Table of Contents

Abstract

In this thesis a variety of approaches are examined and used to explore the dynamics, patterns and structure of ecological communities. I address the problem of "how it is possible for a number of species to coexist ... all competing for the same sorts of materials" (Hutchinson 1961). An ensemble model is used in an attempt to capture those factors that make for long-term community coexistence. The model is also used as a vehicle to explore - as well as to generate questions and hypotheses relating to - topics currently being examined by community ecologists. For example, the persistence and stability of ecological communities, or the true (sometimes hidden) nature of the interaction between a pair of species can be analysed with the aid of the model. I also study the problem of how, by directly analysing field-data, one might detect evidence of any community-wide processes that explain coexistence.

The model makes use of the Generalized Lotka-Volterra equations, and is primarily based on the fundamental consumer-resource interaction, so that in the main, competition communities are investigated. The design of the model permits an analytical study of multi-species systems (say 5 to 100 species). This contrasts with analyses of models normally presented in the literature which usually describe communities of only two or three interacting species. One feature of the ensemble model is that it makes allowance for environmental variations (which cause structural and/or population disturbances) by simulating the totality of possible states to which an ecosystem can be disturbed. It was found that feasibility - the requirement that all equilibrium populations of a system are positive - is a key factor. In fact, virtually all of the model's feasible states were stable. Feasibility was thus found to be a more critical factor than stability - even though it is the latter property which is normally concentrated on, in studies of

model-ecosystems.

The model presents an interpretation of communities that spend most of their lifetime close to an equilibrium. This limited view was then naturally extended, and it became possible to analyse communities that experience a relatively high disturbance rate, and therefore spend only a minor part of their lifetime close to any equilibrium. It is shown that persistent communities can possess the important qualities of conservation and recovery, without necessarily appearing to possess a stable equilibrium.

The model demonstrates that environmental variability may promote coexistence. An examination is made of how community coexistence depends on species' relative competitive abilities and upon their abilities to "spread risks". As well, the response of a community to species invasions is analysed, and a species extinction curve is derived that corresponds qualitatively to that obtained from field-data on the Hawaiian avifauna.

The notion of a competition community is then discussed. Although a pair of species might appear to be competing when viewed in isolation, their interaction could well be facilitative if viewed within a community context. This phenomenon appears to be prevalent in nearly all of the observed competition communities I examined, and can be attributed to hidden "indirect effects" between species. The ensemble model provides an explanation as to why these facilitations occur so frequently.

A detailed null test is performed in order to deduce whether bird distributions on some archipelagos are nothing more than random assemblages, as has been argued by Connor and Simberloff (1979). The design of the null test is unique and makes use of a specially formulated C-score statistic to determine the checkerboard patterns

within biogeographic data. The test adheres faithfully to the constraints outlined by Connor and Simberloff, whereas other attempts reported in the literature have failed to do so. The data is shown to have signicantly large checkerboard distributions when compared to a null model. Even so, analysis of the New Hebrides bird data (when examined at the family level) indicates that it is the "coexistence principle" which shapes community organization, rather than the "competitive exclusion principle".

I declare that this thesis contains no material which has been accepted for the award of any other degree or diploma in any University and that, to the best of my knowledge, this thesis contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

Lewis Stone.

Dated: May 1988.

Acknowledgements

I could never have taken the challenge to begin this thesis if it were not for the enormous influence and inspiration passed on to me by some of the finest mathematicians, under whom I studied at Monash University. In particular, I am greatly indebted to Dr. M. Deakin, Dr. M. Gutmann, Dr. H. Lausch, Dr. B. Morton and the unforgettable (late) Dr. Carl Moppert, who all, each in their own unique way, spurred me on.

Some of the many wonderful problems in the discipline of Ecology took on a reality and dimension I would never have conceived of, if it were not for the enthusiastic discussions and promptings by Dr. S. Lake and Dr. D. O'Dowd (Zoology Dept., Monash). Both freely gave their time to me, for which I am most grateful.

Whilst working at Monash, I had the good fortune to share my ideas with George Nassios, a co-worker in the field. His own personal interest in the subject turned what could have been an isolating experience, into an enjoyable exchange. The computing assistance given by Mr. B. J. Milne (Computer Science, Monash) was also greatly appreciated. Were it not for his help, some of the statistical analyses I designed may never have been implemented

I also would like to acknowledge the hospitality of the Physics Department at Monash University. Not only did they provide me with an office, and computing facilities, but for three years supported me with a Departmental Research Scholarship. In the final months of my work, Dr. A. Smith, of this same Department, acted in a supervisory role and was most supportive.

My appreciation must always go to Gail, Panayotta, and the close friends who stood by me through this work. I am also grateful to my mother Cecelia, who was always ready and available to proof-read, even if the manuscript wasn't.

Above all, I would like to thank my supervisor Dr. Alan Roberts for his most extraordinary help in every manner. His unfailing and often unbridled enthusiasm, at even the darkest of times or over the smallest of matters, never ceased to amaze me. He made - what was initially for me - an impossible and seemingly painful project, something very enjoyable, meaningful, and in the end a reality.

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Chapter 1

Issues in Community Ecology

§1 Introduction and Thesis Overview

The last decade has been a period of great upheaval for those actively involved in theoretical ecology. It has resulted in a very healthy reappraisal of well accepted concepts that normally went unchallenged or were taken for granted. Generally speaking, theoretical ecologists are beginning to recognize how much more subtle our living environment is than they had previously assumed. The notion of structures in community ecology has been widely modified by the realization that inter-relationships amongst living organisms can be in such a state of flux that they are difficult to characterize or pinpoint at any moment. In an unknown range of cases they may be secondary in importance to environmental variations.

Because of the recognition and acceptance of the great variability in natural and ecological processes, many of the traditional methods of investigating ecosystems have been discarded, and newer techniques are being called for and designed. In this dissertation I examine some of these more recent methods and use them to investigate the role of natural variability and its effects on the "total relations" within an ecosystem.

In order to appreciate some of the ideas and results advanced in this thesis, it is important to have some familiarity with their historical background. Therefore Chapter 1 overviews some of the current issues in community ecology from this perspective. Some have been given particular emphasis: the "Balance of Nature" concept; the concept of community as "superorganism"; the theory of interspecific competition; the mathematical modelling of ecological systems. All of the above have played a part in developing the notion of an ecological "community".

The dynamics and structure of ecosystems are examined using a simulation approach. In Chapter 2 an ensemble method for modelling ecosystems is put forward. Chapter 3 elaborates the ensemble model's full range of behaviour when the system undergoes (simulated) environmental disturbance. The discussion, although highly qualitative, evolves from an examination of the model's (analytically obtained) feasibility characteristics. It gives an interpretation of communities that, at least in appearance, do not seem to be governed by deterministic processes. Chapter 4 then outlines possible mechanisms that might be conducive to community coexistence, making use of results obtained from the model.

In Chapter 5 I draw attention to some of the unusual - if not paradoxical - aspects of what are normally considered to be competition communities. It is usually understood that in a competition community each species suffers from the presence of every other. However, this is frequently not the case. I discuss and model how two species that are competitors as an isolated pair can, when put in the context of a community, have a mutualistic association because of indirect interactions.

Finally, in Chapter 6 I explore the notion of ecological structure and patterns, not with a dynamical simulation model, but using a statistical null model applied to field-data. Using raw data on birds in the New Hebrides and bats in the Antilles, the null model was used to investigate whether colonization patterns were an outcome of "chance or competition" - in the words used by Connor and Simberloff (1979) in originally posing the problem. The problem has remained an issue of major controversy ever since.

§2 The Community

'Oekologie', (or 'ecology' as it is freely translated), was a term devised by the German zoologist Haeckel in 1866 (see McIntosh 1985, p.2), and was envisaged to be a study of those universal laws which shape the living world. It has since become a fully recognized science in its own right.

Haeckel, in 1870, defined ecology as:

"the body of knowledge concerning the economy of nature-

the investigation of the total relations of the animal both to its inorganic and to its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact..."

(Translated in Allee et al 1949:frontispiece).

In attempting to delineate the "total relations" of species to its environment, a notion of "community" developed. One very general definition of community is that given by Krebs (1985) as "any assemblage of populations of living organisms in a prescribed area or habitat" (p.435). An important issue dealt with in Chapter 6 is how it may be decided whether a community is anything more than just a random assemblage. What are the "total relations" within the community to which Haeckel refers us? If significant biological processes are believed to "govern" a community, then criteria are required to convince us that this is so.

A long popular view has been to think of ecosystems as harmonious entities which, if left unhampered, will remain in a state of natural balance. This "Balance of Nature" concept has a long history going back millenia, as briefly documented in Appendix 1. Needless to say, there is an attractiveness and convenience in the utopian idea of a "perfect world" with its own natural harmony and organization. However,

this viewpoint has always been controversial. The problems in asserting that ecosystems have, or have not, some innate biological structuring have been debated since at least the time of Aristotle (see Appendix 1).

Statistical tests are often made use of in order to resolve these sorts of questions, but - as we shall see - such tests nearly always require simplifying assumptions to be made; assumptions which may in the end make any conclusion achieved quite open to challenge. For example, McIntosh (1980) reports that Haeckel (in the nineteenth century) came to grips with such problems in his encounters with Hensen. The latter's innovative analyses of plankton communities assumed uniform environmental conditions, so that individuals of the plankton populations were taken to be evenly spread over the sea. Haeckel took strong objection to this assumption, claiming that he knew from first hand experience that plankton populations were aggregated. This led him to reject some of Hensen's counter-intuitive findings.

Early this century the idea that communities had some underlying organizing structure became influential. Clements put forward what was to become Ecology's first paradigm (Simberloff 1980). He elaborated the theory that the community was not just a loose collection of populations but was in itself a "superorganism". In Clements (1935) we read:

"[T]he community is a complex organism of a wholly different order from the individual plant or animal, but nevertheless an organic entity with functions and structure. As a whole, it is not merely greater than the sum of its constituent species and individuals, but these in turn are something different in the community from what they are when detached from it" (pp.342-343).

Seen in this way, zoologists such as Shelford, Elton, Emerson and Allee found the concept appropriate for their work. Its holistic approach made

the view highly appealing to the scientific world. Systems theory was utilized so that the "superorganism" could be analytically dissected in order to find the true balancing mechanisms of Nature.

On the other hand, this view of community had its opponents. H.A. Gleason, in the early part of this century, challenged the idea of community as "superorganism" with his individualistic concept. Gleason, a self-described "good man gone wrong" (quoted in McIntosh 1985, p.137), try as he might, found little evidence of a superorganism in his field-data. Instead his studies showed that communities were a collection of species in loose and varying associations, influenced by chance factors more than anything else. He wrote in 1926 that a forest community "is not an organism, scarcely even a vegetational unit, but merely a coincidence" (quoted in Richardson 1980, p.465).

Gleason's challenge was in the main ignored until nearly 1950. Unexpectedly, it was then resurrected and has gained noticeable support in recent years. Two highly persuasive and articulate proponents of this line of thought were the Australian zoologists Andrewartha and Birch. As early as 1954, they elaborated fully their "Theory of Environment", in the now well known text "The Distribution and Abundance of Animals". Apparently their formulation was inspired by Darwin's ideas that "food", "weather", and "other animals" were part of the "web of complex relations" shaping the "struggle for existence". To this they found it necessary to add a fourth component - "a place in which to live". The struggle became, they emphasized, one of the individual against its often unpredictable environment.

A number of field workers began to test and confirm that a species' local ecological environment (or Autecology) frequently had more effect than any perceived community-wide force. Connell came to this point of view when he "went to Australia in 1962 to study reef and

forest communities. A hurricane promptly swept through my study areas and wiped everything out" (quoted in Lewin 1983b, p.739).

Over the last decade many articles have appeared in the ecological literature specifically to highlight the great role environmental variations play in communities. A large number of these studies conclude that when communities experience environmental disturbances, biological structuring processes can be highly intermittent at best.

§3 Competition as a Community Structure

§3.1 Background

Interspecific competition may be defined as "a negative effect of one species upon the population size of another arising from their joint exploitation of environmental resources" (Grant 1986, p.174). It occurs under conditions when the supply of resources is limited. This exploitative competition, which I will in the main be dealing with, is distinct from interference competition. The latter is achieved by aggressive interactions or other interfering mechanisms (eg., the production of toxins).

For the major part of this century, competition has been popularly thought to be a significant operational community process. Often, it was taken to be the force which gave rise to the "Balance of Nature". In Nicholson (1933), for example, we read that "the evidence for the existence of balance in animal populations is overwhelmingly great" (p.137). Furthermore, "any factor that produces balance is almost necessarily some form of competition, for balance can be produced only if increasing density decreases the chance of survival of an average individual" (p.140).

As Brown (1981) comments: "Among both theoretical and field ecologists there was widespread belief that interspecific competition was the primary factor which limits diversity, and that working out the mechanisms of competitive interaction was the key to understanding the organization of communities" (p.881). den Boer (1980) wrote that "assumptions about exclusion as well as thoughts about coexistence are generally deduced from the same presupposition: competition is the major or even the principal process that determines the distribution of species" (p.283).

In recent years ecologists have become highly divided in their opinion regarding the role of competition (Diamond and Case 1986a, Haila 1982, Harvey and May 1985, Lewin 1983a, Roughgarden 1983, Schoener 1982, Simberloff 1982, 1983a, 1984, Strong et al 1984). Their differences point to the great difficulty of observing or conclusively demonstrating the significance of this process. Until recently, there have been very few properly designed field experiments made specifically for this purpose (Connell 1983a, Schoener 1983). The many statistical tests already made to detect competition have lately been under challenge. Their assumptions have been considered simplistic, restrictive and unrealistic, and the conclusions reached were often found to depend crucially on these assumptions.

To confound the issue further, many other factors tend to drown out patterns that would normally be expected in the presence of competitive interactions. Environmental effects like the weather, or biological processes such as mutualism, predation or indirect interactions, might not only mask observation of competition but could well be at least equally significant in shaping ecosystems. But, whether or not competition is the dominant ecological process, it emerged with considerable status and its development is briefly outlined below.

§3.2 Theory of Interspecific Competition

The initial development of a competition theory went through three phases (Haila 1982):

1) Early twentieth-century plant ecologists formulated the theory of competition for space by individuals of the same and different species. There was a direct link between this theory and the phenomenon of succession.

2) The Lotka-Volterra models of the 1920's provided a theoretical design that predicted the effects of competition.

3) Laboratory experiments of Gause, Park and Birch were made in order to "verify" the Lotka-Volterra equations.

These phases were all important in leading to the acceptance of what is known as the Gause competitive-exclusion principle. Schoener (1974) gives a generally accepted version, stating that "species cannot exist for long if they too similarly use the same kinds of resources" (p.27).

A corollary of the Gause principle is that coexistence is only possible if there are sufficient differences in species usage of resources. Because of this, a good deal of study has been done to determine what these differences might be.

The totality of resources utilized by a species was defined as the species ecological niche. Hutchinson (1957) found it useful to describe the niche as a region in n-dimensional hyperspace, where each dimension referred to a particular environmental resource. If resources were limited, competition between two species was predicted to be high when overlap in their niche space was great – i.e., the species were ecologically similar. Little overlap implied only weak competition since the two species shared only a small portion of their required resources.

According to the theory, competition can lead to the evolution of differences between species in their resource utilization. For example, two related bird species that originally competed for the same seeds might evolve different beak sizes. In this way differences in their food preferences would evolve, the bird with the larger beak eating larger seed than the bird with the smaller beak. Shared resources would reduce with the evolution of this "character displacement", and so also would competition.

§4 Ecological Modelling and Competition Theory

§4.1 The Development of Ecological Models

It was in the early 1920's that a theoretical mathematical population ecology emerged. Initiated independently by Lotka (1925) and Volterra (1926, 1928), models of two-species interactions developed. The models were based on the single-species logistic equation due to Verhulst (1838).

The philosophy of modellers who utilized the Lotka-Volterra equations was reductionist in approach. Fundamental knowledge of the basic biological interaction was sought by studying two species when extracted from their community. The hope was to develop an understanding of the basic unit of interaction. Only when this was clear, could one begin to comprehend the community as a collection of pairwise interactions.

Volterra (1926) developed, and MacArthur and Levins (1967), MacArthur (1969, 1970) further extended, equations believed capable of depicting an n-species competition community. In MacArthur's frequently used formulation the equations rested on the assumption that communities, as well as their resources, exist in a steady state of equilibrium. The assumption of equilibrium is often made in many

scientific investigations of physical phenomena, and is usually legitimate, since many mechanical and physical systems do reach an equilibrium. Appealing to the "Balance of Nature" argument gave justification for the equilibrium approach in ecological analyses.

Utilizing the equations it was possible to make predictions about species packing, population structure, stability and diversity. MacArthur (1969) deduced a certain quadratic form from these equations which was "what competition minimizes." His last vision was to strengthen the metaphor that species packing was of the same nature as crystal packing. The physicist May (1973a, p.12) also awaited the day when "perfect crystal" models would be developed in ecology.

§4.2 Some Problems Encountered With Models and Their Underlying Assumptions

A major criticism of ecological modelling is that in many cases the underlying assumptions are too rigid (Brown 1981, Pielou 1977, Simberloff 1982, Wiens 1977,1984). Models often only provide a "crude caricature of multispecies systems" (May et al 1979, p.268), and suffer from the over-simplifications necessary, when describing large ecosystems in terms of mathematical entities. In the words of Andrewartha and Birch (1984) "there is a tendency to oversimplify. If a theory is beautiful for its logic or its intuition, it may come to be held so securely that it becomes invulnerable to challenge by "ugly facts"; the facts must be made to fit the theory and in doing so may lose some sharpness" (p.131).

One serious shortcoming with the Lotka-Volterra models is their underlying deterministic basis. As a result they are unable to incorporate the striking stochastic variability so prevalent in natural ecosystems. Simberloff (1980) outlined the operational characteristics

of such models where "'everything effects everything else' (Watt 1966) (which) includes not only its tidiness but its determinism, for if all components are included in the system and linked to all others by deterministic equations, then no exogenous, random input is possible" (p.29). Thus "its most fundamental features are determinism and interest in a high-level ideal entity."

Many ecologists are unhappy with the notion of deterministic communities. Predictable stable point equilibria seem divorced from reality. To treat all communities as if they were at equilibrium gives a false representation of the complexities of Nature. On the other hand, it cannot be ignored that there are some ecosystems which, in appearance at least, are quite close to an equilibrium. These ecosystems have been observed in relatively steady states for periods sometimes extended, sometimes short.

Wiens (1984) suggested: "Natural communities should be viewed as being arrayed along a gradient of states ranging from equilibrium to non-equilibrium" (p.451). He argued forcibly (Wiens 1977) that any assumption of equilibrium (which in fact "lies at the heart of the classical Lotka-Volterra competition formulation" (p.591)), is unrealistic. His studies showed that, because of environmental variability, populations are usually kept well below their carrying capacity, and resources are frequently in a state of abundance. Thus competitive equilibrium is not attained since competition itself is not a significant interaction. It is only when these periods of plenty are marred – or punctuated – by "ecological crunches" that competition occurs, owing to scarcity in resources. Wiens' own field-studies of avian communities found little sign of equilibrium communities, and little evidence that competition is a major on-going process.

According to Grant (1986), the challenge Wiens presented was often taken seriously and uncritically in the literature. Schoener (1982) was one of the few who openly opposed his view; he argued that "ecological crunches" are quite frequent, implying that competition is a major community process. Grant (1986) fully reassessed Wiens' paper, defending the four major assumptions Wiens thought dubious. Using data on Darwin's ground finches, he tested these assumptions, and in the main they held good. His study was particularly interesting in that it found that the finch populations tracked their limiting resources closely. This was in contrast to the bird communities of Wiens and Rotenberry (1981), but quite in keeping with normal competition theory and indicative of equilibrium (Cody 1981). Grant finally concluded that "the theoretical arguments derived from the use of Lotka-Volterra models are not rendered untenable by unrealistic assumptions" (p.191).

Both Lawlor (1980) and Yodzis (1981) aimed to contribute in this area when they analysed observed data of "real" ecosystems. Each concluded that there were good indications of some equilibrium process, with its associated stability, in the many webs analysed. Yodzis remarked that either his results were a "monumental coincidence, or the equilibrium viewpoint is really appropriate for quite a few real communities" (p.674).

The above discussion brings home the two opposing points of view; communities existing and maintained at competitive equilibrium, versus communities dominated by environmental effects. Both of these opposing views figure prominently in the current literature.

§4.3 The Influence of Mathematics

Diamond (1978) suggested that competition theory was almost non-existent before 1959. This was indicated in his (lengthily titled) paper: "Niche shifts and the rediscovery of interspecific competition.

Why did field biologists so long overlook the widespread evidence for interspecific competition, that had already impressed Darwin?" We are told that: "Only with the development of mathematical niche models in the late 1950's and 1960's could niche studies [and thus competition - L.S.]) be related to quantitative theory and hence rise above lowly scientific status" (p.330).

Jackson (1981) reviewed the literature, and found that Diamond's point "simply is not true" (p.889), since "much of what is considered original to the modern niche theory of competition, except the mathematics, was well formulated and understood by many plant ecologists.....as early as 1914" (p.893). He in fact accused "successful, creative scientists", presumably those in agreement with Diamond's views, as writers of "revisionist history" (p.889). Jackson supported his contention with evidence from 336 papers written in the period 1920-1959, taken from four journals. Each of these papers in some way dealt with interspecific competition.

The views expressed by Diamond are indicative of the great influence mathematical competition theory had come to exert. Various reasons have been put forward to explain why the mathematical theory was considered by some to be of such great importance. Cohen (1971) referred to "physics-envy", whilst May (1973a) hoped to raise the status of the discipline of Ecology "so that it would be equal to other branches of science and engineering" (p.12). Simberloff (1984) was a little more philosophical and argued that in this century, when the belief in god wanes, then a scientific theory of competition as a homeostatic process maintaining Nature's balance is a catchy alternative.

We see in all this scientific enterprise a good deal of enthusiasm and curiosity in pinpointing ecological laws. However there were always sceptics to be found, many of whom were well equipped to

"stocktake" (Pielou 1981) and critically evaluate the endeavour. The quotations presented below are cited deliberately to show the differing responses to the mathematical theory.

- Reviewing Lotka's book Charles Elton wrote: "Like most mathematicians he takes the hopeful biologist to the edge of a pond, points out that a good swim will help his work, and then pushes him in and leaves him to drown." (Quoted in McIntosh 1985, p.176).

- Levins (1968) felt that "theoretical work often diverged too far from life and became exercises in mathematics inspired by biology rather than an analysis of living systems" (pp.3-4).

- May (1973a), with reference to ecological "systems analysis" suggests that some "massive computer studies could benefit most from the installation of an on-line incinerator" (p.10).

-Van Valen and Pitelka (1974) claim that "mathematical ecology has now entered the Establishment and appears to be pursuing a policy of competitive exclusion" and that this is partly a result of "intellectual censorship in Ecology" (p.925).

- McIntosh (1985) remarked that "ecological models themselves became an object of study independent of organisms" (p.282).

- On the other hand, many theoreticians would be claiming that "(w)ithin two decades new paradigms had transformed large areas of ecology into a structured, predictive science that combined powerful quantitative theories with the recognition of widespread patterns in nature" (Cody and Diamond 1975, p.vii).

The profusion of negative responses (some of which are quite scathing) to mathematical methods indicate the difficulties and frustrations experienced by some very earnest ecologists. There are those who are now finding themselves "out of their depths" grappling with complex mathematics and thus becoming alienated from the ecological

problem at hand. To exacerbate the situation further, it is becoming increasingly apparent that even the most advanced mathematical models will never be capable of capturing the bewildering complexity of the "living" world. In general, biological detail must be sacrificed for any model to be mathematically tractable.

Despite this, the effort to come to terms with new mathematical "tools" does bring rewards. The very process involved in such modelling plays a useful role in the quest to understand ecology. Although models can at best only capture simple, general characteristics of ecosystems, in doing so they become a useful aid in generating hypotheses, inspiring field experiments, and broadening our conceptual understanding of natural processes (see Pielou 1981 and Taylor 1985 for a full discussion).

Only with the passage of time will a clearer perspective evolve with which we may better place and appreciate the role of mathematical modelling. Colwell perhaps best synthesizes the current mood when he says that Ecology "is undergoing .... a salubrious readjustment in the balance between our increasingly detailed appreciation of nature and the domain of our theories and models" (quoted in Lewin 1983b, p.740).

§5 Assessing the Role of Competition

§5.1 Statistical Distributions of Species as Evidence

Elton (1946) published data on animal and plant communities which upon statistical analysis revealed "effects of competition between species of the same genus" (p.66). In the very next volume of the same journal, Williams (1947) found no indication of competition in these same communities. He characterized Elton's finding as a mathematical result to be expected from the small sample size used.

Diamond (1975) and Connor and Simberloff (1979) have analysed bird distributions on archipelagos. Diamond argued that mainland birds colonized an archipelago according to certain assembly rules that were determined by competitive processes. Competition was held to be responsible for shaping the species' distribution patterns, and explained why he found only certain "permissible combinations" of species. On the other hand, Connor and Simberloff analysed similar data and saw no grounds for rejecting a null hypothesis that the birds had colonized the islands randomly.

In the same vein, den Boer (1980) tested the hypothesis that: "Taxonomically closely related species are also ecologically closely related, and will thus be found coexisting in the same sites more frequently than could be expected by a random distribution of species" (p.300). He confirmed this hypothesis in a detailed study of carabid beetles. den Boer then called for a replacement of the competitive-exclusion principle with the above "coexistence principle".

The above important analyses represent only a few of the bewildering number of attempts to deduce biological structures from species distributions. In all, the ambiguity and differences of the results obtained, when analyzing species abundance data for the effects of competition, have not yet led to a consensus. Rather, they show the need for finer, more detailed and more powerful tests (Toft and Shea 1983).

§5.2 Morphological Character Displacements and Size Ratios

Competition theory predicted that there were limits to how similar competing species might be if they were to coexist. This prompted many ecologists to examine morphological characteristics to determine whether there was any limit to their similarity in size. In an attempt to find evidence for character displacement Hutchinson (1959) measured and ranked the sizes of mouthparts amongst coexisting congeneric species of insects, birds, and mammals.

In his classic paper "Homage to Santa Rosalia, or why are there so many kinds of animals?" Hutchinson proposed that "where species co-occur, the ratio of the larger to the smaller form varies from 1.1 to 1.4, the mean ratio being 1.28 or roughly 1.3. This latter figure may tentatively be used as an indication of the kind of difference necessary to permit two species to co-occur in different niches but at the same level of a food-web" (p.152).

Since then, ecologists have often taken 1.3 to be a biological constant. Many field workers have successfully "confirmed" the "1.3 rule" after examining various measurements of organisms. Moreover, when "confirmed", it was considered to be evidence that competition was operational. It was argued that character displacements came about by evolutionary means as a result of competitive pressure. However, there are some who are dubious about this rule - Simberloff and Boecklen (1981) for instance, who have noted the variability of the ratio reported in the literature, suggested it be better termed the "1.x" rule.

Horn and May (1977) extended the rule to include not just coexisting competitors but also ensembles of recorders, string instruments, bicycle wheels and iron skillets. They suggested that the "rule may well derive from generalities about assembling sets of tools,

rather than from any biological peculiarities" (p.661).

More recently a controversy has brewed over the method used in testing the "1.3 rule". Many researchers contend that the observed size ratios would be indistinguishable from any randomly-assembled array, given realistic size constraints/variability of the organisms (Boecklen and NeSmith 1985, Maiorana 1978, Roth 1981, Simberloff and Boecklen 1981, Strong and Simberloff 1981, Wiens 1982). Hence the occurrence of the size ratio 1.3 between two species may have little to do with any ecological process.

Eadie et al (1987) tidied up the whole controversy by formally demonstrating that the size ratios of "things" can be expected to fall roughly within the range set by Hutchinson, given that "things" in the world are lognormally or loguniformly distributed. "Unless one is willing to argue that a lognormal distribution of sizes will arise only in response to inter- and intraspecific competition, then the observation of a lognormal distribution of body sizes ... will tell us little about the mechanisms structuring animal communities" (p.8).

On the other hand, Schoener (1984) made use of null tests and found that "for cases with moderately large sample sizes (N=20-50), ratios are significantly larger than expected from a null model....more ratios occur in the interval 1.2 to 1.4 than in any other sized interval.......this result boils down to ...... the result on limiting similarity" (pp.268-269).

We might draw the general conclusion that - until better tests are performed (perhaps along the lines of Schoener (1984)), and more reliable evidence found - competition cannot yet be taken to be responsible for measures in "character displacement".

§5.3 Experimental Evidence

The most convincing test for detecting competition is by experimental manipulations, or perturbations, of populations. For example, by changing the abundance of one species and monitoring the response it has on another, some indication can be obtained as to the type of interaction between these two species (see Connell 1983a for details of experimental designs). If the response to such manipulation shows a negative correlation with density, fecundity, growth, or perhaps a niche shift, then competition can be inferred.

Connell (1983a), who finds conventional competition theory unacceptable, reviewed the literature to assess the results of these experimental tests. He analysed 72 studies including 527 field experiments with 215 species from six journals published in the years 1974 to 1982. "(C)ompetition was found in most of the studies, in somewhat more than half of the species, and in about two-fifths of the experiments" (p.682).

Schoener (1983), who has often acknowledged the usefulness of competition theory, also reviewed the literature on field experiments although with a database somewhat different to Connell's. He reported: "Rare until recently, field experimental studies of interspecific competition now number well over 150. Competition was found in 90% of the studies and 76% of their species, indicating its pervasive importance in ecological systems" (p.276).

§6 Discussion

We have seen that it is not a simple task to observe the competitive process, or be sure of its role in any particular ecosystem. Analyses of species' distribution patterns, size ratios, or of morphological character displacements, as yet offer no convincing evidence that competition is a major organizing community process. The most reliable information comes from the results of field experiments which seem to indicate that competitive interactions are fairly common in ecosystems. However, as Birch's (1979) review of competitive exclusion shows, little ground has been gained in our understanding of the elusive quality of competition. He found: "In natural populations there is a spectrum of effects of one species on another from nil to complete exclusion" (p.197). No clear general patterns could be discerned.

Taking a different slant, Strong (1983) contends that it is usually birds, lizards or other invertebrates that are studied when attempting to examine the role of competition in ecological communities. He points out that these species constitute only (approximately) 4% of the biotic world (see Figure 1). Strong argues that for the insect kingdom, which contains the great bulk of the total species diversity, autecology and weather appear to be the major governing factors. In most insect communities, evidence of density-dependent growth as assumed by the competition theory, is distinctly lacking.

Of late, much attention has been given to the role of predation in communities. This often overlooked form of disturbance can prevent species from attaining any competitive equilibrium (Connell 1975, 1978, Huston 1979). The work of Paine (1966, 1974) has shown that predators can be the "keystone" members of communities. One of his classic experiments demonstrated how a fifteen species intertidal

community collapsed to eight species when the predatory starfish
<u>Pisaster</u> was removed.

Even more recently, focus has centred upon the importance of
mutualism in ecological communities (see Boucher <u>et al</u> 1982, Boucher
1985a for general reviews). Boucher (1985b) suggests that it is possible
(but it still needs to be demonstrated) that "mutualism is the major
organizing principle in nature" (p.23).

In any ecological analysis, then, it is simply not enough to
assume that competition alone governs community structure. Environmental
factors such as terrain or weather, or biological processes like
predation or mutualism, are very active forces. (Kropotkin (1902) in
fact stressed this point, when he argued that weather was more important
in controlling populations than competition.) Birch (1979) makes clear
that "a simple approach which ignores these factors gives poor
understanding." For those who attempt to portray ecological processes in
the future, he suggests "a stochastic approach which takes into account
the patchiness of the environment in space and time, the role of chance
events and the spreading of risks within life histories" (p.218), as a
more realistic alternative. It is this sort of approach that will be
attempted throughout this thesis.

Appendix

Ecology of the Ancients

The earliest human societies often attempted to interpret and creatively respond to the natural beauties they beheld, together with the calamities and suffering they frequently experienced. Some very interesting insights may be obtained concerning their ecological consciousness by examining the myths, rituals and creation stories they developed. Popper (1962) believes that "historically speaking all or nearly all - scientific theories originate from myths", and that "a myth may contain important anticipations of a scientific theory" (p.38).

Organic, pre-literate societies, and those that developed from them, laid much emphasis on ritual and ceremony. Murray Bookchin (1982) stresses that their purposes were not at all manipulatory in origin but rather were of a participatory nature. By acting out myths, rites and traditions, early peoples obtained a heightened awareness that they themselves played an important role in the functioning of the cosmic order. He cites Dorothee Lee's observation of the Hopi Indians:

"Every aspect of nature, plants and rocks and animals, colors and cardinal directions and numbers and sex distinctions, the dead and the living, all have a cooperative share in the maintenance of universal order. Eventually, the effort of each individual, human or not, goes into this huge whole. And here, too, it is every aspect of a person which counts. The entire being of the Hopi individual affects the balance of nature; and as each individual develops his inner potential, so he enhances his inner participation, so does the entire universe become invigorated" (pp.46-47).

The role and relationship that gods or deities played in these societies are revealing and give insight into the ecological outlook of ancient peoples. The first written records come from the Sumerians some

five thousand years ago. Samuel Kramer translated the following Epic of Emmerkar depicting Paradise.

"The land Dilmun is a pure place, the land Dilmun is a clean place,

The land Dilmun is a clean place, the land Dilmun is a bright place.

In Dilmun the raven uttered no cry.

The kite uttered not the cry of the kite,

The lion killed not,

The wolf snatched not the lamb,

Unknown was the kid-killing dog,

Unknown was the grain-devouring boar...

The sick-eyed says not 'I am sick-eyed',

The sick-headed says not 'I am sick-headed',

Its (Dilmun's) old woman says not 'I am an old woman'..... "

(Quoted from Hooke 1963, p.114.)

We hear in this the aspiration for a "perfect world," free of struggle and fear; where the problems of basic needs and health have been overcome, and life is led in complete harmony. But this poem is not an isolated Sumerian dream. The same thematic (and even stylistic) content has been found in the early writings of many peoples. For instance, the poem certainly has unusual similarities with the better known description of Paradise written in the Old Testament many years later:

"The wolf also shall dwell with the lamb,

and the leopard shall lie down with the kid;

and the calf and the young lion and the fatling together;

and a little child shall lead them.

And the cow and the bear shall feed;

their young ones shall lie down together:

and the lion shall eat straw like the ox,

And the sucking child play on the hole of the cobra,

and the weaned child shall put his hand on the viper's nest.

(Isaiah 11, 6-10).

Ancient ecological practices also say certain things about the deepest desires and insecurities of man. Agriculture was of vital importance in many early societies. The complete dependence man had ᐧ on crops and produce can be understood when examining the measures resorted to, so as to ensure a successful yield. In Bengal, Ecuador and a host of other places throughout the world, Frazer (1955) documents many cases of human sacrifices and bloody rites practiced by natives to their gods. If the gods had been satisfied then good crops could be looked forward to. Often the flesh, hearts, blood or ashes of the victims were buried in the ground symbolically to replenish and fertilize the soil.

The demands of the gods were often great. Enforcement of rituals and later regulations governing man's conduct became essential to keep natural order and stability. Otherwise it was to be expected that the gods would show their displeasure with revenge; perhaps destroying crops, inflicting general hardships or some other form of punishment. We remind the reader of plagues which have been documented from earliest times in pictures, prayers, laments and historical writings. Almost all of them were reported to be of supernatural or godly origin brought about as punishment for man's corrupt ways.

What emerges here is the beginnings of the concept of Balance of Nature. Further, this balance has a large element of causality in it. Certain actions were known to have particular effects, and could often be traced to particular gods.

Ecology in Greek Thought

Greek metaphysical philosophy developed in detail the notion that all god's creations were part of a constant and harmonious whole. The Harmony of the Spheres was developed by the Pythagoreans, the Hyppocratic physicians saw health as depending on a balance of body humors, while Euclid outlined what seemed a rigorous, infallible geometry. All of these formulations are strongly tinged with a theological dimension. It is as if the ways of god's creations work together, as an organism in perfect orderliness, efficiency and beauty. With this vision behind them, Greek scholars began to formulate the Balance of Nature concept. Egerton (1968, 1973) has masterfully documented the views of the Greek scholars on this subject and I draw on his work to outline their character.

In the fifth century BCE, Herodotus assembled a large number of biological observations and provides us with the earliest indications of some natural balance. Many of these descriptions are of such extraordinary character, that they are believed to be complete fabrications invented for the explicit purpose of demonstrating that nature is kept in check. Herodotus implied that balance amongst animal populations came about by predation and from the differing reproductive capabilities amongst species. The following excerpt brings this to light:

"For timid animals which are a prey to others are all made to produce young abundantly, that so the species may not be entirely eaten up and lost; while savage and noxious creatures are made very unfruitful" (III 108).

Again, to support the contention of regulation, Herodotus gives us a marvellous report of a mutually beneficial relationship between a crocodile and trochilus (or Egyptian plover). As the crocodile "lives chiefly in the river, it has the inside of its mouth constantly covered with leeches; hence it happens that, while all the other birds and beasts avoid it, with the trochilus it lives at peace, since it owes much to that bird: for the crocodile, when he leaves the water ... is in the habit of lying with his mouth wide open, ... at such times the trochilus goes into his mouth and devours the leeches. This benefits the crocodile, who is pleased, and takes care not to hurt the trochilus" (II,68).

As was indicated previously, hand in hand with a Balance of Nature concept is the view of the biotic community working as an organismic process. This theory of the community as superorganism, where each species is actually an "organ" to some super-being is given explicit support in Plato's writings. He asks:

"In the likeness of what animal did the creator make the world?" Timmaeus (30 c-d) answers that god made the world not as any one species, but rather as "one visible animal comprehending within itself all other animals of a kindred nature."

Greek thought had an enormous influence on Western civilization. Popper maintained that it still dominated nineteenth century thought (refer to Simberloff 1980). The Balance of Nature concept over this period has almost ingrained itself into man's consciousness.

However, there was one great voice amongst the Greek scholars that remained silent in his views of the above theory, even though he had ample opportunity and interest in these matters. Aristotle, the influential commentator on Greek scientific thought, appeared to have

reservations concerning the synthesis (Egerton 1973). In all his many writings on the natural world, reference to a Balance of Nature is extremely rare.

Aristotle's reluctance to accept the theory of a holistic superorganism was perhaps the first evidence we have for some seed of doubt as to its validity. His ambivalence is perhaps a reflection of an interest in his own theory of teleology, that emphasised the individual to be the most worthy area of study. Never did Aristotle attempt to apply teleological thinking on a community level, nor does the idea of superorganism appear to be hinted at. In most cases he concluded that a species is governed mainly by its physiological limitations - eg., size, age, reproductive ability. In **Physica** he argued that environmental effects, even though they are often random in character, are essential to life.

"Zeus does not send the rain in order to make the corn grow: it comes of necessity .... It is merely concurrent that this having happened, the corn grows" (II.8.15 - 25).

(Note how this notion of concurrency has similarites to the "coincidences" mentioned by Gleason [see §2].)
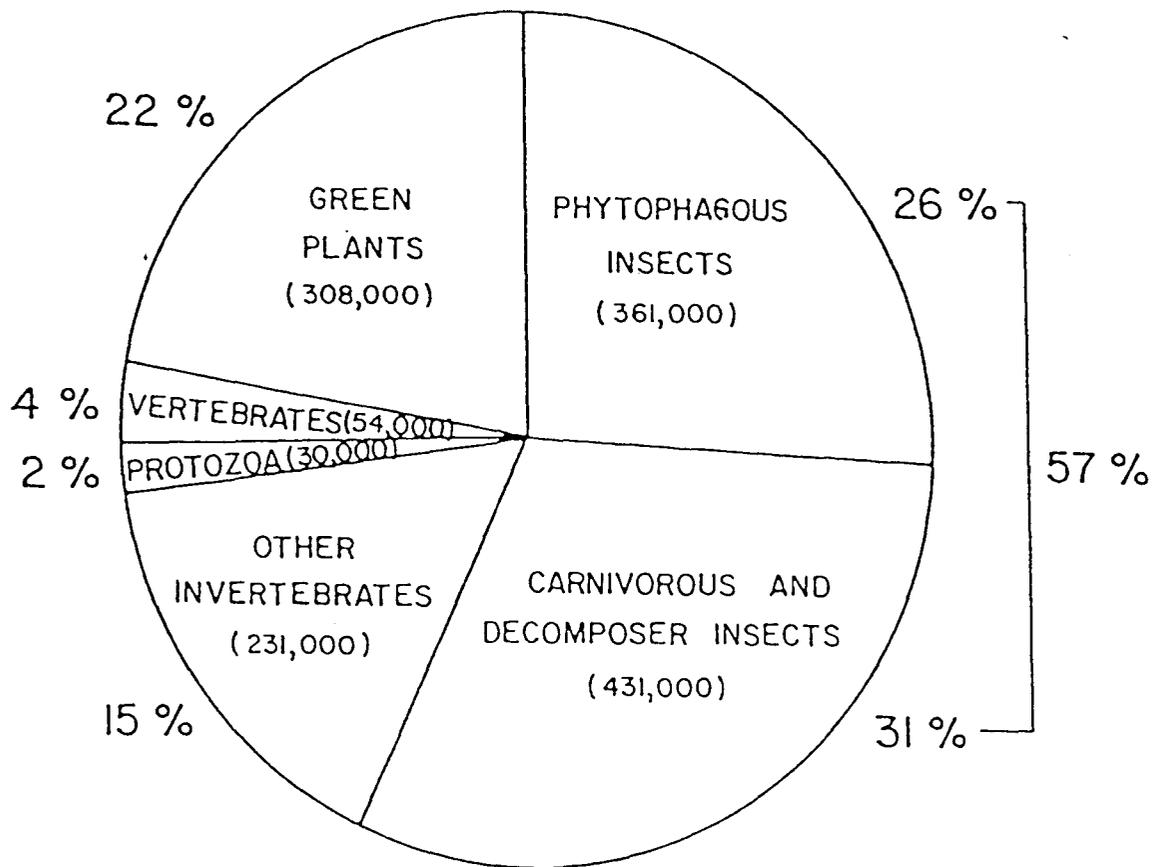
Figure 1. The approximate numbers (in parentheses) and proportions of different sorts of macroscopic species now on earth. (Reproduced from Strong 1983, p.646 .)

Chapter 2

The GLV Ensemble Model

§1 Modelling in Fluctuating Environments

Fluctuations are very much part of any natural community. Weather, climate, resources, species densities, population sizes, and interaction strengths all vary over time and space in a stochastic manner. A type of fluctuation has its characteristic scale; to evaluate its effects on an ecosystem, observations need to be taken over a suitably chosen spatial region and time period. Fluctuations may be cyclical with the seasons, or completely erratic like cyclones. If the intensity of a fluctuation is great, it may entirely destroy a community. Disturbances of a less extreme nature can still be large enough to mask observable community patterns, making difficult the task of ever perceiving ecological processes.

Chapter 1 pointed out that many experimental field-studies have found competition operative in varying degrees. Many of the patterns expected in the presence of this interaction are often heavily masked and subdued by environmental disturbances. In the bulk of this dissertation, I model and explore the effects that fluctuating environmental conditions might have on communities in which competition occurs.

Initially, one of the most important tasks when modelling ecosystems was to determine whether a particular model possessed a stable equilibrium point. If so, then the ecosystem being investigated was predicted to be capable of recovering after environmental disturbances, and always able to return to its original equilibrium state. Thus a study of environmental variations was taken to be unnecessary, and the deterministic model seemed generally suitable.

One of the underlying weaknesses in this argument lay in the very restrictive technique by which disturbances were modelled. They were taken to modify species population densities only, whilst leaving all other system parameters unchanged. However, environmental disturbances significantly alter many other important factors. Species interaction strengths, recruitment-rates, birth-rates, carrying capacities, resource availability and spatial heterogeneity, are a few of the many environmentally dependent parameters that fluctuate with disturbance (usually simultaneously) and so modify the specifications of the system. Further, the possibility of an ecosystem attaining an equilibrium may depend upon both the intensity and frequency of the disturbances. Continual perturbation of an ecosystem might prevent the possibility of an equilibrium ever being achieved and may in many cases make the notion of a stable equilibrium seem irrelevant.

Recently interest has been shown in stochastic models because they simulate the effects of random fluctuations and spontaneous events with far more realism than the widely-used deterministic models (Chesson 1986, May 1973b, 1981, Roberts 1974, 1984). These models can be useful as an aid in helping grasp the many elusive notions of randomness. Their construction encourages the development of thinking processes which recognize that "noise.... is music to the ecologist" (Simberloff 1980, p.25) and that randomness can play a crucial role. Wiens (1977 p.591), for example, states that "documentation of the competition process in nature may be extremely difficult if environments vary." Because stochastic models can give insights into the behaviour of systems undergoing constant changes, they can be used as an aid for those who have to deal with the sorts of problems described by Wiens.

A Model of Communities Governed by Consumer-Resource Interactions

There are many situations when species within communities display little evidence that their population densities have some constancy over time. This has called for the design of models that are applicable in non-equilibrium settings. Such models recognize that ecosystems are constantly undergoing perturbations and are never, perhaps, at any steady equilibrium value.

The approach used here is to examine the characteristics of the totality of possible states a particular ecosystem might experience, given that it is undergoing environmental fluctuations. The final picture obtained from examining this "ensemble" of disturbed states is quite different from that found by the usual analyses which examine a single, unchanging system, whose defining parameters remain constant for all time. Because of its stochastic design, the ensemble model can predict the survival prospects for a particular type of community, when it is subjected to significant environmental changes.

As a starting point, the ensemble approach will be utilized to examine the simplest community structures. Tilman (1986), in his discussion of elementary mechanisms structuring communities, suggested: "Because all species are consumers and all, eventually, are consumed by other species, consumer-resource interaction is one of the most fundamental processes of ecology" (p.5). Tilman implies that a model with deliberately simplified structure, but stressing the consumer-resource interaction as a basic building block, can explain quite a variety of patterns within real ecosystems. This is assisted by incorporating environmental phenomena such as the effects of physical limiting factors, spatial heterogeneity, and fluctuating resources.

The approach followed here is based on the frequently-used Lotka-Volterra competition model, portraying a single trophic community governed by the consumer-resource interaction. One unusual aspect of the model investigated is that it describes, and makes accurate predictions for large multi-species systems. This contrasts with the many models described in the literature that are very often applicable ,to communities of only two or three interacting species.

§2 The Model Defined

§2.1 The GLV Model

Non-linear population models are often represented in the form

$$\frac{dN_i}{dt} = N_i \ F_i(N_1,N_2,\ldots\ldots\ldots N_m) \quad \text{for } i = 1,2,\ldots m. \tag{1}$$

The model describes an m-species community, with N_i representing the population density of the (i)th species. When in a steady state, the rate of change of each population N_i is zero and the equilibrium population levels $N_i = N_i^*$ may be found by setting the right-hand side of (1) to zero. If there is an equilibrium solution in which <u>all</u> populations are non-zero, then this may be determined by solving:

$$F_i(N_1^*,N_2^*,\ldots\ldots\ldots\ldots,N_m^*) = 0 \quad \text{for } i = 1,2,\ldots\ldots m. \tag{2}$$

In the frequently used Lotka-Volterra model, the F_i are replaced by their first-order Taylor expansions about equilibrium - i.e.,

$$F_i = \frac{r_i}{k_i} \ (k_i + \sum_{j=1}^{m} \alpha_{ij} N_j) \quad . \tag{3}$$

Here r_i is the birth-rate of the (i)th species, k_i its carrying capacity, and α_{ij} the interaction coefficient representing the effect species j has on species i.

I have re-parametrized the model by taking

$$a_{ij} = \frac{\alpha_{ij}}{k_i}, \tag{4}$$

so that (1) becomes:-

$$\frac{dN_i}{dt} = r_i N_i \left(1 + \sum_{j=1}^{m} a_{ij} N_j\right) \qquad i = 1, 2, \ldots, m . \tag{5}$$

The above equations, that characterize multi-species ecosystems, have become known as the Generalized Lotka-Volterra (GLV) model. Owing to the vast number of systems described by (4), the equations have been normalized as recommended by Gilpin and Case (1976, 1981), Pomerantz and Gilpin (1979) and Roberts (1974, 1984) by taking all species to be self-regulated with $a_{ii} = -1$. This in effect scales to 1 each equilibrium population in the absence of other species. In addition, the above authors scaled the carrying capacities to 1, so that $a_{ij} = \alpha_{ij}$. However, this scaling is not needed and not adopted in the model presented here.

§2.2 Feasible and Unfeasible Systems

Taking into account all combinations of populations that might be zero at equilibrium, the GLV Equations 5 can be seen to have 2^m sets of equilibrium solutions. Since I am concerned only with m-species communities, there is no need to examine equilibrium solutions of Equations 5 save that (at most one) solution which has all m-populations non-zero. (Any other equilibrium solution to (5), possessing k equilibrium populations that are zero, is treated as an equilibrium for a community with [m-k]-species.)

If there is an equilibrium solution to (5) where all m-species have non-zero populations, then it can be found by setting all F_i in (3) to zero. In matrix form:

$$\underline{\underline{A}}\ \underline{N}^* = -\underline{e}\ , \qquad \text{or} \qquad \underline{N}^* = -\underline{\underline{A}}^{-1}\underline{e}\ , \qquad (6)$$

where $\underline{N}^*$ is the vector of equilibrial populations N_i^*,

$\underline{e}$ is a vector with entries $e_i = 1$,

and $\underline{\underline{A}} = (a_{ij})$ is the normalized interaction matrix with entries $a_{ij} = \dfrac{\alpha_{ij}}{k_i}$.

Two types of equilibrium points that might be solutions to Equation (6) can now be distinguished:

a) those that are **feasible** - i.e., where all $N_i^* > 0$;

and

b) those that are **unfeasible**, where one or more equilibrium populations of the model are "negative" or zero[†].

Obviously no real ecosystem can exist at an unfeasible equilibrium point that has "negative" populations; hence, when examining equilibrium communities, I will in the main be dealing with feasible equilibria. It will be shown in Chapter 3 that a study of feasible equilibria can also be useful when trying to explain the behaviour of some communities that are apparently non-equilibrial.

[†] For the ensemble of models to be described in §2.4, those systems with solutions to Equation 6 having one or more species with $N_i^* = 0$, are of measure zero.

§2.3 The Uniform Competition Model

In what can be termed the "uniform competition model" (or simply the "uniform model"), each pair of species has a negative direct interaction, all of the same strength c - i.e.,

$$a_{ij} = -c, \qquad 0 \leq c < 1, \quad \text{for all } i, j \quad i \neq j. \tag{7}$$

This model depicts each species competing with equal strength. To find the equilibrium populations N_i^*, we note that all species are interchangeable and hence $N_i^* = N^*$ for all i. At equilibrium, Equation 6 yields:

$$-N^* - (m-1)c\, N^* = -1 \qquad \text{or} \qquad N^* = \frac{1}{1 + (m-1)c} \ . \tag{8}$$

Since $0 \leq c < 1$, the populations are all guaranteed positive, and thus the uniform model is feasible. In Appendix 1 it is shown that this model is always globally stable for the above range of the parameter c. Hence the uniform deterministic model predicts that large competitive communities will satisfy two potentially advantageous features of viable ecosystems - namely, feasibility and stability. We will see, nevertheless, that these seemingly stable and well-organized systems may be highly fragile in the presence of environmental fluctuations.

§2.4 The Stochastic Ensemble Model

In the spirit of May (1972) and Roberts (1974, 1984), the limited uniform model may be "brought to life" by incorporating stochasticity. A large ensemble of competitive communities may be specified all of which, on the average, resemble the uniform model with mean interaction strength -c.

To incorporate stochasticity, we let the interaction matrix $\underline{\underline{A}}$ be of the form:

$$\underline{\underline{A}} = \underline{\underline{A}}_0 + \underline{\underline{B}} \qquad (9)$$

where $\underline{\underline{A}}_0$ is the matrix of the uniform model detailed in §2.3, while $\underline{\underline{B}}$ is a matrix of small perturbations: $\qquad \underline{\underline{B}} = (-b_{ij})$.

The b_{ij} are taken from a uniform probability distribution so that:

$$\langle b_{ij} \rangle = 0 \quad ,$$
$$\text{Var}(b_{ij}) = \sigma^2 \quad , \qquad (10)$$
$$\text{and} \qquad b_{ii} = 0 \ .$$

The community matrix now has elements:

$$a_{ii} = -1 \qquad \text{and} \quad a_{ij} = -(c + b_{ij}) \ .$$

In this model, environmental fluctuations make the interaction strengths vary about the community's mean strength of competition. Thus two communities may both have the same average interaction strength $-c$, but the one undergoing stronger perturbation will show a greater variation in its interaction coefficients. Hence the stochastic model associates increasing disturbance with an increase in σ^2 (the variance of the perturbations b_{ij}).

The maximum change in the coefficients a_{ij}, due to environmental disturbance, will be taken as a fraction v ($0 \leqslant v \leqslant 1$) of their mean c. In this model, the b_{ij} are drawn from a distribution uniform in the interval $[-cv, +cv]$, so that the a_{ij} remain in the interval $[c-cv, c+cv]$. For a uniform distribution, the σ in Equation 10 is:

$$\sigma = \frac{cv}{\sqrt{3}} \ . \qquad (11)$$

If v = 0, then there are no perturbations present, and the interaction coefficients have the values of the uniform model.

When v = 1, a strong disturbance is causing interaction coefficients to change by as much as 100% of their parameter values set by the uniform model.

By keeping v < 1, when c < 0.5[†], we ensure that the communities modelled are of pure competition only (since all interactions must then be negative).

An ensemble of m-species competitive systems can be constructed in which every pairwise interaction has mean strength -c and variance σ^2. The ensemble can be specified completely by the parameters (m,c,σ); however, as will later become apparent, it is more convenient to specify the ensemble by the triple (m,c,γ), where γ is defined as:

$$\gamma = \frac{\sqrt{(m-1)}\,\sigma}{1-c} \qquad . \qquad (12)$$

[†] When c > 0.5, it is necessary to keep v < (1-c)/c, to ensure systems of pure competition.

§3 Stability of the Model

In the remaining part of this Chapter I will demonstrate that feasible GLV models (as parameterized in §2.4) are virtually[†] always globally stable. The result itself is of considerable importance and made use of throughout Chapter 3, where I outline the responses of the ensemble model to a variety of environmental disturbances. The mathematical details required to prove this result are presented below; however, they can be skipped without breaking the continuity of the thesis.

The GLV Equations 5 can, using Equations 6, be put in the form:

$$\frac{dN_i}{dt} = N_i \sum_{j=1}^{m} a_{ij}(N_j - N_j^*) \quad .$$

$$(13)$$

Taking $n_j = N_j - N_j^*$, then to first order in n_j we have the linear model:

$$\frac{dn_i}{dt} = \sum_{j=1}^{m} N_i^* a_{ij} n_j$$

or, in matrix form, $\quad \dot{\underline{n}} = \underline{\underline{S}} \cdot \underline{n} \quad .$

$$(14)$$

The stability matrix $\underline{\underline{S}} = (s_{ij})$ has as its elements

$$s_{ij} = N_i^* a_{ij}$$

or, in matrix form, $\quad \underline{\underline{S}} = \underline{\underline{D}} \, \underline{\underline{A}} \, , \quad$ where $\underline{\underline{D}} = \text{diag}(N_i^*)$.

$$(15)$$

Because no species in an ecosystem can ever have a negative population, it is meaningless to examine the stability of a model with negative equilibrium populations. The question of stability only arises for those ecological models that possess a feasible equilibrium.

[†] The (slight) qualification implied by the word "virtually" will be made more precise below.

A feasible GLV model is said to be <u>locally stable</u> if, when its populations are disturbed from equilibrium by a "small amount", they return to their former steady-state. For "small" perturbations the linear model given in (14) accurately approximates the behaviour of the GLV equations. This linear model is known to be locally stable when all the eigenvalues λ_j, of the matrix $\underline{\underline{S}}$, satisfy the condition

$$\text{Re}(\lambda_j) < 0 \qquad \text{for } j = 1,2,\ldots\ldots m.$$

Throughout this dissertation I will refer to any matrix that satisfies the above eigenvalue property as locally stable. Hence local stability of the GLV model is synonymous with local stability of the stability matrix $\underline{\underline{S}}$. For a fuller mathematical treatment of this type of stability analysis refer to May (1973a).

Quite distinct from local stability and stronger than it, is <u>global stability</u>. A feasible system that is globally stable will return to equilibrium no matter what size of perturbation disturbs it. Lyapunov developed powerful techniques with which to determine whether global stability holds. To make use of these results, it is helpful to define the matrix $\underline{\underline{X}}$ as **Lyapunov stable** whenever there exists a positive definite diagonal matrix $\underline{\underline{W}}$ such that the symmetric matrix

$$\underline{\underline{G}} = \underline{\underline{W}}\,\underline{\underline{X}} + \underline{\underline{X}}^T\underline{\underline{W}} \tag{16}$$

has all its eigenvalues (which are necessarily real) negative. ($\underline{\underline{G}}$ is then said to be negative definite.)

It was shown by Tuljapurkar and Semura (1975), and Tuljapurkar (1976), that **any feasible GLV model with a Lyapunov stable interaction matrix $\underline{\underline{A}}$ will always be globally stable.** (Volterra in 1928 put forward this same test for global stability, but without allowance for feasibility [see Harrison 1979].) Further mathematical discussion concerning the global stability properties of the GLV equations can be

found in the work of Case and Casten (1979) and Goh (1977).

§4 Competition Systems - Feasibility Implies Stability

§4.1 Computer Results

The results of the following stability investigation were obtained by analysing various random ensembles of competition systems, each distinguishable by its particular combinations of the variables (m,c,γ). Good familiarity with the model was obtained by many Monte Carlo computer simulations over a wide range of parameters. It became clear that:

virtually all feasible systems are stable (nearly always globally stable) while unfeasible systems possess unstable $\underline{\underline{S}}$ matrices.

The (slight) qualification implied by the word "virtually" is made more precise below.

I define the matrix $\underline{\underline{A}}$ to be G(L)-stable if $\underline{\underline{A}} + \underline{\underline{A}}^T$ is negative definite. Any matrix that is G(L)-stable must be Lyapunov stable (take $\underline{\underline{W}}$ = $\underline{\underline{I}}$ in (16)). Hence, according to the results of Tuljapurka and Semura (mentioned above), two requirements sufficient to ensure global stability are:

1) the GLV model is feasible;

2) the interaction matrix $\underline{\underline{A}}$ is G(L)-stable.[†]

[†] Note that an interaction matrix which is not G(L)-stable may nevertheless be Lyapunov stable - so that global stability of the model might still be possible.

Figures 1a,b and c give graphical results for communities with c = 0.4, and m = 8,14,20 species respectively. Fourteen values of γ were examined from γ = 0 to γ = 1.3 in steps of 0.1. The graphs were obtained by generating on the computer 200 random matrices for each particular combination of (m,c,γ).

For each set of 200 samples the following statistics were collected:

i) %G(L) - the percentage of interaction matrices ($\underline{A}$) in an ensemble of 200 samples that were found to be G(L)-stable;

ii) %F - the percentage of feasible systems;

iii) %F&G(L) - the percentage of systems that were both feasible and possessed interaction matrices that were G(L)-stable.

Each of Figures 1a,b and c displays superimposed graphs of all three above statistics. What is immediately noticable in all three figures, is that the interaction matrix $\underline{A}$ is always Lyapunov stable whenever γ < 0.6. Therefore all feasible systems are certainly globally stable when $0 \leqslant \gamma <$ .6. The high stability of the interaction matrices over this parameter range will be accounted for when the statistical properties of their eigenvalues are examined.

Even when γ > 0.6, one sees by comparing the statistics %F and %F&G(L), that almost all feasible systems have an interaction matrix $\underline{A}$ that is G(L)-stable. From the statistics collected it was deduced that for communities of size:

a) m = 8, only 15 of the 1,348 feasible models possessed interaction matrices that were not G(L)-stable;

b) m = 14, only 5 of the 1,184 feasible models possessed interaction matrices that were not G(L)-stable;

c) m = 20, only 1 of the 1,092 feasible models possessed an interaction matrix that was not G(L)-stable.

But, as mentioned above, any of those interaction matrices that were not G(L)-stable may still be Lyapunov stable.

The above empirical results show that feasible systems are nearly always globally stable.

Figure 2 displays the local stability properties (determined from an eigenvalue analysis) of the $\underline{A}$ and $\underline{S}$ matrices, obtained from Monte Carlo computer simulations. It was found that for those model communities of size:

a) $m = 8$, only 3 of the 1,348 feasible models were unstable.

b) $m = 14$, only 1 of the 1,184 feasible models was unstable.

c) $m = 20$, of the 1,092 feasible models not one was unstable.

Further, all unfeasible models possessed $\underline{S}$ matrices that were unstable. Hence, "virtually" all models were found feasible and stable (nearly always globally stable), while unfeasible models were found to have unstable $\underline{S}$ matrices.

§4.2 Mathematical Results

Global Stability

In Appendix 1, a mathematical argument is given that demonstrates why nearly all the interaction matrices are G(L)-stable when $\gamma < 0.71$. Thus, in this parameter range, feasible systems will nearly always be globally stable.

Unfortunately, the global stability properties of those feasible systems with $\gamma > 0.71$, cannot be predicted. However, Appendix 1 (Property 1.2) shows that these latter systems, are in any case associated with a low probability of feasibility. (The probability decreases as the community size m increases, being less than 0.3 for 8-species systems, and less than 0.15 for 14-species systems.) Because of their low probability of feasibility, models that are not globally

stable would characterize very few observed ecosystems, as discussed below.

Local Stability

Since it is difficult to predict the global stability properties of those rare feasible systems that occur when $\gamma > 0.71$, I have examined their local stability in Appendix 2. It was found that feasible systems can be expected to be at least locally stable when $\gamma < 1$ and unstable when $\gamma > 1$. Thus when $.71 < \gamma < 1$, feasible models are expected to be at least locally stable.

Appendix 2 also shows that systems with feasible but unstable equilibria rarely occur. The probability of feasibility for these unstable systems is particularly slight, and they are therefore unrealistic, as discussed below. (The probability decreases as the community size m increases, being less than 0.1 for 8 species systems, and less than 0.05 for 14 species systems.)

Models Possessing a Low Probability of Feasibility

A model-community that possesses a low probability of feasibility, is likely to have a relatively short lifetime when experiencing environmental disturbances. In terms of the ensemble picture, one could imagine the community being successively perturbed towards different equilibrium points, most of which are unfeasible. Hence, before long, it suffers a loss of species.

Because feasible models that are not globally stable occur only for parameter values at which the chance of feasibility is slight, it is difficult to treat them as realistic since they correspond to those ecosystems unable to withstand a series of perturbations. Thus they could represent only a negligible fraction of observed persistent ecosystems. (Chapter 3 outlines in further detail this interpretation.)

§5 Mutualist Systems – Feasibility Implies Stability

A very general model is studied in the following analysis of mutualist systems. The only requirement is that the interaction matrix $\underline{\underline{A}}$ have entries:

$$a_{ii} < 0 \quad \text{and} \quad a_{ij} > 0.$$

Thus all species have a direct positive effect on one another.

Roberts (personal communication) found, by utilizing a theorem of Schneider, that all feasible mutualist systems in this form are globally stable. M-matrix theory quickly demonstrates this feature. The interaction matrix may be written in the form:

$$-\underline{\underline{A}} = s\underline{\underline{I}} - \underline{\underline{P}} ,$$

with $\underline{\underline{P}}$ a non-negative matrix whose spectral radius is less than s.

Thus $-\underline{\underline{A}}$ will be an M-matrix if there exists a positive vector p so that:

$$-\underline{\underline{A}}\, p > 0 \tag{17}$$

(see Berman and Plemmons 1979, p.136,128).

However, all feasible systems must satisfy the equilibrium condition (Equation 6) which reads:

$$-\underline{\underline{A}}\, \underline{N}^* = \underline{e} > 0. \tag{18}$$

By taking $p = \underline{N}^*$, the condition (17) is satisfied. $\underline{\underline{A}}$ is thus necessarily an M-matrix and is therefore Lyapunov stable. Because Lyapunov stability is preserved by pre- and post-multiplication with any positive diagonal matrix, then $\underline{\underline{S}}$ must also be Lyapunov stable.

This is quite contrary to conventional theory which until recently pronounced mutualism as destabilizing. Conclusions such as these were often based on Lotka-Volterra models and predicted mutualists as "populations undergoing unbounded exponential growth, in an orgy of reciprocal benefaction" (May 1982 p.803). However, for the very general model in which each species benefits every other, the above result demonstrates that all feasible communities are globally stable.

§6 Stability of Random Versus Feasible Systems

Goh and Jennings (1977) set out to show that the subset of feasible systems had no distinguishing features as far as stability was concerned. They concluded that "the subset of Lotka-Volterra models, each of which has a feasible equilibrium, has the same stability property as a set of linear models which is assembled randomly in the same manner" (p.70). Unfortunately this style of argument confuses the issue at stake, and is but another ill posed test in the ecological literature. The question that should be addressed is whether the subset of feasible GLV models differs in its stability behaviour from those GLV models (rather than linear models) which are randomly assembled.

Goh and Jennings (p.66) noted that "in Roberts' experiments the fraction of models with a feasible equilibrium does not behave like the function 2^{-m}. Hence the samples in Roberts' experiment are not sufficiently random. It follows that we should not conclude from Roberts' experiment that a Lotka-Volterra model with a feasible equilibrium tends to be stable." This criticism however has no validity since the fraction of feasible models in Roberts' experiments should not be expected to behave like 2^{-m} (as I make clear in Chapter 3). The difference in behaviour between the models of Goh and Jennings, and Roberts stems from the two distinctly different parameterizations they use. Whereas Goh and Jennings had as parameters –

$$b_i = {}^+_-1, \quad a_{ii} = {}^+_-1, \quad a_{ij} = {}^+_-z \quad i \neq j, \tag{19}$$

Roberts took –

$$b_i = +1, \quad a_{ii} = -1, \quad a_{ij} = {}^+_-z \quad i \neq j \tag{20}$$

(where the positive and negative signs were equally likely). Because the models have different parametrizations, it should be no surprise that they have markedly differing feasibility and stability properties. These

differences arise therefore, not from sampling errors on the part of Roberts, as Goh and Jennings claim, but simply from the study of two different models.

A glance at Table 1 (Appendix 5) quickly reveals that the feasible subset of the m-species GLV model (as parametrized in (20)) is dramatically more stable (see column headed %SLS/F) than those m-species models randomly assembled (see column headed %SLS). In light of Goh and Jennings' remarks, it is necessary to point out that there appears a very clear difference in stability properties between feasible and random systems.

§7 Discussion

It was seen in §5 that feasible systems are much more stable than those randomly assembled. This was also the conclusion reached by both Lawlor (1980) and Yodzis (1981) when they examined data for some real webs. On constructing the appropriate community matrices, they found the stability of these "real systems" to be much greater than that of the same matrices after a randomization process. Although the studies did not make allowance for the constraint of feasibility, they reinforce our conclusion that randomly-assembled systems do not have the high stability properties of the feasible set.

Whilst it has been common in the past to examine whether or not an ecological model has an interaction matrix that is stable, this study demonstrates that it can be far more important to determine whether a system has a feasible equilibrium point. For the particular GLV model analysed here, virtually all feasible competition and mutualist systems were globally stable. "Negative" equilibrium populations, characteristic of unfeasible models, were found highly destabilizing (Appendix 6) even when the interaction matrix was stable. Feasibility thus emerges here as the overriding criterion upon which system stability depends.

Although feasible (and thus stable) models best represent those ecosystems that are equilibrial, I will show in the next chapter that they can play an important role in the study of communities that appear to be non-equilibrial.

Appendix 1. Global Stability of the Model

Property 1.1) Large feasible systems (i.e., as m → ∞) are nearly always globally stable when $\gamma < 0.71$. (Empirically it is found that decreasing the system size m, increases the likelihood that a feasible system will be globally stable when $\gamma > 0.71$).

Proof:

The interaction matrix $\underline{\underline{A}}$ may be written as $\underline{\underline{A}} = -[(1-c)\underline{\underline{I}} + \underline{\underline{B}} + c\underline{\underline{U}}]$ where $\underline{\underline{U}}$ is the m-x-m matrix with all entries $u_{ij} = 1$.

It is useful to study the matrix $\underset{\sim}{\underline{\underline{A}}} = -[(1-c)\underline{\underline{I}} + \underline{\underline{B}}] = \underline{\underline{A}} + c\underline{\underline{U}}$. $\qquad (21)$

The matrix $\underset{\sim}{\underline{\underline{A}}}$ is Lyapunov stable if a positive definite diagonal matrix $\underline{\underline{W}}$ can be found

so that $\qquad \underline{\underline{G}} = \frac{1}{2} (\underline{\underline{W}} \underset{\sim}{\underline{\underline{A}}} + \underset{\sim}{\underline{\underline{A}}}^{T}\underline{\underline{W}})$ is negative definite.

(Note that $\underline{\underline{G}}$ is symmetric, and is negative definite when all its eigenvalues λ_j (which are real) satisfy $\lambda_j < 0.$)

If we choose $\underline{\underline{W}} = \underline{\underline{I}}$ (which is positive definite) then:

$$\underline{\underline{G}} = (g_{ij}) \text{ where } g_{ii} = -(1-c) \quad \text{and} \quad g_{ij} = \frac{1}{2} (b_{ij} + b_{ji}).$$

[†] Note that for the uniform model (with $\underline{\underline{B}} = 0$), the stability matrix $\underline{\underline{S}} = \underline{\underline{DA}}$ is symmetric and possesses eigenvalues $\lambda = -1$, and $\lambda = -(1-c)/(1+[m-1]c)$ ([m-1]-fold). Thus the uniform model (with $0 \leqslant c < 1$) always possesses a Lyapunov stable stability matrix (and interaction matrix) and so is globally stable. If $c > 1$ then the uniform model has a stability matrix with [m-1] positive eigenvalues and so is unstable.

Since Var (b_{ij}) = σ^2, then we must have Var (g_{ij}) = $\dfrac{\sigma^2}{2}$ for i≠j.

Invoking the Wigner theorem (Appendix 4), which is applicable as m → ∞, it results that the matrix $\underline{\underline{G}}$ + $(1-c)\underline{\underline{I}}$ has eigenvalues distributed according to the semi-circle law, with density

$$d(x) = \begin{cases} \dfrac{(2m\sigma^2 - x^2)^{1/2}}{m\pi\sigma^2} & \text{when } |x| < \sqrt{(2m)}\sigma \ , \\[2mm] 0 & \text{when } |x| > \sqrt{(2m)}\sigma \ . \end{cases}$$

Hence the eigenvalues of $\underline{\underline{G}}$ have the distribution given above, but shifted $(1-c)$ to the left.

Thus $\underline{\underline{G}}$ is stable (having all its eigenvalues $\lambda_j < 0$), when

$$\gamma < \dfrac{1}{\sqrt{2}} = 0.71 \quad , \quad \text{where } \gamma = \dfrac{\sqrt{m}\sigma}{1-c} \ ,$$

in which case $\underline{\underline{\tilde{A}}}$ will be Lyapunov stable. Appendix 3 (Property 3.3) shows that this implies the matrix $\underline{\underline{A}}$ will also be Lyapunov stable.

Thus all large feasible systems (as m → ∞) with $\gamma < 0.71$ are globally stable.

The important question remains: does the above result apply to those systems of intermediate-sizes (say 5 < m < 100), which have most interest for us? I have found from empirical results that it does apply. In fact decreasing the matrix size m, increases the likelihood of finding an interaction matrix that is G(L)-stable when $\gamma > 0.71$. Figure 3 plots the probability of G(L)-stability for randomly generated matrices of sizes m = 4, 8, 14, 20 and 50, all constructed with c = 0.4 . Nineteen values of γ were examined, from γ = 0 to γ = 1.8, in steps of 0.05. For each particular combination of (m, c, γ), the computer generated 200 random matrices, and tested them for G(L)-stability.

It is clear from Figure 3 that, when $\gamma < .71$, matrices in the intermediate-size range $(5 < m < 100)$ are $G(L)$-stable with very high probability. The graph shows how the critical transition from stability to instability, at $\gamma = 0.71$, sharpens as m increases. Moreover, it shows that a significant subset of matrices are $G(L)$-stable when $.71 < \gamma < 1$; the smaller the matrix size m, the larger is this subset.

Property 1.2) The ambiguous parameter range $(\gamma > 0.71)$, in which it is difficult to predict global stability, is in any case associated with a low probability of feasibility.

To see this, it is necessary to make use of the feasibility predictions calculated in Chapter 3. When $\gamma = 0.7$, the following probabilities of feasibility were obtained (see Figure 3, Chapter 3).

m	Pr(Feasible)
8	0.3
14	0.15
20	0.05
100	0.00

These probabilities all decrease when γ increases beyond $\gamma = 0.7$. Hence those interaction matrices that cannot be shown with high probability to be $G(L)$-stable (i.e., when $\gamma > 0.7$) have in any case a low probability of feasibility.

Appendix 2. Local Stability of the Model

In Appendix 1, the interaction matrix $\underline{\underline{A}}$ was (upon application of Wigner's theorem) found Lyapunov stable when $\gamma < 0.71$. Unfortunately it is difficult to make any prediction concerning the global stability properties for those feasible systems that occur when $\gamma > 0.71$ (without resorting to empirical Monte Carlo methods). However, it is possible to make some comments regarding local stability.

Property 2.1) Large feasible systems (i.e., as $m \to \infty$) possess an $\underline{\underline{\tilde{A}}}$ matrix (see (21) p.57) that is locally stable when $\gamma < 1$. When $\gamma > 1$, $\underline{\underline{\tilde{A}}}$ is unstable, and the probability of feasibility is slight. (Empirically it is found that decreasing the system size m, increases the likelihood of finding a locally stable interaction matrix, when $\gamma > 1$.)

Making use of the May-Wigner theorem, it is shown in Appendix 4 that the modified interaction matrix $\underline{\underline{\tilde{A}}}$ is, for large m (i.e., as $m \to \infty$), certainly locally stable when $\gamma < 1$, and certainly unstable when $\gamma > 1$. Moreover, it was found empirically that a significant subset of intermediate-sized matrices ($5 < m < 100$), are locally stable when $\gamma > 1$; the smaller the matrix size m, the greater is this subset.

Since nearly all feasible systems (and certainly all of size $m \geqslant 20$, as Chapter 3 shows) occur in the parameter range $\gamma < 1$, they are therefore predicted to have a locally stable interaction matrix $\underline{\underline{\tilde{A}}}$. Those feasible systems that occur for values of $\gamma > 1$ (eg., when $\underline{\underline{\tilde{A}}}$ is unstable) must in any case have a very slight probability of feasibility. The estimates of Chapter 3 find this probability to be less than 0.1 in 8-species systems, and less than 0.05 in 14-species systems (the probability decreasing with the community size m).

Property 2.2) A feasible system possessing a locally stable $\tilde{\underline{A}}$ matrix will have a stability matrix $\underline{S}$ that is locally stable.

Although $\tilde{\underline{A}}$ may be locally stable, this does not necessarily imply that the modified stability matrix $\underline{D}\,\tilde{\underline{A}}$ ($\underline{D} > 0$), will also be locally stable.[†] However, computer simulations have failed to produce a counter-example. (Compare for example, the columns headed (%SLS/F) with (%ALS/F) in Table 1 of Appendix 5.) In every case, with $\underline{D} > 0$, $\tilde{\underline{S}}$ inherited the stability of $\tilde{\underline{A}}$. Because, as Appendix 3 (Property 3.2) shows, $\underline{S}$ must be locally stable whenever $\tilde{\underline{S}}$ has local stability, then $\underline{S}$ will also inherit the stability properties as $\tilde{\underline{A}}$.

[†]The literature has been thoroughly reviewed on this point. $\underline{D}$ stability, (i.e., $\underline{D}\,\tilde{\underline{A}}$ stable for all $\underline{D} > 0$) has been surveyed recently and it appears that there are currently many open questions regarding this property (see Berman and Hershkowitz 1983).

[It may be the "internestedness" of the subsystems within $\tilde{\underline{A}}$ which makes $\underline{D}\,\tilde{\underline{A}}$ inherit the stability characteristics of $\tilde{\underline{A}}$, when $\underline{D} > 0$. For example, one necessary (but not sufficient) condition for $\underline{D}$ stability is that $-\tilde{\underline{A}}$ be a P matrix (i.e., all its principal matrices have positive determinants), as made clear by Johnson (1974). Suppose that $m \to \infty$, and $\tilde{\underline{A}}$ is locally stable. Those principal matrices of $-\tilde{\underline{A}}$ which are large enough for the May-Wigner theorem (see Appendix 4) to be applicable will (by the theorem) have positive determinants. Those principal matrices of smaller dimensions (say less than 50), where the May-Wigner theorem is less accurate, can also be shown to have a positive determinant. This latter property arises because the diagonal elements of the principal matrices are all +1, and since $\tilde{\underline{A}}$ has the dimension $m \to \infty$, and because $\gamma < 1$, then the smaller sized principal matrices will be diagonally dominant.]

Restating and summarizing the above two properties:

2.1) $\overset{\sim}{\underline{\underline{A}}}$ is locally stable for all feasible systems, save in a very few extreme cases, when m is small and the probability of feasibility is itself low.

2.2) The conjecture that, for feasible systems, $\underline{\underline{S}}$ is locally stable whenever $\overset{\sim}{\underline{\underline{A}}}$ is locally stable, has been confirmed by computer experiments.

Because a feasible model is locally stable whenever its matrix $\underline{\underline{S}}$ has local stability, we can conclude from the above that:

<u>All large feasible systems will be (at least) locally stable while the smaller feasible systems will nearly always be locally stable.</u>

Appendix 3. Some Properties of the Matrices $\underline{\underline{S}}$ and $\underline{\underline{A}}$.

Property 3.1) The stability matrix $\underline{\underline{S}}$ possesses an eigenvalue $\rho = -1$, which has associated with it the eigenvector $\underline{N}^*$.

Proof:

$\underline{\underline{S}}$ can be seen to satisfy:

$$\sum_{j=1}^{m} N_j^* S_{ij} = -N_i^* \ [N_i^* + \sum_{\substack{j=1 \\ j \neq i}}^{m} N_j^*(c+b_{ij})] = -N_i^* \ ,$$

for $i = 1, 2, \ldots\ldots m$,

having made use of equilibrium condition (2):

$$F_i = 1 - N_i^* - \sum_{\substack{j=1 \\ j \neq i}} (c+b_{ij})N_j^* = 0, \qquad \text{for } i = 1, 2, \ldots\ldots m.$$

In matrix form, $\qquad \underline{\underline{S}}.\underline{N}^* = -1 \ \underline{N}^*.$

Thus $\underline{N}^*$ **is a right eigenvector of** $\underline{\underline{S}}$ **corresponding to the eigenvalue** $\rho = -1.$

Property 3.2) The modified stability matrix $\underline{\underline{\tilde{S}}}$ has $[m-1]$ eigenvalues in common with $\underline{\underline{S}}$. ($\underline{\underline{\tilde{S}}}$ does not possess the eigenvalue $\rho = -1$ belonging to $\underline{\underline{S}}$.) Hence $\underline{\underline{S}}$ is locally stable whenever $\underline{\underline{\tilde{S}}}$ has local stability.

(Recall from Appendix 1 that $\underline{\underline{\tilde{S}}} = \underline{\underline{S}} \pm c\underline{\underline{D}} \ \underline{\underline{U}}$ where $U = (u_{ij})$ with $u_{ij} = 1.$)

Proof:

The left eigenvectors of a matrix are orthogonal to their non-corresponding right eigenvectors (see Aitken 1958, p.81). In particular, if we use $\underline{v}_i$ for the left eigenvectors of $\underline{\underline{S}}$, then

$$\underline{v}_i^T . \underline{N}^* = 0 \ , \qquad \text{where } \underline{v}_i^T \text{ corresponds to any eigenvalue } \lambda \neq \rho.$$

Take any eigenvalue $\lambda \neq \rho$, and its corresponding left eigenvector $\underline{v}^T$ of $\underline{\underline{S}}$, and note that

$$(\underline{v}^T \cdot \underline{\underline{\widetilde{S}}})_i = (\underline{v}^T \cdot \underline{\underline{S}})_i + c\underline{v}^T \cdot \underline{\underline{N}}^* = (\underline{v}^T \cdot \underline{\underline{S}})_i$$

(since $\underline{v}^T \cdot \underline{\underline{N}}^* = 0$).

This immediately gives $\underline{v}^T \cdot \underline{\underline{S}} = \underline{v}^T \cdot \underline{\underline{\widetilde{S}}} = \lambda \underline{v}^T$

so that $\underline{\underline{\widetilde{S}}}$ and $\underline{\underline{S}}$ have the eigenvalue λ in common.

Because we already know that $\rho = -1$ is one eigenvalue of $\underline{\underline{S}}$, we need only be concerned with finding the other m-1 eigenvalues, which can be obtained from a study of $\underline{\underline{\widetilde{S}}} = \underline{\underline{D}} \, \underline{\underline{\widetilde{A}}}$.

Property 3.3) $\underline{\underline{A}}$ is Lyapunov stable whenever $\underline{\underline{\widetilde{A}}}$ is Lyapunov Stable

Proof:

Assume that $\underline{\underline{\widetilde{A}}}$ is Lyapunov stable and recall from Appendix 1 that:

$$\underline{\underline{A}} = -[(1-c)\underline{\underline{I}} + \underline{\underline{B}} + c\underline{\underline{U}}] \, , \quad \text{where } \underline{\underline{U}} \text{ has all entries } u_{ij} = 1,$$

where $\underline{\underline{\widetilde{A}}} = \underline{\underline{A}} + c\underline{\underline{U}} = -[(1-c)\underline{\underline{I}} + \underline{\underline{B}}]$.

Note that $-\underline{\underline{U}}$ is symmetric, with eigenvalues $\lambda = -m$, $\lambda = 0$ ([m-1]-fold). Hence $-\underline{\underline{U}}$ is a negative semi-definite matrix.

Since by assumption $\underline{\underline{\widetilde{A}}}$ is Lyapunov stable, then there exists a positive definite diagonal matrix $\underline{\underline{W}}$, such that:

$$\underline{\underline{\widetilde{L}}} = \underline{\underline{W}} \, \underline{\underline{\widetilde{A}}} + \underline{\underline{\widetilde{A}}}^T \underline{\underline{W}} \text{ is negative definite.}$$

$$\text{Let } \underline{\underline{L}} = \underline{\underline{W}} \, \underline{\underline{A}} + \underline{\underline{A}}^T \underline{\underline{W}} = \underline{\underline{\widetilde{L}}} - (c\underline{\underline{W}} \, \underline{\underline{U}} + c\underline{\underline{U}} \, \underline{\underline{W}}) \, .$$

If $\underline{x} \neq 0$ is any real vector,

$$\underline{x}^T \underline{\underline{L}} \, \underline{x} = \underline{x}^T \underline{\underline{\widetilde{L}}} \, \underline{x} - c\underline{x}^T(\underline{\underline{W}} \, \underline{\underline{U}} + \underline{\underline{U}} \, \underline{\underline{W}}) \underline{x} < 0 \, .$$

This follows because $\underline{\underline{\widetilde{L}}}$ and $-\underline{\underline{U}}$ are negative definite and negative semi-definite respectively, so that $\underline{\underline{L}}$ must be negative definite and $\underline{\underline{A}}$ Lyapunov stable.

<u>Property 3.4)</u> Let the total sum of the equilibrium populations, $\sum N_i{}^*$,

be T. If $\tilde{\underline{A}}$ is Lyapunov stable, and the equilibrium is feasible, then

$T < 1/c$.

<u>Proof:</u>

We first note that $\tilde{\underline{\underline{S}}}.\underline{N}^* = -(1-cT)\underline{N}^*$, which shows that $-(1-cT)$ is an

eigenvalue of $\tilde{\underline{\underline{S}}}$.

Recall that if $\tilde{\underline{A}}$ is Lyapunov stable, then so too is $\tilde{\underline{\underline{S}}} = \underline{\underline{D}}\,\tilde{\underline{A}}$ (assuming

the equilibrium is feasible so that $\underline{\underline{D}} > 0$). Thus all the eigenvalues of

$\tilde{\underline{\underline{S}}}$ have negative real parts; but $-(1-cT)$ is an eigenvalue of $\tilde{\underline{\underline{S}}}$, so that

we must have $(1-cT) > 0$, or $T < 1/c$.

If $\tilde{\underline{A}}$ is locally stable (but not Lyapunov stable), the question of

whether or not $\tilde{\underline{\underline{S}}} = \underline{\underline{D}}\,\tilde{\underline{A}}$ is locally stable remains to be answered. As

discussed in Appendix 2, it appears that $\tilde{\underline{\underline{S}}}$ inherits the stability

properties of $\tilde{\underline{A}}$. If this be the case, then whenever $\tilde{\underline{A}}$ is locally stable,

we must again have $(1-cT) > 0$, or $T < 1/c$.

Appendix 4.

The Wigner Semi-Circle Law.

The study of the distribution of eigenvalues in matrices with random entries led Wigner (1955, 1958, 1967) to formulate what has become known as the semi-circle law. The theorem applies to hermitian matrices $\underline{A}$ as follows:

If the elements a_{ij} of $\underline{A}$ are independently chosen from some statistical distribution, and for all i,j

$$a_{ij} = \bar{a}_{ji}, \quad E(a_{ij}) = 0, \quad Var(a_{ij}) = \sigma^2,$$

then the eigenvalues, which are all real, are distributed as m → ∞, according to the semi-circle law - i.e., with density d(x), where

$$d(x) = \begin{vmatrix} \dfrac{\left(4m\sigma^2 - x^2\right)^{1/2}}{2m\pi\sigma^2} & \text{when } |x| < 2\sqrt{(m)}\sigma, \\ 0 & \text{when } |x| > 2\sqrt{(m)}\sigma. \end{vmatrix}$$

The May-Wigner Stability Theorem.

The question of a critical regime at which large complex systems switch from being stable to unstable was investigated by May (1972), who made use of Wigner's semi-circle law. He obtained the following simple result which allows the stability of matrices of the same form as $\tilde{\underline{A}}$ (analysed in Appendix 3) to be determined:

Let $\underline{A} = \underline{B} - \underline{I}$ be an m-x-m matrix where the matrix $\underline{B} = (b_{ij})$ has entries chosen from some statistical distribution as given in (10).

Let $P(m,\sigma)$ be the probability that a locally stable matrix will be drawn from such an ensemble.

If we define $\gamma_{May} = \sqrt{(m-1)}\sigma$, then May found that for large m,

$P \to 1$ and $\underline{A}$ is certainly stable when $\gamma_{May} < 1$

$P \to 0$ and $\underline{A}$ is certainly unstable when $\gamma_{May} > 1$.

The transition from stability to instability is very sharp and highly critical as $\gamma_{May} \to 1$.

Applying the May-Wigner theorem to the matrix $\tilde{\underline{A}}$ is straightforward. If gamma is defined by

$$\gamma = \frac{\sqrt{(m-1)}\sigma}{1-c} \quad , \quad \text{then for large m,}$$

$\tilde{\underline{A}}$ is certainly stable for $\gamma < 1$ and certainly unstable for $\gamma > 1$.

Since May never published a formal proof of the above theorem[†][*], I made use of computer Monte Carlo techniques, in a similar way to McMurtrie (1975), to check its validity. It was also possible to determine whether the theorem had application for matrices of intermediate-sizes (say $5 < m < 100$). Figure 4 plots the probability of stability for randomly-generated matrices of sizes $m = 4$, 8, 14, 20 and 50, all constructed with $c = 0.4$. Nineteen values of γ were examined, from $\gamma = 0$ to $\gamma = 1.8$, in steps of 0.05. For each particular combination of (m,c,γ), the computer generated 200 random matrices, and tested them for stability.

The graph shows how the critical transition from stability to instability, at $\gamma = 1.0$, sharpens as m increases. It is clear that a matrix in the intermediate-size range $(5 < m < 100)$ is locally-stable with very high probability when $\gamma < 1.0$. Moreover, a significant subset of matrices are Lyapunov stable when $\gamma > 1.0$, but the larger the matrix size m, the smaller is this subset.

[†] See Hastings (1982) for a proof in the case of difference equations.

[*] Further, note that queries have been raised concerning May's adaption of Wigner's result to a non-symmetric matrix (P. Taylor personal communication).

Appendix 5.

```
..................................
: 8-species,  C = 0.4,  samples = 200 :
..................................
```

GAMMA	%SLS	%F	%SLS/F	%G(L)/F	%ALS/F
0.10,	100.00	100.00	100.00	100.00	100.00
0.20,	100.00	100.00	100.00	100.00	100.00
0.30,	100.00	100.00	100.00	100.00	100.00
0.40,	92.00	92.00	100.00	100.00	100.00
0.50,	68.00	68.00	100.00	100.00	100.00
0.60,	44.50	44.50	100.00	100.00	100.00
0.70,	34.50	34.50	100.00	100.00	100.00
0.80,	21.00	21.00	100.00	100.00	100.00
0.90,	10.00	10.50	95.24	90.48	95.24
1.00,	6.00	6.50	92.31	69.23	92.31

```
..................................
: 16-species,  C = 0.4,  samples = 200 :
..................................
```

GAMMA	%SLS	%F	%SLS/F	%G(L)/F	%ALS/F
0.10,	100.00	100.00	100.00	100.00	100.00
0.20,	100.00	100.00	100.00	100.00	100.00
0.30,	97.00	97.00	100.00	100.00	100.00
0.40,	86.50	86.50	100.00	100.00	100.00
0.50,	51.00	51.00	100.00	100.00	100.00
0.60,	24.00	24.00	100.00	100.00	100.00
0.70,	10.50	10.50	100.00	95.24	100.00
0.80,	4.00	4.00	100.00	75.00	100.00
0.90,	1.50	1.50	100.00	33.33	100.00
1.00,	0.50	0.50	100.00	0.00	100.00
1.10,	0.00	0.50	0.00	0.00	0.00
1.20,	0.00	0.00	0.00	0.00	0.00
1.30,	0.00	0.00	0.00	0.00	0.00

Table 1.

%SLS = percentage of $\underline{S}$ matrices that were Locally Stable.

%F = percentage of Feasible systems in the ensemble sample.

%SLS/F = percentage of Feasible systems that were Locally Stable.

%G(L)/F = percentage of Feasible systems found Globally Stable by the G(L)-test.

%ALS/F = percentage of Feasible systems found to possess a locally stable interaction matrix $\underline{A}$.

Appendix 6.

Unfeasible m-species Equilibria are Unstable.

It is shown here that, if the interaction matrix $\underline{\underline{A}}$ is stable, then it i it only requires one, or any other odd number of negative equilibrium populations, to bring about instability of the system.

Since by assumption $\underline{\underline{A}}$ is stable, then all the eigenvalues λ_j of $(-\underline{\underline{A}})$ satisfy $\text{Re}(\lambda_j) > 0$ so that $|-\underline{\underline{A}}| = \prod_j \lambda_j > 0$.

As well, $|\underline{\underline{D}}| > 0$ because the system is feasible.

Hence $|-\underline{\underline{S}}| = |-\underline{\underline{A}}| \, |\underline{\underline{D}}| = \prod_j \nu_j > 0$, ν_j being the eigenvalues of $(-\underline{\underline{S}})$.

If there are an odd number of negative equilibrium populations, $|\underline{\underline{D}}| < 0$, so that now $|-\underline{\underline{S}}| = \prod_j \nu_j < 0$

This can be true only if there is an eigenvalue of $(-\underline{\underline{S}})$ with a negative real part, making $\underline{\underline{S}}$ unstable.

Roberts (1974) made it quite clear that "negative" equilibrium populations or "ghost species" are highly destabilizing. Suppose for example $N_1^* < 0$. The first row of the stability matrix would now have all positive entries since:

$$s_{11} = -N_1^* > 0, \text{ while } s_{1j} = -N_1^*(c+b_{1j}) > 0.$$

Therefore the ghost species acts like a real species (with positive equilibrium population), but with a positive birth rate $a_{11} = +1$. Moreover, all other species will be conferring benefits to it. The total effect is that the population of species-1 will have a rate of increase eventually proportional to N_1^{*2}, and the community will be unstable.
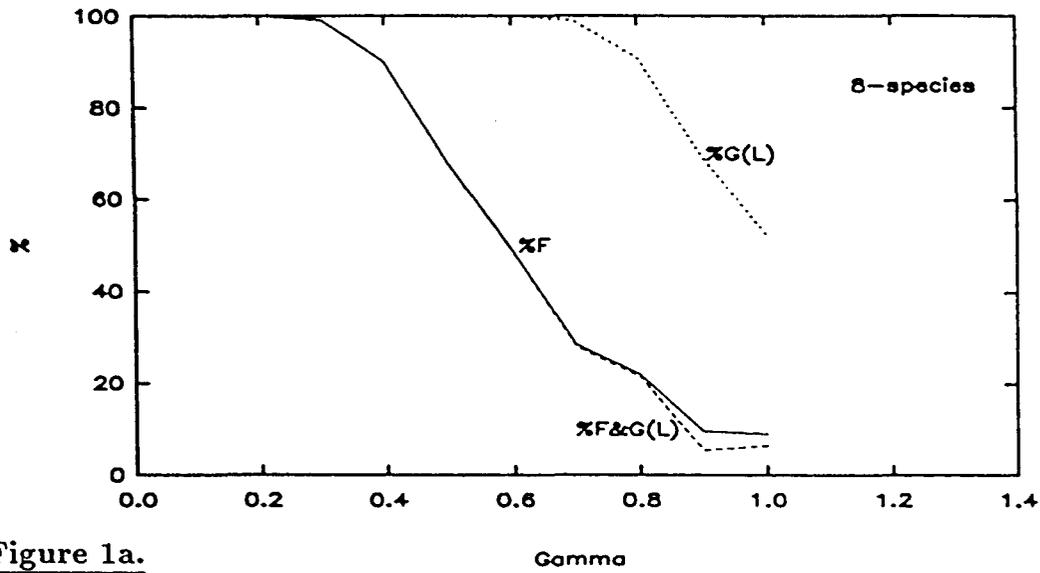
Figure 1a.
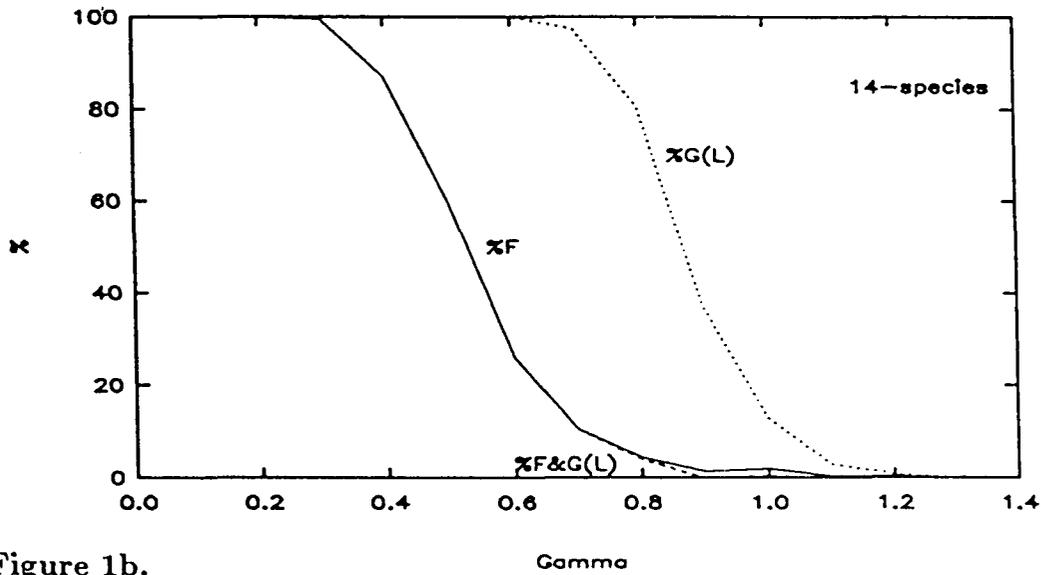
Figure 1b.
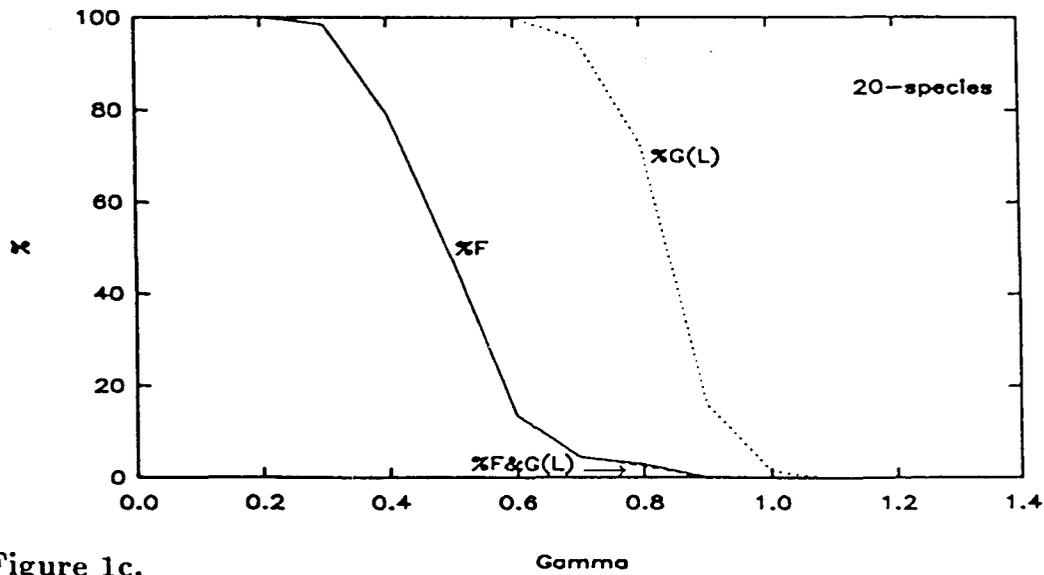
Figure 1c.

%G(L)   - the percentage of interaction matrices that were G(L)-stable.
%F   - the percentage of systems that were feasible.
%F&G(L)   - the percentage of systems that were feasible and possessed
             interaction matrices that were G(L)-stable.
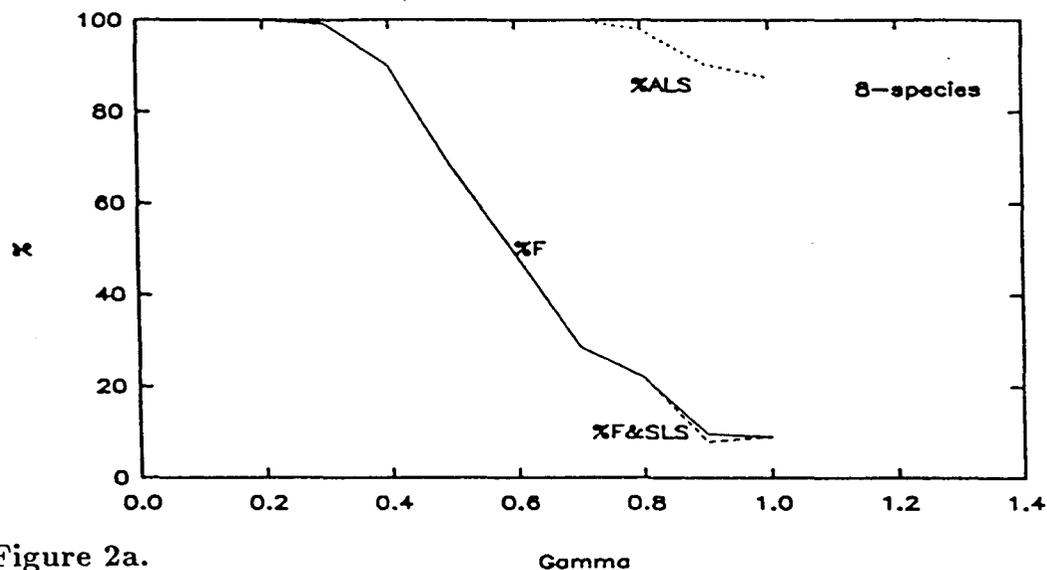
Figure 2a.
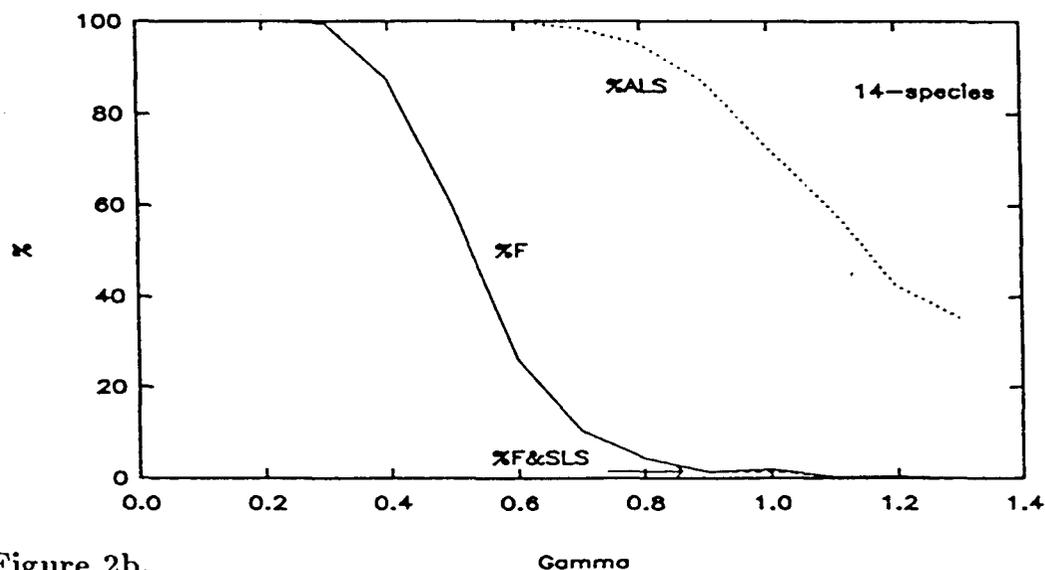
Figure 2b.
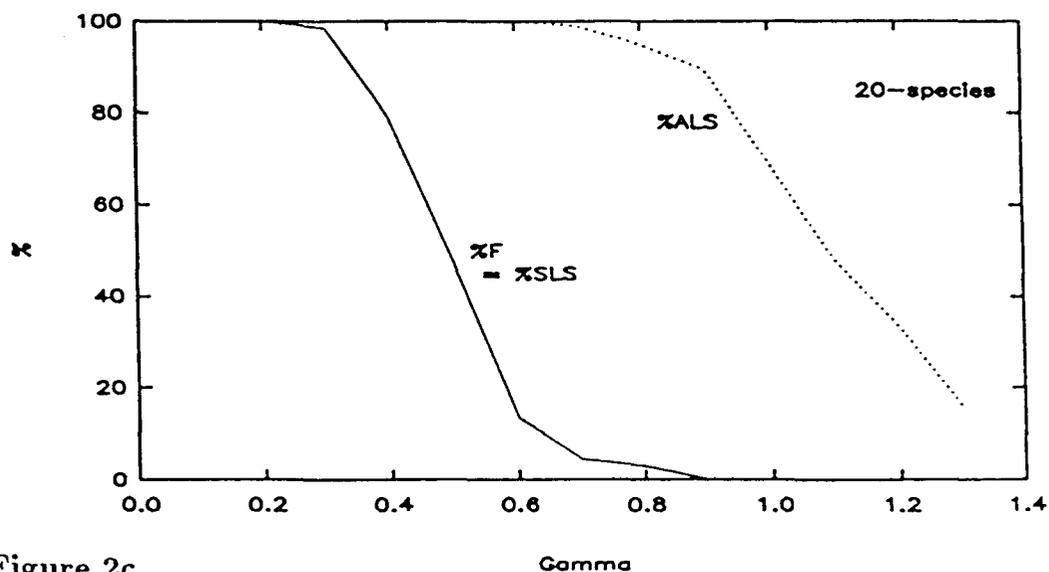
Figure 2c.

%ALS   - the percentage of interaction matrices $\underline{A}$ that were locally stable.
%F   - the percentage of systems that were feasible.
%F&SLS   - the percentage of systems that were feasible and possessed
            a locally stable $\underline{S}$ matrix.
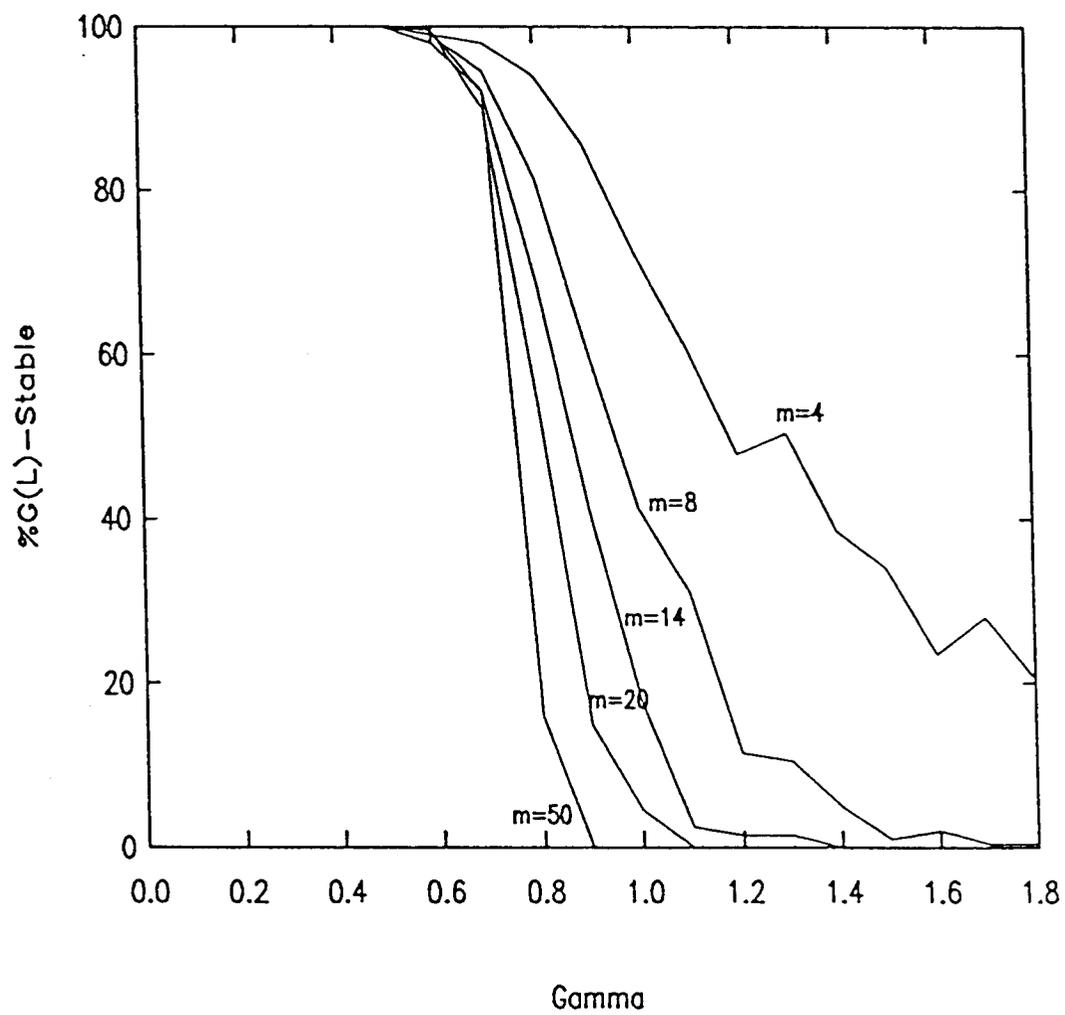
Figure 3. The % of interaction matrices ($\underline{A}$) that were found G(L)-stable.
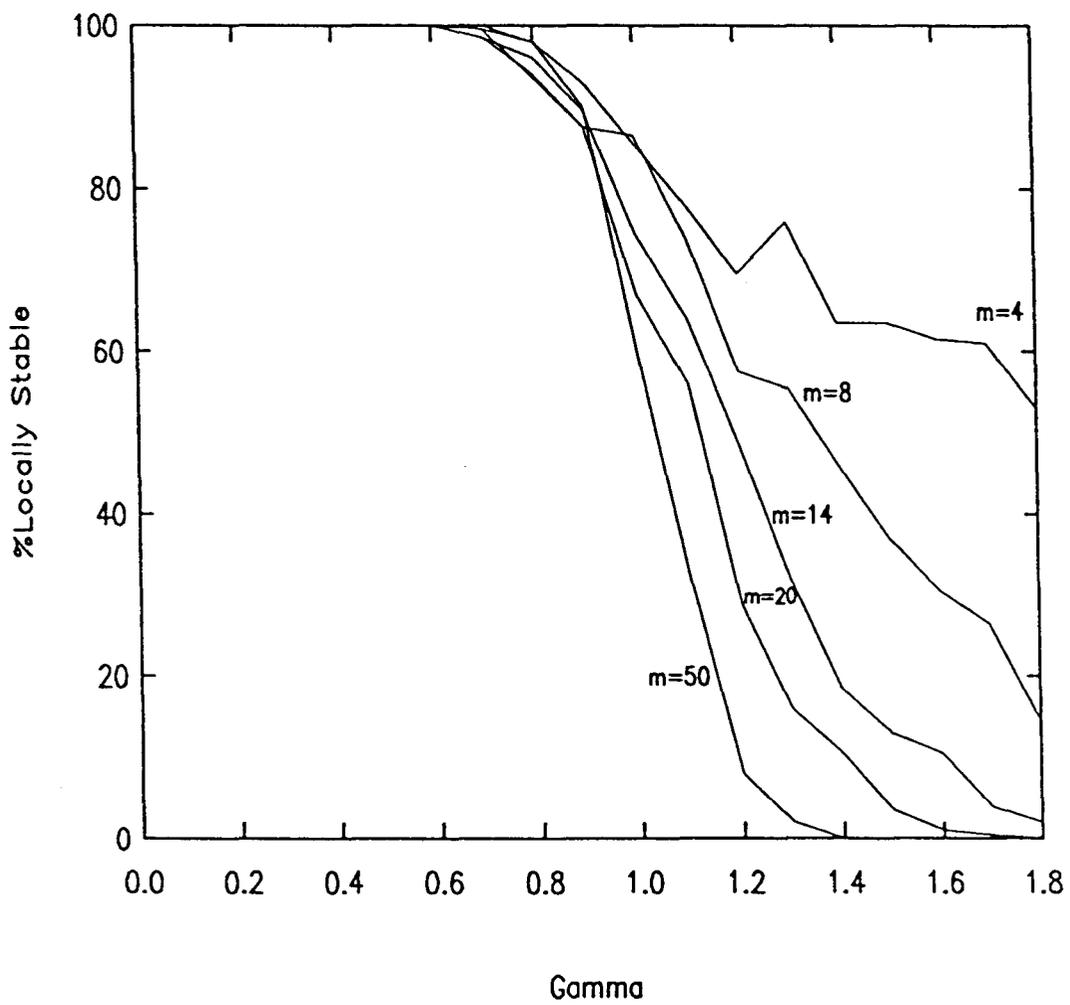
Figure 4. The % of interaction matrices ($\underline{A}$) that were found locally stable.

Chapter 3

Persistence of Ecological Systems Undergoing Environmental Disturbance

§1 Introduction

The difficulties in demonstrating that real communities possess stable equilibria have led some ecologists to modify and recast existing theories concerning community stability and the Balance of Nature concept (Botkin and Sobel 1975, Connell and Sousa 1983, Holling 1973). In their terms, stability may be understood as that property which keeps constant (or very close to constant) the species composition within a community over long periods of time. Apart from the ability to recover and conserve their species after disturbances, many communities have little in common with the features predicted by "mathematical stability" or the "Balance of Nature". These latter views suppose that populations continuously approach or actually attain a point equilibrium, after experiencing environmental disturbances. However, in many ecosystems populations may exhibit little sign of ever approaching an equilibrium, yet nevertheless manage to persist and maintain constancy in species composition. These points are elaborated in more detail below, and it is indicated how the important features of community conservation and recovery might still be found in an ecosystem, even when it appears to be an assemblage of stochastically disturbed non-equilibrium populations.

A theoretical formulation that makes use of the ensemble model, develops the idea further. The study of equilibrium models is used to give a picture of the feasibility and stability characteristics of a random ensemble of ecological systems and provides insight into the behaviour of some ecosystems that appear to be non-equilibrial. I model communities that undergo a series of environmental disturbances, as though they were attracted to a succession of equilibrium states. These

states all lie within a defined ensemble. I also examine the effects of those environmental changes that might directly depress populations without perturbing the equilibrium point of the system.

How a community responds to its environment depends on the rate and magnitude of the disturbances it experiences, relative to its own ability to recover. The ensemble model explores the full spectrum of possible relative rates and examines the requirements of community coexistence over this spectrum. If the model-community tracks environmental changes swiftly, then it exhibits the critical feasibility and stability traits of the ensemble in the large. On the other hand, model-communities that respond more slowly to environmental changes effectively filter out dangerous disturbances, and so increase their chances of coexistence.

§2 Ecological Persistence and Stability

The concept of stability has been given a variety of differing interpretations by ecologists. Many of the prevailing views stem from mathematical studies of the classical competition theory. These studies assumed stable point equilibria, where species' densities were maintained over time. This assumption was a consequence of the belief that species had density-dependent growth (i.e., each species' growth varies according to its instantaneous density) so that population levels were stabilized. The degree of stability was characterized by the ability of a community to return to equilibrium after a disturbance. The faster the return, the more stable a community was considered.

For equilibrium communities, global stability is viewed as the most desirable form of stability possible. It guarantees that no matter what the size of the perturbation, the populations will always follow a trajectory moving back towards their equilibrium point so that constancy

in population densities will be continually approached. This picture of stability supported the long-held view that there was a "Balance of Nature".

Over the last two decades, the above view that natural communities possess stable equilibria, has increasingly been under challenge. Even a stable community, with the ability to recover from disturbances, may rarely reach equilibrium if disturbance rates are high. Connell (1978 p.1302) points out: "in recent years it has become clear that the frequency of natural disturbance and the rate of environmental change are often much faster than the rates of recovery from perturbations", in which case it is unlikely that populations will be found at equilibrium levels.

In order to determine the role and attributes of stability, Connell and Sousa (1983) analysed census data from available long-term field studies. They concluded that "ideas of population or community stability based upon the existence of equilibrium states have seldom if ever been tested adequately because of the difficulty of defining the equilibria, measuring the strength of the disturbing forces and measuring the rate or degree of recovery in natural communities. Given the difficulties of testing these notions of stability it seems more useful to study the broader class of mechanisms which ensure population persistence regardless of whether equilibria can be identified" (pp.805-806).

This led Connell and Sousa to perceive ecological stability as very much broader in scope than its usual meaning, when it is associated with a stable equilibrium point. They felt: "Rather than the physicist's classical ideas of stability, the concept of persistence within stochastically defined bounds is.... more applicable to real ecological systems" (p.808). The theory of stochastic boundedness appeared to be a

more plausible explanation that accounted for the continuum of temporal variability.

Indeed, as Holling (1973) pointed out, the usual notion of stability as meaning a constancy in population numbers can give an entirely misleading understanding of ecosystems. The budworm-forest community in Canada suitably demonstrates this point. Under normal conditions the budworm is at low population density. However, approximately every forty years it erupts to epidemic levels. In doing so, it defoliates and destroys the spruce and fir trees it lives on, thus causing its own demise. The budworm crashes to its usual state of low density, whereupon the forests begin to regenerate and the cycle begins again.

Holling makes clear that budworm outbreaks maintain forest diversity (by keeping in check the competitively dominant fir trees), whilst destruction of the forest prevents the budworm from remaining at epidemic levels. Because of these cyclical conditions, the budworm population is seen to alternately explode and crash. Such "boom and bust" behaviour would be considered highly unstable in terms of constancy in density. However, Holling (p.15) demonstrates that "it is because of this instability that it [the community - L.S.] has an enormous resilience", which allows long-term persistence.

This phenomenon is prevalent and essential, in many types of communities. Heinselman (1973), for example, makes clear that recurring periods of severe fire damage in the forests in Minnesota U.S.A. are "an essential factor in maintaining the kind of long-term stability and diversity recorded" in this region. Sousa (1984) is of a similar view, and remarks: "There is now abundant evidence that in the absence of such [temporal and spatial - L.S.] variability many species would cease to exist" (p.354).

It seems then that there are many situations where species' densities within a community do not remain constant over time and have no apparent equilibrium - not even an asymptotic one. For these communities, it is irrelevant to define stability as a return to an equilibrium state. Despite the lack of evidence, it has still been convenient to assume that natural communities possess, and often reside at (or close to), a stable equilibrium point. If the stability were global, the following properties (amongst others) would be predicted:

1) <u>Community conservation.</u> The community is "conserved" and maintains its species composition.

2) <u>Community recovery.</u> The community is resilient and can recover from events that perturb species to low density.

(See Chesson and Case (1986) for a further discussion of these properties and overview of the question in general.)

Even though both of these features are outcomes predicted for an equilibrium system that possesses global stability, they could equally well have alternative explanations, and perhaps occur in ecosystems lacking any equilibrium point whatever. Hence there is a need to put forward alternative theories in community ecology that explain persistence, other than the usual approach where a stable equilibrium, often justified by the "Balance of Nature" concept, is simply assumed.

§3 Modelling the Effects of Environmental Disturbances
§3.1 Structural and Population Disturbances

In this chapter, a model is presented which simulates a community as it undergoes environmental disturbance. The model is shown to have the properties of community conservation and recovery that are usually associated with global stability, even when it displays density-vague behaviour with no apparent sign of possessing an equilibrium. Such

circumstances might occur in the setting outlined by Connell and Sousa (1983), and Strong (1986), where species populations sporadically or continuously fluctuate (because of autecological or environmental disturbances), yet remain within fixed bounds over time, showing no tendency to be attracted to any particular equilibrium point.

The model explored here treats the m population densities N_i as the components of the vector $\underline{N}$, in m-dimensional phase-space. This provides a simple picture of the population trajectory as it develops in time, when environmental disturbances are present. In the absence of disturbances, a community and its dynamics can, at any instant, be completely described by two sets of parameters:

1) $\underline{N}$, the vector of population densities;

2) $\underline{\underline{A}} = (a_{ij})$, the normalized interaction matrix (or community matrix) that prescribes the community's unique **dynamical mode**, density-dependence relations and environmental tracking ability. ($\underline{\underline{A}}$ also determines a single m-species equilibrium point $\underline{N}^*$, that the community's populations may achieve.)

The community's state may be represented by the set of parameters $(\underline{N}, \underline{\underline{A}})$. The dynamical mode and equilibrium point are said to be **feasible**, if the corresponding equilibrium populations N_i^* are all positive. (Note that a community can be in a feasible state or mode, even when the populations are not at equilibrium.)

I characterize two types of environmental disturbances that can affect the community in its state $(\underline{N}, \underline{\underline{A}})$. Structural disturbances effectively alter the dynamical mode by changing the entries of the normalized community matrix $\underline{\underline{A}}$. (Such disturbances have similarities to the "press" experiments described by Bender et al (1984).) Population disturbances act directly on the components of the population vector $\underline{N}$. (These disturbances are similar to the "pulse" experiments described by

Bender <u>et al</u> (1984).) A more detailed outline of the two disturbances is given below.

Structural disturbances occur when the dynamical mode is altered - i.e., when the internal community interactions a_{ij} are modified as a result of changed environmental and biological conditions[†]. That interactions continually change over time is a point that is very often neglected in ecological models (Abrams 1980), yet it is an extremely common phenomenon.

With particular reference to competition, Huston (1979 p.82) remarked that its "elusive quality.... results from the constantly changing intensity and focus of competitive interactions. Species may compete for an endless array of resources, but do not compete at all times for all possible resources. In general, competition will be for specific limiting resources, which change through time and space, as well as through a species' life history stages.... Cases may arise in which competition at one stage or place has no effect on the ultimate population size because limiting competition occurs at another stage, place or time.... In addition, genetic changes may be constantly occurring within populations which will change their competitive

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[†] It must be remembered that the interactions a_{ij} have been normalized as recommended in Chapter 2, so that:

$$a_{ij} = \alpha_{ij}/k_i \ ,$$

where α_{ij} is the real interaction between species i and j,

and k_i is the carrying capacity of species i.

Hence any changes to the "normalized" interaction matrix $\underline{\underline{A}} = (a_{ij})$ may reflect changes in carrying capacities, as well as in pairwise interactions.

interactions ... and even differences in age may drastically alter the direction of interactions... Constant competitive coefficients may well be meaningless except in uniform stable environments which never exist in nature."

The design of the model used here permits environmental effects to structurally modify the system itself and allows an investigation especially when environmental parameters (such as interactions, carrying capacities, resource levels, recruitment rates, and density-dependent growth relations) vary over time. Since all pair-wise species interactions are written down in the community matrix $\underline{\underline{A}}$, a structural disturbance can be modelled by appropriate changes to the elements of this matrix. A community's dynamical mode then alters, and the populations become attracted towards a new equilibrium point (specified by the "post-disturbance" interaction matrix). Whether species composition will be conserved is highly dependent on the nature of the new equilibrium point. By making allowance for environmental variations in this way, the model seeks to be more general and realistic than the usual analyses that model population disturbances only.

Population disturbances occur when the populations $\underline{N}$ have been perturbed from equilibrium, either infinitesimally or macroscopically, whilst all other system parameters remain constant. The consequences of such changes in population densities can be determined by the routine mathematical (local or global) stability analyses so frequently used by modellers. Systems that are stable to these disturbances should recover to their initial equilibrium. However, because the technique assumes that an equilibrium is possible, and that disturbances do not alter important factors like biological interactions or carrying capacities, some ecologists maintain that by itself it can give only a limited representation of real ecosystems.

A Simple Example

Figure 1 (reproduced from Pimm 1984, p.410) displays the population density of Song Thrushes in English farmlands, over the years 1962 to 1978. As Pimm (1984) notes, the population's crash and subsequent recovery may be modelled either by perturbing population levels or by perturbing structural parameters like the carrying capacities. Pimm argues that in general, such behaviour is best modelled by treating disturbance as a population perturbation only, and ignoring structural disturbances.

The aim here is not to select the most convenient way of simulating the crash, but rather to present a satisfying model that incorporates all realistic ecological events and processes. Pimm points out that the crash was caused by the unusually cold and harsh winter, in which a good deal of food resources were covered in snow and the habitat's carrying capacity was significantly reduced. Viewed from this angle, the community could be seen to have experienced structural disturbances, resulting in lowered carrying capacities. The thrushes could then attain an equilibrium only at some very low population density, which they crash towards. Simultaneously, population disturbances also came into play. The unusually sharp reduction, during the crash period, suggests that the thrush population was in part reduced by exogenous factors, as would be expected in periods of intense coldness.

Figure 1b (reproduced from Lack 1967, p.4) displays the population levels (measured by occupied nests) of British Herons, over a thirty year period. Because the time period is of greater length than the data used by Pimm (Figure 1a), the effects of structural disturbances are more easily seen. It would appear that the Herons in the Thames drainage area keep fairly close to an equilibrium level (of approximately 320

occupied nests) for the fourteen-year period between 1933 and 1947. After the particularly hard winter of 1947 the population rises to what seems to be a new equilibrium level (of approximately 480 occupied nests) which it holds with some constancy for another ten years. The two equilibrium levels might well be a result of structural disturbances, whilst fluctuations about these apparent equilibrium points could to some extent be attributed to population disturbances.

§3.2 Density-Dependent Growth

The "Balance of Nature" concept implicitly assumes that populations track environmental disturbances in a way that regulates them at constant density levels. Balance is maintained by the negative feedback inherent in density-dependent growth. If a population is perturbed to a level higher than its equilibrium value, it is predicted that it will decay back to equilibrium. Conversely, a reduced population will increase back to equilibrium. Thus the populations are seen to have the capacity to recover from any disturbance.

This density-dependent regulation has often been at the core of much ecological theory, so that species are usually modelled to be attracted towards an equilibrium, which they "track" after any disturbance (see Murdoch 1970). Figure 2, for example, displays how the logistic model simulates a population's growth to equilibrium, after it has been reduced to low density. The general shape of the curve, however, is an artifact of the logistic equations. Another density-dependent model might give a quite different shape, yet achieve the same result - i.e., an asymptotic approach to equilibrium.

A growing number of ecologists are challenging the idea that population growth is usually density-dependent (eg., Andrewartha and Birch 1954, Strong 1983, 1986), or that such growth plays an important

role in stabilizing communities (eg., den Boer 1986). Ecological field-studies offer only scant evidence of density-dependent growth (Connell and Sousa 1983, Strong 1986). Strong argues that, if it does occur, then it is usually only when populations are at particularly high or low densities. He suggests that many populations spend most of their time at intermediate densities where population changes are related to environmental or autecological factors, more than anything else. At these levels their growth is described as **density-vague** and the population changes resemble a "random walk".

I have chosen to use the GLV model (as outlined in Chapter 2) so that upon disturbance, a species recovers to its equilibrium level, in a manner quite similar to that predicted by the logistic curve. (The same results, however, would be obtained from most types of density-dependent models, including those based on difference equations.) Although the formulation incorporates density-dependent growth, I will show that a variety of behavioural responses are possible when disturbances come into play. Even though the model is based on equations that simulate density-dependent growth of populations to equilibrium, it is found that there are many occasions when density-vague behaviour dominates.

§3.3 "Hard" and "Soft" Disturbances

The method I use here treats a structural disturbance as a pulse or spike of given strength that occurs within an infinitesimal time-period. Because of their instantaneous nature, I refer to them as "hard" disturbances. A "soft" environmental change might have the same overall "energy" yet it would act gradually, spread out over a much greater time-period.

Whereas seasonal disturbances, such as patterns in rainfall, temperature and humidity, might be classed as "soft", a two-day bush-fire or a hurricane would be considered "hard". A great many disturbances are "soft", occurring gradually over time. I make the simplifying assumption that these can be approximated by a series of "hard" disturbances, constructed so as to have equivalent ecological effects over the same period of time.

§4 The Rate of Environmental Disturbance

The gradient that exists, extending from unstable environments where disturbances are frequent and imposing, to environments that are relatively stable and undisturbed over time, must be allowed for when investigating and hypothesizing community processes. In general, the stability of the environment can be characterized only if some definite time-scale is adopted. In the reference frame of a community, the perceived environmental stability will depend very much upon the rate of environmental disturbance, relative to the speeds with which species may recover.

Generally speaking, the recovery time of a species depends on its generation time. In fact, in persisting communities, the two periods are often of the same order of magnitude, since survival from disturbance can in many cases depend on how quickly the next offspring restores the population. Southwood et al (1974), in a study of single-species models, found the recovery time of a species inversely proportional to its growth rate r, whilst r is inversely proportional to generation time. Together these relations imply that recovery time is directly proportional to generation time. As can be seen in Figure 1, for example, the thrushes which breed annually are able to recover in a matter of several generations.

I define the community's rate of recovery, R_{rec} as the average speed at which a population approaches its equilibrium point after it has been perturbed to a level that is very close to extinction (all other species being maintained near to equilibrium levels). Appendix 2 gives details for obtaining R_{rec} when using the GLV model. Suppose then that the rate of environmental disturbances is R_D. This leads us to define the **Relative Disturbance Rate (RDR)** as

$$RDR = \frac{R_D}{R_{rec}} \; .$$

With this parametrization it becomes possible to examine the characteristics of a given community over a wide spectrum of environmental conditions, ranging from relative stability where disturbances rarely occur (RDR < 1) and a community is capable of easily tracking its environment, to instability (RDR >> 1) where environmental changes are too frequent to be tracked.

Suppose RDR $\simeq$ 1, so that the rate of disturbance is approximately equal to the community's recovery rate. This parametrization would describe a stable environment. The community will exhibit "fine-tuned tracking" of environmental changes, since there is always enough time for populations to recover from disturbances and approach constancy in density levels. If **RDR** $\ll$ 1 (i.e., relatively infrequent disturbances), then the community will exhibit "fast-tracking" behaviour. Because the community's recovery rate is faster than the rate of disturbance, it will always respond to environmental changes relatively quickly. As a result such communities will spend most of their lifetimes fairly close to equilibrium. Communities in which RDR < 1 would have similarities to those avian ecosystems studied by Cody (1981), in which species were observed to track variations in resource levels and environmental conditions closely, so that equilibrium was often maintained.

Suppose RDR $\gg$ 1, so that the rate of disturbance is significantly greater than the rate at which the community can recover. In these circumstances, there is insufficient time for communities to recover from an environmental change before the next oncoming disturbance. In the reference frame of the species, the environment is unstable. The species will exhibit "slow-tracking" behaviour, since they are never able to approach an equilibrium state too closely. If disturbances are particularly harsh, populations will display irregular density levels over time, their growth being determined more by abiotic factors than anything else. However, because tracking rates are slow, many of the effects that might result from dangerous disturbances will be evened out or smoothed over. The above scenario would conform with Wiens' (1977) observations of grassland avifaunas in Wisconsin, suggesting that these were frequently disturbed and that the tracking rates of species were not fast enough to keep populations at equilibrium levels. As a result species are often kept below their carrying-capacities, in a state where resources are plentiful and the need to compete reduced.

Southwood et al (1974) and Southwood (1977, 1981) have elaborated in depth how species evolve ecological strategies to suit the particular habitat they reside in. Those in relatively undisturbed and permanent habitats do not require the same sorts of strategies as those in habitats where, for example, environmental disturbances are severe and frequent. Relatively stable conditions favor communities with characteristics predicted by the equilibrium theory, in which biological interactions will be significant and resources will be competed for and become limited. Species evolve a K-strategy that emphasises maintaining or increasing competitive ability so that populations remain at levels close to equilibrium. If mortality jumps because of environmental

disturbance, populations will return quickly to equilibrium so that their share of resources is not secured by any competitors.

At the other end of the spectrum, in highly unstable environments, populations would be frequently subjected to major disturbances such as floods, fires and droughts. Communities would tend to be loose assemblages, for which the stochastic environmental disturbances weigh far more heavily than biological interactions. Evolutionary pressure would encourage species to evolve an r-strategy, with the emphasis placed on reproduction. Populations would have rapid growth rates at low densities, be opportunistic and, because of the changing environmental conditions, develop a "boom and bust" behaviour.

Summary

Unstable Environments:	Stable Environments:
1) Frequent stochastic effects. RDR $\gg$ 1.	1) Relatively undisturbed over time RDR $\ll$ 1.
2) Intense disturbances.	2) Weak disturbances.
3) Slow tracking rate.	3) Fast tracking rate.
4) Loose assemblage of independent species.	4) Tight competitive community.
5) r-strategists favored. (with opportunistic populations).	5) K-strategists favored. (with equilibrium populations).
6) Density-vague.	6) Density-dependent.
7) Abundance of resources (so that populations are below carrying capacities).	7) Resources limited (so that populations are close to carrying capacities).

§5 The Ensemble of Dynamical Modes and its Feasibility Characteristics

§5.1 The Ensemble of Structurally Disturbed Ecological Systems

In Chapter 2, I characterized the totality of possible community matrices $\underline{A}$ one might expect from an m-species competitive community in which

a) the species pair-wise interactions, after normalization, have a mean strength $-c$;

b) disturbances introduce independent random variations in all pair-wise interactions, of RMS strength σ.

This ensemble of matrices was defined by (m,c,γ), where $\gamma = \dfrac{\sqrt{(m-1)}\sigma}{1-c}$.

Each interaction matrix in the ensemble represents a distinct ecological system, having its own unique dynamics and density-dependence relations. The ensemble was considered to represent the totality of possible interaction matrices (or dynamical modes) a particular competition community might possess over its complete lifetime, given that it is undergoing structural disturbances of mean strength represented by γ. Each matrix has its own equilibrium solution $\underline{N} = \underline{N}^*$. Hence the ensemble of matrices gives rise to a corresponding ensemble of equilibrium points which could be envisaged in the form of a "stochastic cloud". If the community's trajectory at any stage of its lifetime approaches an equilibrium point, then this point must reside within the stochastic cloud. Thus a study of the ensemble of equilibrium points may yield information regarding the likelihood of community coexistence.

Lawlor (1978) pointed out that real ecosystems are not random and therefore it was inappropriate to compare results found from analyses of "random ensembles" with observations of the real world. Of considerable interest then are those characteristics that make ecosystems different

from random assemblages. The proposal of Roberts (1984), that established ecosystems must be **feasible** (i.e., **all** equilibrium populations are positive) to coexist, allows progress to be made in this direction. Roberts suggested examining an ensemble of ecological models that described the total multiplicity of modes an ecosystem might be disturbed to. He then proceeded to examine the distinguishing features of the feasible subset.

Roberts originally used the term "feasible" in the context of **equilibrium** populations. As has been made clear throughout this dissertation, the assumption of equilibrium is often inapplicable. Nevertheless, I begin by studying the characteristics of an ensemble of equilibrium states, and later make use of the results so that the model's behaviour, when in a non-equilibrium setting, may be explicated.

Roberts' early work in the main relied on computer experiments. Recently (1984), he calculated analytically an approximate "probability of survival" for a community that was described by the ensemble (m,c,γ). The higher the probability, the more likely it is that the community has m-species coexistence. The analysis gave a framework of the kind called for by Holling (1973 p.2), who believed progress could be made only "by viewing the behaviour of ecological systems in terms of the probability of extinction of their elements, and by shifting emphasis from the equilibrium states to the conditions for persistence." The ensemble model was thus a promising probabilistic technique that could be used to investigate what allows large complex ecosystems to survive.

§5.2 Predicting Feasibility of the Model

An ensemble of interaction matrices is defined by the set of parameters (m,c,γ). For the model described in Chapter 2, each interaction matrix has a corresponding equilibrium point that may or may

not be feasible. Roberts (1984), using the method of averaged environments, calculated the probability that any matrix drawn at random from the ensemble would be feasible. These results are now derived, but without environmental averaging.

The ensemble of matrices gives rise to an ensemble of equilibrium points. The equilibrium population of each species can be examined over the complete ensemble and be given in terms of a probability distribution. For feasibility it is necessary to determine the probability species i has a "positive" equilibrium - i.e., $N_i^* > 0$.

The model's populations over the ensemble (m,c,γ) are given by (see Appendix 1):

$$N_i^* = \kappa(1 - X_i), \qquad \text{where } \kappa > 0, \tag{1}$$

and $\quad N_i^* > 0, \qquad \text{if } X_i < 1.$

The distribution of the X_i was found to be asymptotically Normal as $m \to \infty$ - but even for m as small as m = 5, the Normal distribution provided an adequate approximation. It was found that (for $\gamma < 1$):

$$\langle X_i \rangle = 0 ,$$

$$\text{Var}(X_i) \simeq \gamma^2(1 + \gamma^2 + \gamma^4), \qquad \text{where } \gamma = \frac{\sqrt{(m-1)}\sigma}{1-c} . \tag{2}$$

$$\text{Thus } P = \text{Pr}(N_i^* > 0) = \text{Pr}(X_i < 1) = \text{Pr}(Z < \frac{1}{\sqrt{\text{Var}(X_i)}}) . \tag{3}$$

Here Z is a Normal variate with $\langle Z \rangle = 0$ and $\text{Var}(Z) = 1$.

Note that the probability P is a function of γ - i.e.,

$$P = P(\gamma). \tag{4}$$

An estimate of the probability of system feasibility $\text{Pr}(F)$, is given by the probability that all m equilibrial populations (N_i^*) are greater than zero so that:

$$\text{Pr}(F) = \text{Pr}(\text{System Feasible}) = P^m. \tag{5}$$

This estimate assumes that all equilibrium populations are independent of one another – i.e., that the covariance between any two populations is negligible for the stochastic setting given in Chapter 2. This is the case for all the systems over the parameter ranges of interest (i.e., ranges that allow the construction or generation of feasible systems) and does not become a limitation for the purposes of this work.

§5.3 Results – Feasibility of Communities With Fixed Size m

One way of testing the predictive ability of (5) is to construct samples from an ensemble of "random communities" with the aid of a computer, and compare the feasibility results given by the computer to those given by the analytic approximation. The prediction has been verified over a large range of the parameters (m,c,γ). Figure 3 for example, displays the feasibility features of models with a fixed number of species, $(m = 8,14,20,100)$, while the value of γ in the community is varied. The mean competition strength was kept fixed throughout as $c = 0.25$. For a given value of γ and size m, 500 random interaction matrices $\underline{A}$ were generated. A tally was kept of all feasible models so that the resultant graphs in Figure 3 could be plotted. These graphs may be used to read off the probability of "drawing" a feasible mode (or interaction matrix) from the ensemble (m,c,γ).

The graphs show that there is an extremely close match between the prediction given by Equation 5 (the continuous curve) and the actual Monte Carlo results. To check this further, it should be noted that when estimating p, the probability of an event, from N samples all obtained by the Monte Carlo method, the expected sampling error is given by:

$$\text{error} = \sqrt{(pq/N)} \qquad \text{where } q = 1 - p. \qquad (6)$$

The error is expressed as a fraction of the probability p. For example, at $p = q = 0.5$, and with $N = 500$ samples, a Monte Carlo experiment would

be expected to have probability p = 0.5 ± 0.03 . By using this method to obtain expected error, there seems to be no clear evidence of inaccuracy for the feasibility predictions given by Equation 5 .

§6 Dynamics of Communities Under Structural Disturbances

in Stable Environments - RDR < 1

§6.1 Surviving a Single Structural Disturbance - RDR < 1

This section will consider only those environments in which the Relative Disturbance Rate is low (RDR < 1), so that communities are "fast-tracking" - i.e., there is always sufficient time for populations to approach closely their new equilibrium levels after an environmental change. Hence, after a single structural disturbance:

1) either the new mode is feasible; in which case the community will asymptotically approach the equilibrium point of that mode, and species composition will be preserved;

2) or else the new mode is unfeasible; in which case at least one species extinction will occur (see Appendix 3).

Because of this, a community's probability of survival after a single structural disturbance, can be taken to be synonymous with $Pr(F)$ (the chance of asymptotically approaching a feasible equilibrium point). Similarly, the chance of an extinction occurring is represented by $[1 - Pr(F)]$.

Upon re-examining the feasibility predictions in Figure 3, it is apparent that the probability of survival for large communities rapidly dwindles as γ rises, and is often quite low well before γ approaches one. Interestingly, this shows these systems to be more delicate than May (1972) found from his study of stability. He conjectured that large systems (i.e., when m → ∞) would be surely stable for $\gamma < 1$ whilst unstable for $\gamma > 1$. The feasibility criterion is far more restrictive

however, and predicts large systems will survive only if $\gamma \ll 1$.

Extinctions

Figure 3 makes clear that the larger the parameter γ, the higher the chance that a species extinction will occur after a single structural disturbance. In ecological terms (for a community with a fixed number of species), γ can be increased in two different ways:

1) by increasing c, the normalized mean strength of competition. Recall that in Chapter 2, the parametrization was made that

$$a_{ij} = \frac{\alpha_{ij}}{k_i} \quad\quad \text{and} \quad\quad \langle a_{ij} \rangle = -c \quad .$$

Hence c may be increased in magnitude by an increase in the mean (unnormalized) strength of competition or by a decrease in the carrying capacity k_i, either of which could easily arise from environmental disturbances;

2) by increasing σ, the mean amount of variation in pair-interaction strength. An increase in σ signals that the competitive differences between species have become greater. Note that an increase in σ might well be due to a higher rate of environmental disturbance. If two communities have the same average (unnormalized) interaction strength, the community experiencing the higher disturbance rate would be expected to have the greater variation in its species interaction strengths - i.e., a greater value of σ.

In the interpretation adopted in this thesis, such increases (in c and/or σ) imply that the system's life history would now be given by a different ensemble having a higher value of γ. Hence the chance of feasibility is reduced, making greater the chance that one or more species become extinct after a disturbance.

The feasibility graphs of Figure 3 have fairly sharp transition regions (the sharpness increasing with m, the community size). If the

model is a guide to the behaviour of real-world systems, then it would appear that to increase the strengths of species' competitive interactions and/or the variation between them, even only slightly, can have detrimental consequences. The same critical behaviour could be expected, if the resources in a habitat were diminished and thus carrying capacities fell. Any of these changes might lead to species extinctions, particularly if the system did not initially have a high probability of feasibility and experienced multiple structural disturbances.

To obtain some insight into how species extinctions come about, the GLV equations were time-developed with the aid of a computer for a model specified by (m,c,γ) = $(10,.25,.75)$, and with RDR = 1 . (In actual fact the time development is a portion of a run to be described in §8.2 and Figure 10a, but without population disturbances.) Figure 7 plots the trajectory for species 4, 9 and 10 (whose equilibria are displayed as squares,triangles and circles respectively) after a structural disturbance at t = 28.6 . The graph shows that because γ is large, the equilibrium populations vary greatly about their expected value $\langle N_i^* \rangle$ = .31 (as determined from the uniform model Equation 8, Chapter 2).

After the disturbance at t = 28.6 , one sees that:

a) the new equilibrium value of species 10 exceeds the expected value by more than 100% ;

b) species 9 actually "overshoots" its equilibrium by almost 50% .

As a result, species 9 and 10 manage to achieve particularly high population levels and in consequence, other competitors in the community suffer. For example, Figure 7 shows that the equilibrium level of species 4 is drastically reduced to zero, and the species is consequently eliminated.

Southwood et al (1974) found the logistic model incapable of simulating a species which, because of a burst in growth, overshoots its carrying capacity and destroys resources. In an effort to model such situations (which can lead to erratic and chaotic behaviour), they resorted to the study of difference equations. However, as Figure 7 shows, the multi-species GLV equations can easily (and perhaps more realistically) elicit such behaviour. In what follows, we will see how populations might appear to have unusual and irregular growth because of the way multiple environmental disturbances affect them.

§6.2 Dynamics Under Multiple Structural Disturbances - RDR < 1

Assume for the moment that each of the possible equilibrium points is feasible and globally stable, and consider now the effects of structural disturbances. At a definite instant in time, the community has a definite dynamical mode; as a result, its populations $\underline{N}$ are attracted towards a single one of the possible equilibrium points which will be asymptotically approached over time (since RDR < 1). If an environmental disturbance is experienced, the entries within the community's interaction matrix change, and the community's dynamical mode is modified. In response, the population trajectory $\underline{N}$ alters its "course", being lured towards a new target equilibrium point (singled out by the "post-disturbance" interaction matrix).

A chain of disturbances would create a succession of target equilibrium points which the community sequentially moves towards. Each of these target points lies within the stochastic cloud. The community's trajectory $\underline{N}$ would meander continuously through the cloud of all possible feasible equilibrium points, and species composition would be conserved.

Suppose now, there is only a high probability - but not a certainty - that the current point within the "stochastic cloud" is feasible. Over time the populations $\underline{N}$ might be lured from target point to target point within the cloud, but even after a large number of disturbances, never enter into a mode that is unfeasible. The community could conceivably survive for a reasonable length of time before entering an unfeasible mode, whose probability is by assumption, small. When such a mode is entered, then one or more species must become extinct (see Appendix 3). This is an acceptable feature of the model, since we know extinction is not a rare phenomenon.

To illustrate the behaviour of "fast-tracking" communities under multiple disturbances, I have time-developed the GLV equations with the aid of a computer for an ensemble specified by (m,c,γ) = $(10, 0.25, 0.25)$ and graphed one of the ten populations in Figure 8, for various values of the Relative Disturbance Rate. These graphs visually display how a population within the community can be attracted towards an equilibrium point (represented by a triangle), that changes every time a structural disturbance takes place. Figure 8a demonstrates how, in stable environments (RDR = 0.1), populations spend most of their time close to equilibrium levels. In contrast, when the environment is less favourable (RDR = 1.0, Figure 8b), as soon as the populations manage to approach equilibrium levels, a new disturbance arrives and noticably alters their behaviour. The populations would appear to be governed by density-dependent growth after they are disturbed, and predictably approach equilibrium levels asymptotically. However, examined over a time-scale that encompasses a number of disturbances (Figure 8b), these population changes can appear non-equilibrial, even though they stem from equilibrium processes.

Effects of Population Disturbances - RDR < 1

For those "fast-tracking" communities that are capable of persisting under continued structural disturbances, it was shown that, in virtually all the dynamical modes they enter, the feasible equilibrium points are globally stable. Because of this global stability, all m-species are able to <u>recover</u> from any population disturbances. Figures 9a and 9b · for example, display the same communities as Figures 8a and 8b (respectively), receiving exactly the same structural disturbances. However, while the communities in Figure 8 suffer no population disturbances, those in Figure 9 experience heavy population reductions. The computer was programmed to depress populations by 90% whenever a structural disturbance occurred. Because the rate of disturbance is relatively low (RDR < 1), and because the communities are nearly always found in dynamical modes that are globally stable, they are endowed with the ability to fully <u>recover</u> from population disturbances (that do not completely eliminate a species). Hence, when RDR < 1, population disturbances can be neglected and it is the structural disturbances which are critical, and upon which continued coexistence is dependent.

§6.3 The Lifetime of Fast-Tracking Communities - RDR < 1

The feasibility predictions given in §5 may now be drawn on to study the survival characteristics of a "fast-tracking" community undergoing disturbances. The lifetime of a community is proportional to the maximum number of structural disturbances it can withstand before a species extinction occurs (since, as made clear in §6.2, models of fast-tracking communities are capable of surviving all population disturbances as long as species are never reduced entirely to extinction level).

The probability that the model-community can survive a single structural disturbance is given by the probability of feasibility

$$p = Pr(F) = P(\gamma)^m \qquad (\text{see Equations 4 and 5}).$$

Let the random variable Y be the total number of such disturbances the model survives before some disturbance gives rise to an unfeasible mode, and causes the extinction of one or more species. Note that Y has the geometric probability distribution function –

$$Pr(Y = y) = p^y (1 - p) , \qquad y = 0,1,2,\ldots\ldots \qquad (7)$$

The probability that a model-community can withstand more than k structural disturbances is:

$$Pr(Y > k) = 1 - \sum_{y=0}^{k} Pr(Y=y) = p^{k+1} . \qquad (8)$$

In Figure 4, I have used the above formula to plot the probability that a 14-species model can survive at least k structural disturbances, against γ (in the interval [0,1]). Four separate graphs are shown, for values of k = 5, 10, 50, 100. The most striking feature of these graphs is the very sharp transition at which the probability falls rapidly from 1 to 0. The sharpness of the transition increases with k. The transition region is also greatly influenced by the feasibility curve $P(\gamma)^m$, and thus will become sharper as m increases. The graphs indicate the unusually small range of values in which γ must lie, so that continued persistence is allowed, namely $\gamma \lesssim 0.4$. These model-communities are thus particularly vulnerable to structural disturbances.

The model may be used to predict the lifetime of a "fast-tracking" community by estimating the expected number of structural disturbances (i.e., $\langle Y \rangle$) before the first unfeasible mode is entered (in which case one or more species will go extinct). For the above geometric distribution (Equation 7), the expected value is given by:

$$\langle Y \rangle = p/(1 - p) \quad .$$

Figure 5 plots $\langle Y \rangle$ against γ for an m-species community $(m = 8,14,20,100)$, and again indicates the critical value of γ (at $\gamma \simeq 0.4$), beyond which continued persistence is unlikely. Throughout the remainder of the thesis, this critical value of γ will be taken to be $\gamma_{crit} \simeq 0.4$.

In Figure 6, $\langle Y \rangle$ is plotted against the feasibility predictions of a 14-species system. The graph strikingly demonstrates that it is essential for fast-tracking communities to possess a high probability of feasibility if they are to withstand even a relatively small number of structural disturbances.

(Figures 4,5 and 6 were arrived at making use of the probabilities given by the Monte Carlo estimates displayed in Figure 3.)

§6.4 Behaviour of Fast-Tracking Communities

The study above treats those communities which spend much of their lifetime close to equilibrium. For such a community to persist, it is important that the parameter γ be less than the critical value $\gamma_{crit} \simeq 0.4$. For those who have little belief in the notion of "equilibrium communities", the above results may appear somewhat artificial. However, in §7 they will be shown to be useful in the study of communities which do not appear to exist in a steady state.

We saw that when RDR < 1, a community will spend most of its lifetime with populations close to their current equilibrium levels (Figures 8a and 9a). How the community behaves is governed by the particular combination of structural and population disturbances. It is quite likely that if the community were examined over a time-scale spanning a moderate number of disturbances, its populations would appear to fluctuate irregularly and show no definite sign that equilibrium

processes were at work (Figures 8b and 9b). This picture of communities that display irregular behaviour, even though they are governed by deterministic processes, will now be developed further.

§7 Dynamics of Communities in Unstable Environments - RDR > 1

§7.1 Slow-Tracking Communities

In this section I examine communities in unstable environments - i.e., with a high Relative Disturbance Rate (RDR > 1). These communities have long characteristic recovery times with respect to the rate of ongoing disturbances - they are "slow-tracking". As explained earlier, a slow-tracking community suffers from an inability to asymptotically approach the current equilibrium point. What frequently happens is that, before a community can closely approach a particular equilibrium point, conditions change and the community is forced to readjust its path in order to track some new target equilibrium point. Because of this continual pattern of readjustment, the community's populations show little sign of any constancy in density, and are erratic and irregular.

Davis (1986) studied the effects of climatic changes on natural communities. The conclusion she arrives at has many similarities to the model's behaviour discussed above. She remarks (p.284):

"Given the slow responses of many species to climatic change and given the instability of the climate at all time scales, many plant and animal communities, or at least components of those communities, will be in disequilibrium, continually adjusting to climate and continually lagging behind and failing to achieve equilibrium before the onset of a new climatic trend. The species composition and the abundances of species within a community cannot be interpreted on the basis of biotic interactions without also considering responses to directional climatic

trends."

It is instructive to compare this description with a computer time development of the model's populations when they have slow-tracking rates (i.e., RDR $\gg$ 1). Figure 8c displays the population of a single species (N_1) in one such run. The ensemble was specified by $(m,c,\gamma) = (10,0.25,0.25)$, with RDR = 5. One sees how N_1 is continually attracted towards its changing target equilibrium point N_1^*, yet is rarely, if ever, capable of attaining an equilibrium level.

The Effects of Population Disturbances - RDR > 1

Figure 9c displays the effects when the time-development program, whose results have already been shown in Figure 8c, is modified to incorporate harsh population reductions. Populations were depressed by 90% every time a structural disturbance occurred. The graph clearly demonstrates how the slow response time of species prevents them from attaining equilibrium. In this example, the populations rarely attain much more than 50% of their equilibrium levels.

§7.2 Temporal Variation Promotes Coexistence

Hutchinson (1961) noted that disturbances, by constantly altering competitive rankings and thus slowing down the exclusion process, could promote coexistence. Connell (1978) developed this line of argument in full when he put forward the "intermediate disturbance hypothesis". He explains that at low levels of disturbance, the community's dominant competitor has the opportunity to competitively exclude all other species. When disturbances are at intermediate frequencies and intensities, populations are often depressed and found below their equilibrium levels. Hence those competitors that might normally dominate the community are suppressed, and are of far less danger to other

species. In these conditions, a higher species diversity may be achieved. Once disturbances increase beyond "intermediate" levels, they may no longer promote coexistence but instead cause severe damage, depleting important resources and even eliminating species.

Figures 10a,b, and c demonstrate how different levels of temporal variation (or Relative Disturbance Rate) might affect a single species within a large community. They also capture important features of the intermediate disturbance hypothesis. In Figure 10a, temporal variation is taken to be relatively low (RDR = 1) so that conditions may allow some competitor/s to attempt to dominate the community. Thus c, the strength of competition will be high, making the parameter γ relatively large. I have chosen γ = 0.75, which for ten-species systems ensures that $Pr(F)$ (the probability of feasibility) is low, and that in all likelihood some species will be eliminated. In this example, the populations are depressed by 50% every time a structural disturbance occurs. After eight disturbances, the time-development shows that the model entered an unfeasible mode[†] in which species 1 was attracted to an equilibrium level of $N_1^* = 0$. Species 1 was then competitively eliminated.

[†] When an unfeasible mode did occur, the equilibrium point of attraction was determined by the method presented in Appendix 3.

Figure 10b shows that when disturbances occur more frequently (i.e., at "intermediate" rates), extinctions can be prevented and coexistence maintained. In this time-development, species 1 experiences the same disturbances as in Figure 10a, but at a faster rate (RDR = 5). One sees that N_1 is attracted many times to the equilibrium level $N_1^* = 0$, but because of its slow tracking rate, the species survives some seventy disturbances and shows every indication that it is capable of persisting further. In Figure 10c environmental disturbances are even more frequent (RDR = 8) and more extreme (populations are depressed by 85% whenever there is a structural disturbance). Under these harsh conditions extinction swiftly follows.

There are a number of reasons why the model predicts coexistence to be more likely at intermediate frequencies than at other frequencies. When the model enters an unfeasible mode, for example, extinction can in some circumstances be prevented if an environmental disturbance soon follows. This is because a perturbation may deflect a population's path away from a dangerous equilibrium point (eg., one where its equilibrium population $N_i^* = 0$), to an equilibrium level that will be advantageous (eg., one where $N_i^* \gg 0$). Hence there may not be sufficient time for any population to reach extinction. Disturbances, if they act in this manner, would be a mechanism preventing populations ever approaching too closely those equilibrium points within the stochastic cloud that are unfeasible. This would be particularly likely when the probability of entering a feasible mode is high.

A close examination of Figure 11a (RDR = 2) reveals that at t $\simeq$ 22, 58, 72 and 78, the mode became unfeasible, with $N_1^* = 0$ (as established by the method described in Appendix 3). Two factors worked simultaneously so that the species survive these dangerous modes (except at t = 78):

a) Before each of the disturbance, N_1 was doing quite well for itself and had high population density. This made it all the more difficult for the species to be reduced to extinction. In simple terms, the populations could be said to "remember their past", so that previous periods of high density enable species to survive in lean times or whenever extinction appears imminent. "Historical factors" are thus important.

b) When an unfeasible mode was entered that was hazardous to species 1's existence (i.e., $N_1^* = 0$), the next structural disturbance usually attracted N_1 to a new positive equilibrium. In doing so, it prevented N_1 from moving any further along its path to extinction. This, of course, would most likely come about for communities that have high probability of feasibility or, put equivalently, under environmental conditions where γ is not too large.

At t $\simeq$ 78 both of the above points were breached. The population was already at very low density when the community entered an unfeasible mode. After being attracted to two successive unfeasible equilibria, the species was finally eliminated.

Perhaps the most remarkable characteristic of communities in unstable environments (RDR > 1), where response times are relatively slow, is that structural disturbances can reach quite a significant magnitude ($\gamma \gg 0.4$) but still allow long-term persistence. Slow-tracking rates endow species with a "memory" so that any traumatic disturbances tend to be averaged out, or filtered, often making them of

little danger. This is because the relatively slow response times allow populations to "remember" their usual or mean density levels, and slowly fluctuate about these levels, even after large disturbances. Hence the m-species investigation has similarities to May's (1981) findings for single species models. He showed that when the recovery rate is relatively fast, populations "are condemned to track environmental fluctuations" whereas, if the recovery rate is relatively long, populations "may average over essentially all fluctuations" (p.25).

If disturbances occur with greater frequency, the community is less able to track them, and "historical factors" can play a part in preventing species extinctions. Figure 11b is an identical community to that in Figure 11a, experiencing the same structural disturbances. However, because the disturbances are more frequent (RDR = 8), the population tends to respond more slowly to environmental changes and the species manages to persist for a lengthy period, rather than go extinct as in Figure 11a.

§7.3 Density-Vague Behaviour and Stochastically Bounded Populations

Figure 11b displays the trajectory of N_1 over time; it has much in common with Strong's (1986) description of liberal population regulation (compare his Figure 15.4). Because all equilibrium points lie within the "stochastic cloud", limits are set on the maximum and minimum population levels a species may reach. These limits are similar to the ceilings and floors described by Strong. Structural perturbations attract N_1 to a series of equilibrium points all of which successively arise because of "density-independent" factors. As well, N_1 follows a trajectory governed by the density-dependent GLV equations. When combined, these contrary effects (one density-dependent and one density-independent) endow N_1 with density-vague behaviour.

Figure 11b demonstrates this behaviour clearly. N_1 is frequently observed altering its direction as it is attracted towards a shifting target equilibrium point. Its resulting trajectory shows little overall sign of density-dependent behaviour, where the instantaneous change in population level should be related to instantaneous density. Had population disturbances also been simulated, there would be even fewer signs that species were density-dependent (eg. Figure 10b).

§8 Conclusion

The ensemble model developed a picture of a community being successively attracted to a series of different equilibrium points that lie within a "stochastic cloud". This would occur whenever the community experienced a succession of structural disturbances. If the community is relatively "fast-tracking", as it would be in stable environments (RDR < 1), long-term survival is only possible if unfeasible modes are rare. This means γ must be small ($\gamma \leqslant 0.4$), implying that structural disturbances can be no more than mild. The community meanders between feasible modes (that are globally stable), and consequently possesses the important qualities of conservation and recovery even though it never remains long in any specific equilibrium state. Structural disturbances, therefore, appear to be the critical factors in stable environments, whereas population disturbances (if they do not depress species to extinction) can normally be recovered from.

In harsher environments the higher frequency of (both structural and population) disturbances ameliorate any destructive effects. This arises because many communities are only capable of tracking environmental changes slowly, so that successive dangerous disturbances tend to cancel one another out. Under extreme conditions, however, the effect become less important and extinctions can easily occur from both

structural and population disturbances. The total picture obtained from the model is in accord with Connell's (1978) "intermediate disturbance hypothesis".

For a community to persist, it is crucial that a suitable ecological strategy, which matches the stability of the environment, is utilized. Southwood (1977 p.337) succinctly refers to habitat stability as a possible "templet" for ecological strategies. The model predicts that in stable environments communities must have populations fairly close to equilibrium levels. A K-strategy, that invests energy into competitive ability, longevity, size and individual offspring (see Southwood 1981 for a complete discussion) would give species a high recovery rate and so maintain and reinforce equilibrium behaviour. In less stable environments, where populations are often perturbed far from equilibrium and at low densities, an r-strategy that invests energy into reproduction would be more appropriate. Large numbers of offspring, high mobility and migration are characteristics that would enhance survival under precarious and uncertain conditions, since all are phenomena tending to average out the effects of disturbances and thus give species a slow-tracking rate.

Many ecologists have pointed out how difficult it is to determine whether real ecosystems are stable (Auerbach 1979, Connell and Sousa 1983, Sutherland 1981). The results here suggest why there has been so much difficulty in this task. If ecosystems are subjected to disturbances and their system parameters left with altered values, the equilibrium populations will generally change. Hence it would be rare to observe a system "returning" or "adjusting" back to its initial equilibrium state; its populations will rather be attracted to some new equilibrium level.

We have seen that the ensemble model can display unusual and erratic behaviour when responding to disturbances. Under these conditions, there might be little evidence for an observer to deduce that the populations are governed by equilibrium processes. This has similarities to the phenomenon of "chaotic" behaviour, which can be exhibited in some deterministic models that make use of a difference equation (May 1975, 1976, May and Oster 1976, Southwood et al 1974). In these latter models, "chaos" occurs only for particular, and perhaps unrealistic, parameter ranges (see eg., Hassell et al 1976, Mueller and Ayala 1981). However, it seems that erratic behaviour can be expected in even the most simple of models, if structural disturbances are allowed for.

In the past, a great and perhaps unnecessary emphasis has been placed on determining under what conditions ecological models will have a single stable equilibrium, and then attempting to suggest how these conditions might be met in the real world. Connell and Sousa (1983) have instead been urging ecologists to focus on the notion that communities have stochastically bounded populations. The ensemble model analysed here has found that such communities can possess the important properties of conservation and recovery, and thus are capable of persisting for extended periods. It was found also that time lags, whereby populations track environmental changes slowly, can be an effective strategy that is conducive to long-term persistence.

Appendix 1

Deriving the Distribution of the Equilibrium Populations

The equilibrium populations N_i^*, are determined by the following perturbation method. At equilibrium we have in matrix form:

$$\underline{\underline{A}} \ \underline{N}^* = -\underline{e} \qquad \text{(see Chapter 2, Equation 6)}$$

where $\underline{\underline{A}} = (\alpha_{ij})$ is the m x m matrix, with entries $\alpha_{ii} = -1$, $\alpha_{ij} = -(c+b_{ij})$,

$\underline{e}$ an m x 1 vector with all components $e_i = 1$,

and $\underline{N}$ is the m x 1 vector of populations N_i^*.

Let $\underline{\underline{U}}$ be the m x m matrix with all entries $u_{ij} = 1$, then

$$\underline{\underline{A}} = -[(1-c)\underline{\underline{I}} + c\underline{\underline{U}} + \underline{\underline{B}}] \ .$$

$$\underline{\underline{A}} \ \underline{N}^* = -[(1-c)\underline{N}^* - cT \ \underline{e} - \underline{\underline{B}} \ \underline{N}^*] = -\underline{e} \quad \text{where } T = \sum_1^m N_i^* \ .$$

$$[(1-c)\underline{\underline{I}} + \underline{\underline{B}}] \ \underline{N}^* = (1-cT)\underline{e}$$

or $\qquad \widetilde{\underline{\underline{A}}} \ \underline{N}^* = -(1-cT)\underline{e} \qquad$ where $\widetilde{\underline{\underline{A}}} = -[(1-c)\underline{\underline{I}} + \underline{\underline{B}}] = \underline{\underline{A}} + c\underline{\underline{U}} \ .$

$$\underline{N}^* = -(1-cT) \ \widetilde{\underline{\underline{A}}}^{-1}\underline{e} = \kappa(\underline{\underline{I}} - \underline{\underline{B}}' + \underline{\underline{B}}'^2 - \ldots) \quad \text{for } \kappa = \frac{1-cT}{1-c} \ . \qquad (9)$$

Here I have used the symbol ' to represent a general division by $(1-c)$, (for example, $a' = a/(1-c)$).

The above series expansion for an inverse matrix is allowable when

$\rho(B') < 1$ (i.e., when $\widetilde{\underline{\underline{A}}}$ is locally stable).

In Chapter 2 (Appendix 3, property 3.4) it was shown that when $\widetilde{\underline{\underline{A}}}$ is globally stable then $(1-cT) > 0$. I also argued there that when $\widetilde{\underline{\underline{A}}}$ is locally stable, $(1-cT)$ could be expected positive, again giving $\kappa > 0$.

With the knowledge that $\kappa > 0$, the probability that a single equilibrium population is positive can be arrived at as follows. Expand (9), obtaining to a third order approximation:

$$N_i^* = \kappa(1 - X_i)$$

where $X_i \simeq B_i' - \sum_j b_{ij}' B_j' + \sum_j b_{ij}' \sum_k b_{jk}' B_k'$ $\qquad$ and $B_i = \sum_j b_{ij} \ .$

Note that when m is large, the Central Limit Theorem shows that the X_i are normally distributed, essentially regardless of the particular probability distribution of the b_{ij} . (An empirical investigation shows that even when m is as small as m = 5, the X_i are approximately normal – at least close enough to give accurate feasibility predictions.)

Given that $\text{Var}(b_{ij}) = \sigma^2$,

one finds that $\langle X_i \rangle = 0$ and $\text{Var}(X_i) \simeq \gamma^2 (1 + \gamma^2 + \gamma^4)$.

Appendix 2

Estimating the Recovery Rate – R_{rec} for the GLV model.

Details are first given here concerning the method of estimating the characteristic return time T_R, for the "uniform model" described in Chapter 2. This has proved to be an adequate approximation for the GLV ensemble model (in which stochastic perturbations are added to the "uniform model"). Assume that (m-1) populations are maintained at their equilibrium level N^*, so that the dynamics of the remaining species would be given by:

$$\dot{N} = rN(1 - N - (m-1)cN^*) \qquad \text{where} \quad N^* = \frac{1}{1 + (m-1)c}$$
$$= rN(N^* - N) .$$

Then $t = \frac{1}{r} \int \frac{dN}{N(N^* - N)} = \frac{1}{rN^*} \ln\left|\frac{N}{N^* - N}\right| + \beta$ (where β is a constant).

At t = 0, let $N = \lambda N^*$ so that $\beta = \frac{-1}{rN^*} \ln\left|\frac{\lambda}{1 - \lambda}\right|$.

Define T_R so that at $t = T_R$, $N = (1 - \lambda)N^*$.

This gives $T_R = \frac{2}{rN^*} \ln\left|\frac{1 - \lambda}{\lambda}\right|$.

The constant λ was chosen to be $\lambda = 0.1$. Hence the return time T_R represents that time for a population, when depressed to 10% of its equilibrium value, to return to 90% of its equilibrium level. If, for example (as in the time developments of Figures 7 - 11), we choose $m = 10$, $c = 0.25$, and $r = 1$, the characteristic return time can be calculated as:

$$T_R = 14.28 \quad .$$

The recovery rate R_{rec} is inversely proportional to T_R and is taken as:

$$R_{rec} = \frac{1}{T_R} \quad .$$

Appendix 3

Some Details of the Time Developments

In all time developments of the GLV equations, the initial values of the populations were set to the equilibrium levels of the uniform model (see Chapter 2, Equation 8). A species extinction was said to occur whenever a population fell below a certain cut-off level. In these time-developments, the cut-off level was taken to be 0.5% of the expected equilibrium populations given by the uniform model

Difficulties arose in trying to determine the equilibrium point of attraction, whenever the mode became unfeasible. In this event, I halted the simulation and stored the instantaneous values of all populations. The GLV equations were then time-developed without introducing further disturbances, until the populations converged to an equilibrium. Once the equilibrium values were established, and that of the first species plotted, I then reset the model to the state it was in at the point of halting the simulation. The simulation was then continued.

Appendix 4

Species Extinctions in Unfeasible Systems

A model possessing an unfeasible m-species equilibrium solution will suffer species losses if time-developed.

The above assertion has been proved by Coste et al (1978) for the GLV competition model making use of time averaging techniques. The stability analysis below confirms their result for the case when the interaction matrix $\underline{\underline{A}}$ is Lyapunov stable (case a). However, when it is not (cases b and c), the analysis tells us only that the result should be expected.

a) Suppose first that the interaction matrix $\underline{\underline{A}}$ is Lyapunov stable (so that $\gamma < 0.71$ [see Chapter 2, Appendix 1]). Takeuchi and Adachi (1980) applied Linear Complementarity theory to the very general equations

$$\frac{dN_i}{dt} = N_i (k_i + \Sigma \alpha_{ij} N_j) \ . \tag{10}$$

They proved that for any set of k_i, if $\underline{\underline{A}}$ is Lyapunov stable (satisfying the Lyapunov test described in Chapter 2, Appendix 1), then (10) has a unique non-negative equilibrium point that is globally stable. Stability here is with reference to the non-negative orthant only. If the system is globally stable, populations initially in this orthant will remain there for all time and asymptotically approach the unique equilibrium point.

Recall that (10) has at most 2^m sets of equilibrium solutions, after taking into account all possible combinations of populations that might be zero at equilibrium. If there is an m-species equilibrium point, it may be found by setting the right hand side of (10) to zero,

- i.e., $$\underline{N}^* = -\underline{\underline{A}}^{-1} \underline{e} \ . \tag{11}$$

If (11) does not possess a feasible equilibrium solution, then the

theorem of Takeuchi and Adachi guarantees that one of the other $(2^m - 1)$ possible equilibrium solutions is globally stable and non-negative. Thus upon time-development of (10), one or more species will become extinct as this equilibrium is approached.

b) If $\underline{A}$ is locally stable but not Lyapunov stable (so that γ is expected to lie somewhere in the interval $.71 < \gamma < 1$), then Chapter 2 (Appendix 2) shows that $(-\underline{A})$ is likely to be a P matrix. Takeuchi and Adachi pointed out that (11) would then possess a unique non-negative equilibrium solution (however we have assumed that it will not be feasible). If this equilibrium is approached then one or more species will become extinct.

If an equilibrium is not approached, then it is difficult to accurately predict the behaviour of the model. However, since each of the other domains of attractions must have an equilibrium with at least one "negative" population, then (as Chapter 2, Appendix 6 shows), instability is expected to arise. These "negative" populations were predicted to result in one or more species exploding, so that other species within the community are competitively excluded.

c) If $\underline{A}$ is unstable (i.e., $\gamma > 1$), so that $(-\underline{A})$ is not a P matrix, then again it is difficult to accurately predict the behaviour of the model. Nevertheless, because the only m-species equilibrium is unfeasible, if any equilibrium is approached, a species extinction must result. One would expect instability to arise because:

i) $\underline{S}$ inherits the instability of the interaction matrix $\underline{A}$;

and/or

ii) all the domains of attraction are likely to have equilibria with one or more destabilizing "negative" populations.

The above stability investigation can be summarized as follows:

If the m populations (not necessarily at equilibrium) of an unfeasible system reside at any time in the positive orthant, and the interaction matrix is Lyapunov stable, then species extinctions will eventually occur.

If, however, it is not Lyapunov stable, extinctions will still be expected to occur because of the destabilizing properties of "negative" equilibrium populations and/or the instability of the interaction matrix.
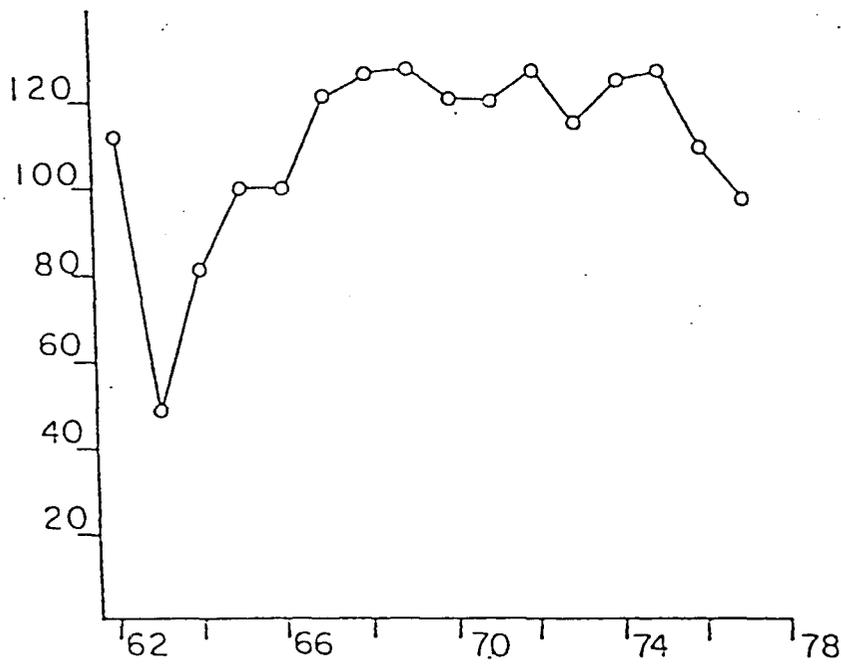
Figure 1a. The population density of Song Thrushes in English farmlands in the years 1962-1978, on a relative scale where the density in 1966 was set to 100. (Reproduced from Pimm 1984, p.410 .)
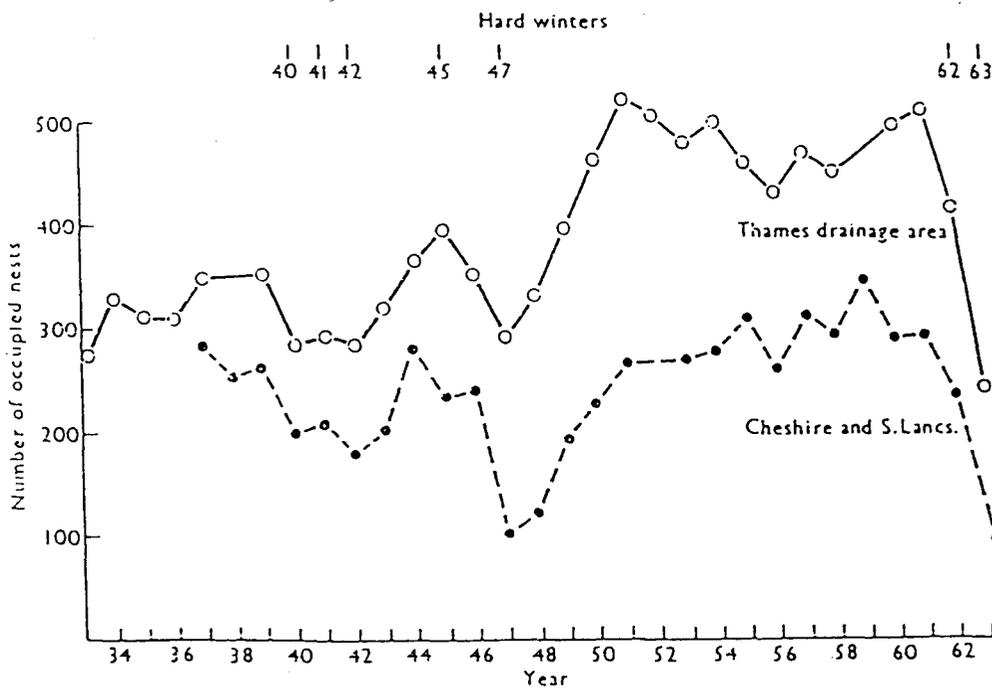
Figure 1b. Number of breeding pairs of Heron, *Ardea cinera*, in two parts of England, 1933-63. (Reproduced from Lack 1967, p.4 .)
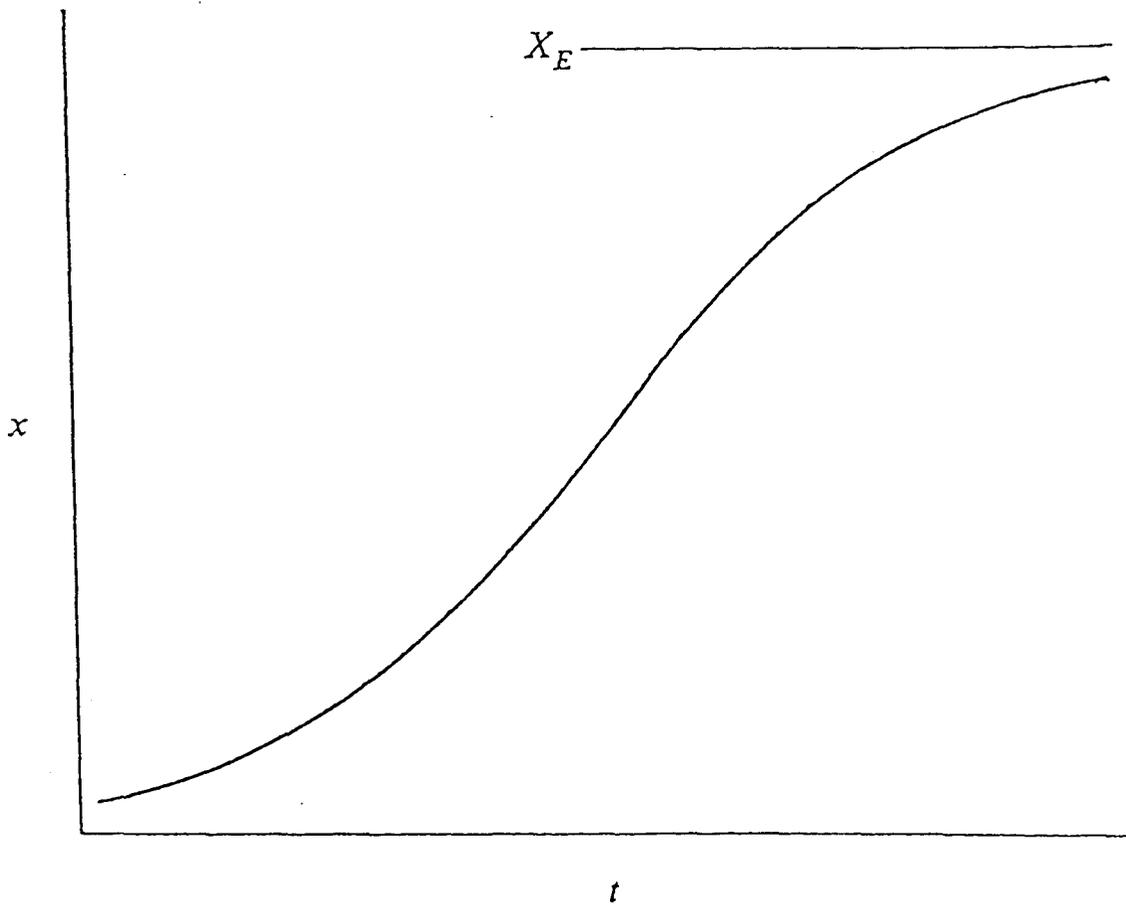
Figure 2.   Population growth as modelled by the logistic equation. The population x asymptotically approaches the equilibrium X_E. (Reproduced from Maynard Smith 1971, p.42 .)
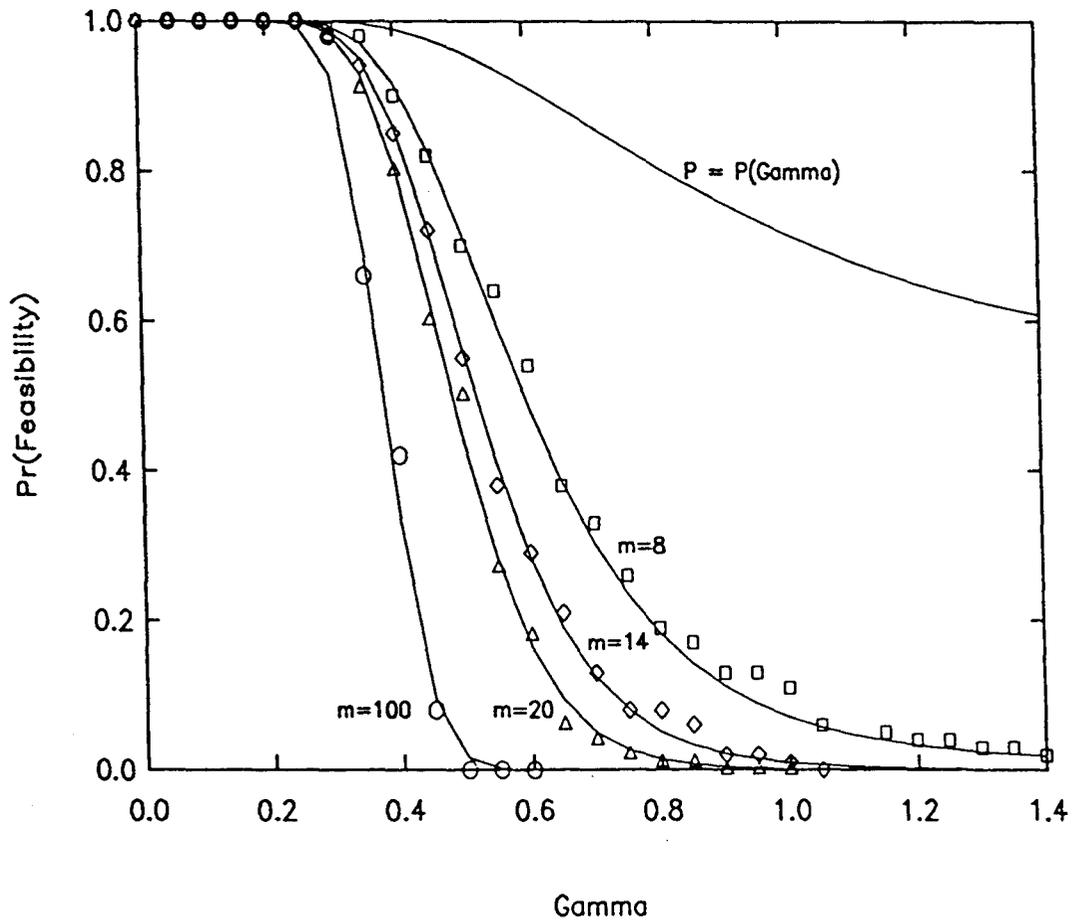
Figure 3. Feasibility predictions for m-species communities with C = 0.25. The theoretical predictions are given by the continuous curves. Each probability marked by a square, circle etc., was obtained from 500 Monte Carlo runs (as discussed in the text).
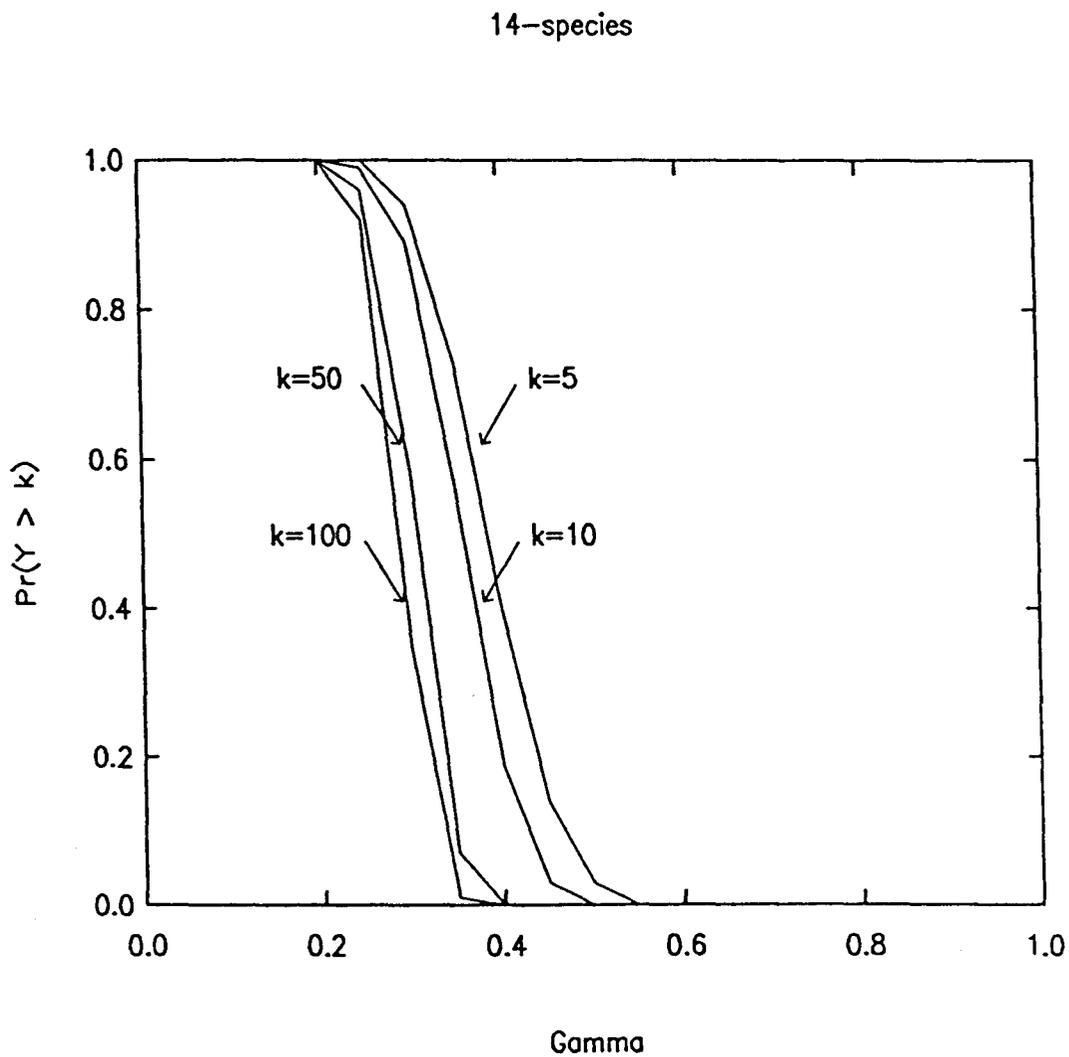
14-species

Figure 4. The probability a 14-species community survives more than
k disturbances, is plotted against Gamma.
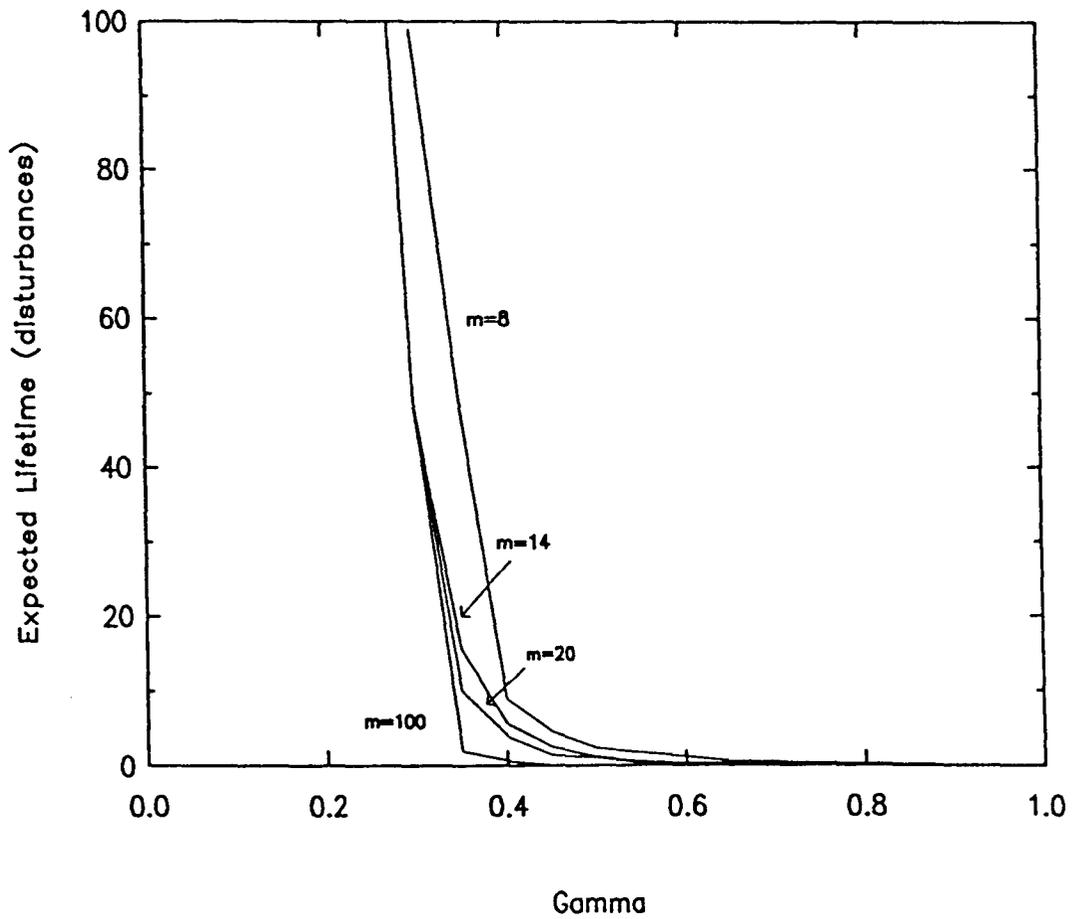
Figure 5. The expected lifetime of an m-species community (expressed as the average number of disturbances it can survive), plotted against Gamma.

14—species
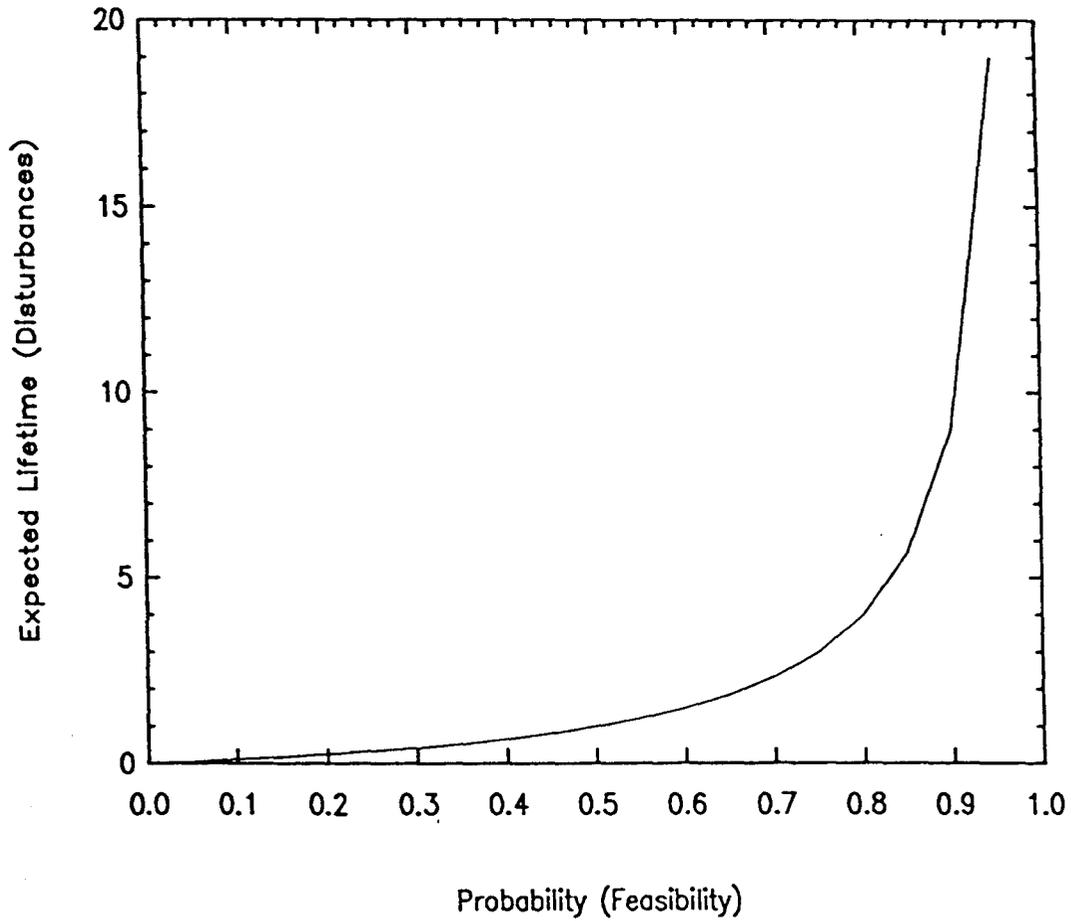
Figure 6. The expected lifetime of a 14-species community (expressed as the average number of disturbances it can survive), plotted against its probability of feasibility.

RDR = 1.00
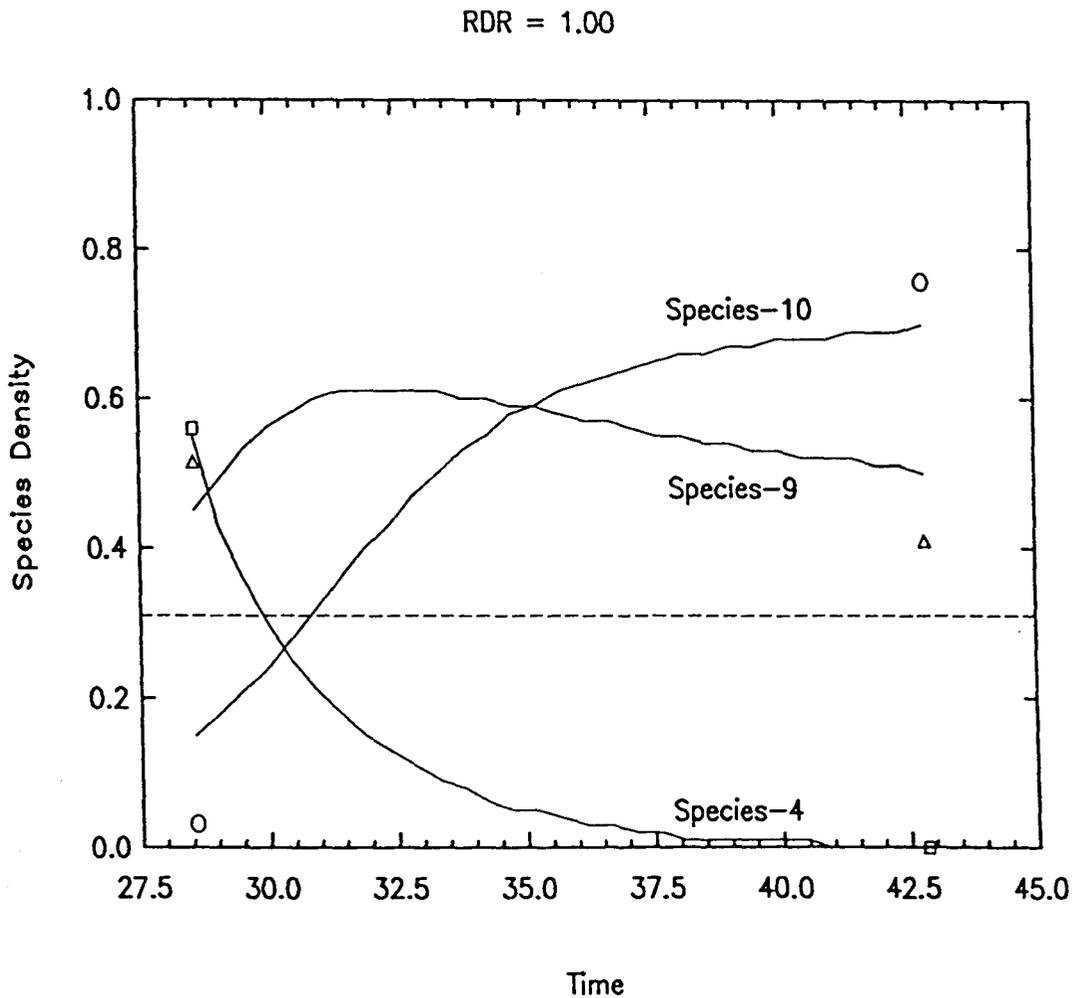
Figure 7. 10-species, Gamma = 0.75, c = 0.25.

$\square$ = equilibrium level of species-4.

$\triangle$ = equilibrium level of species-9.

o = equilibrium level of species-10.

$- - - = < N_i^* >$, the expected equilibrium level.

A structural disturbance occurs at $t = 28.6$ so that species-4 becomes attracted to the new equilibrium level $N_4^* = 0$. The other species similarly track their new equilibrium levels.
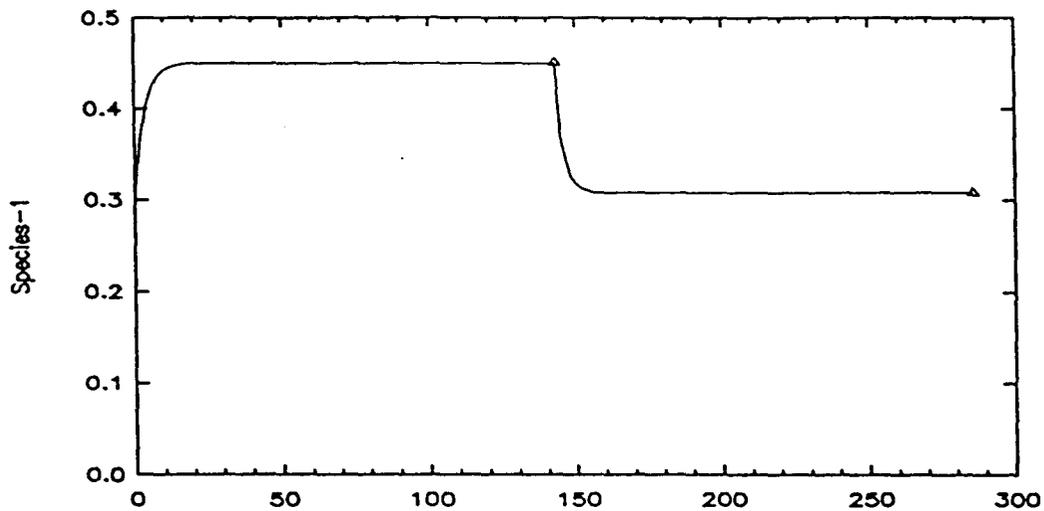
Figure 8a.   RDR = 0.1   Time
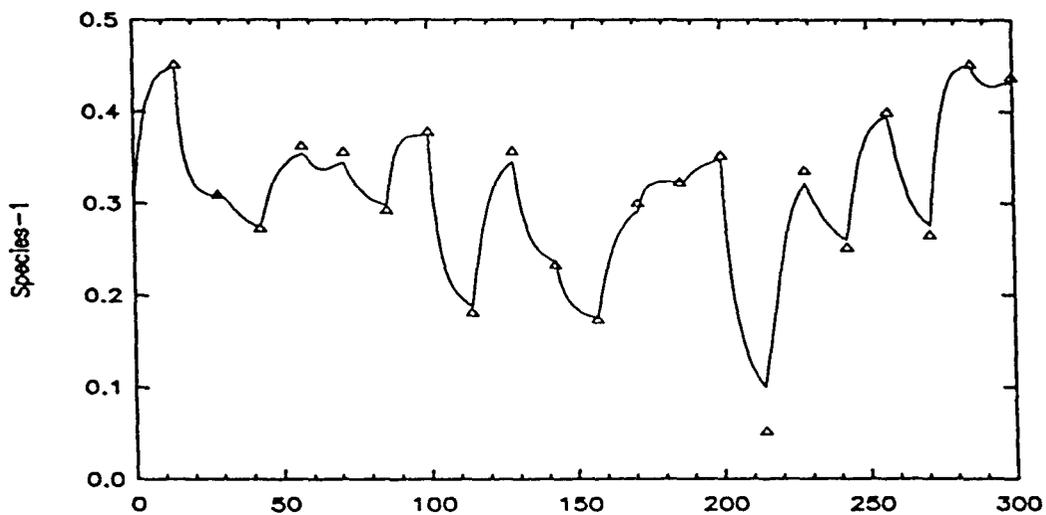
Figure 8b.   RDR = 1.0   Time
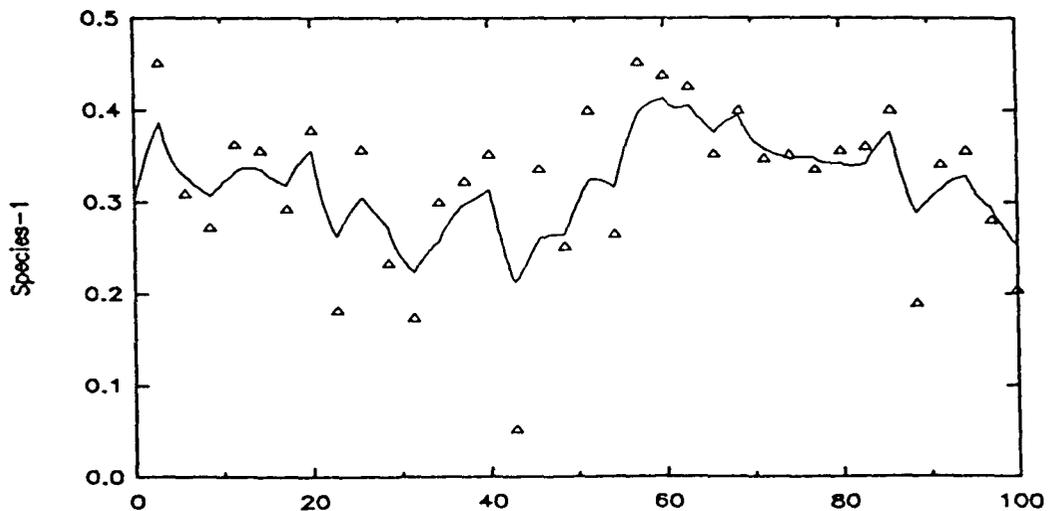
Figure 8c.   RDR = 5.0   Time
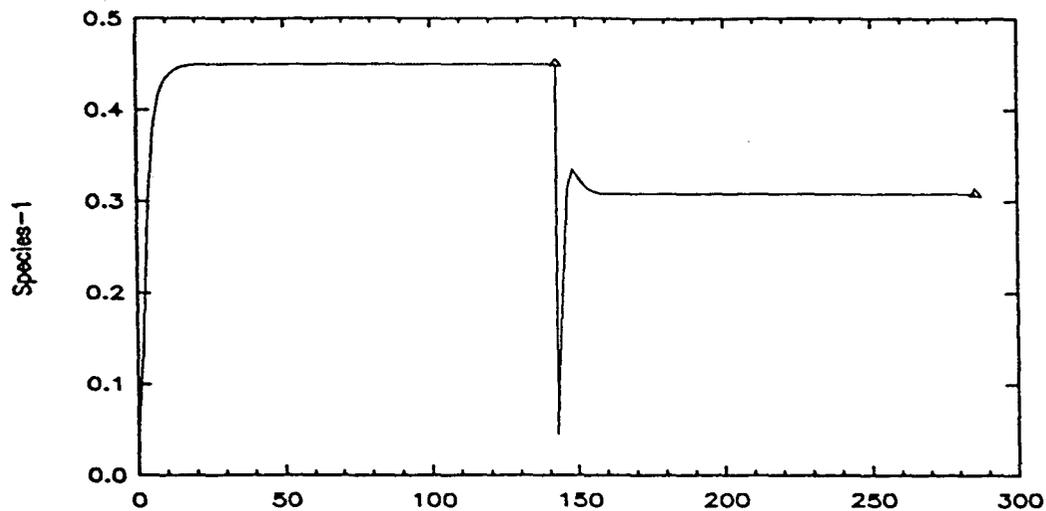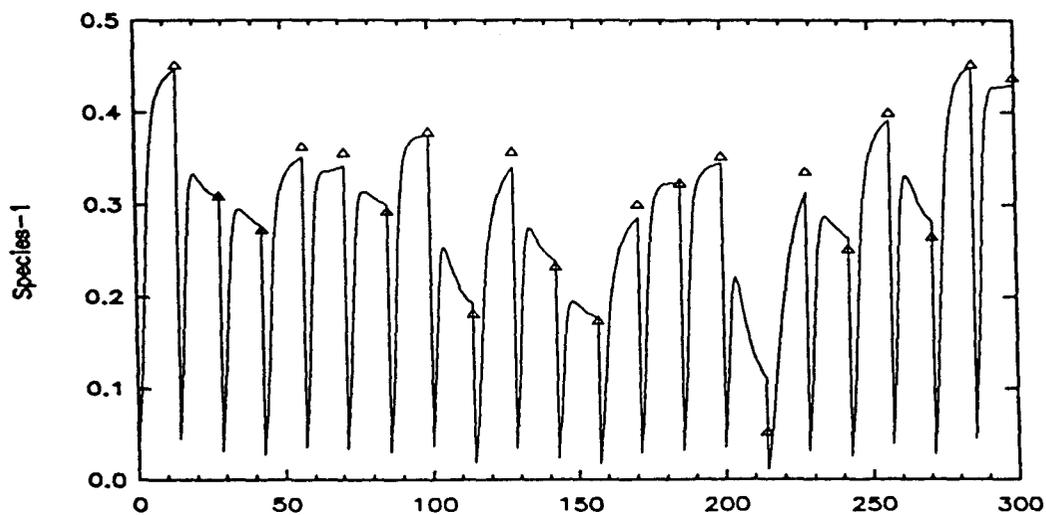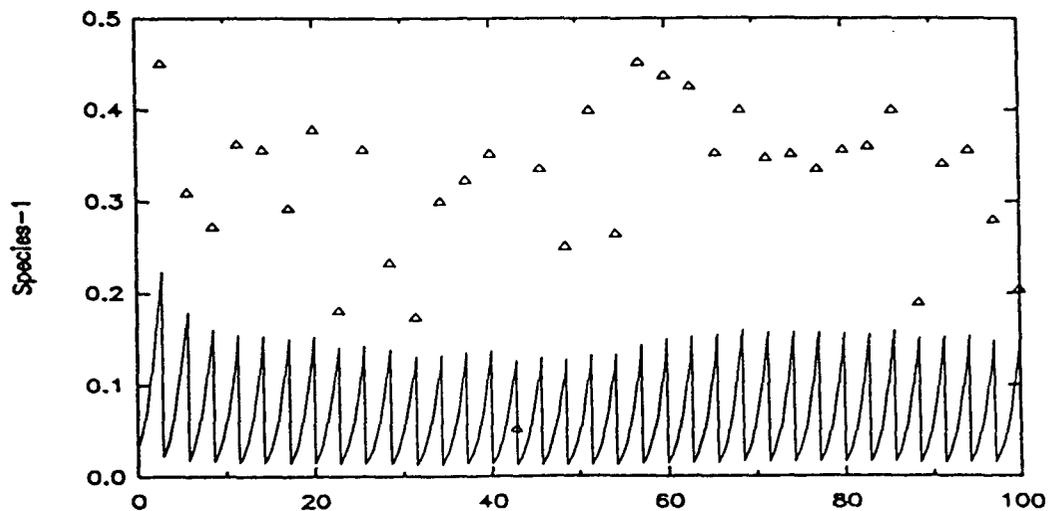
10-species, Gamma = 0.25, C = 0.25

Figure 9a.   RDR = 0.1

Figure 9b.   RDR = 1.0

Figure 9c.   RDR = 5.0

10-species, Gamma = 0.25, C = 0.25, Popn. disturbance = 90%
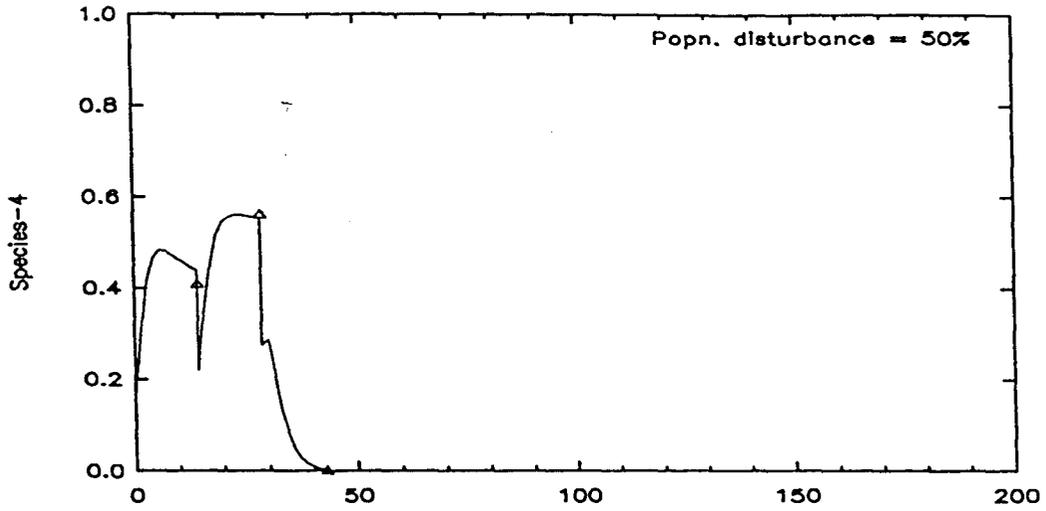
Figure 10a.   RDR = 1.0
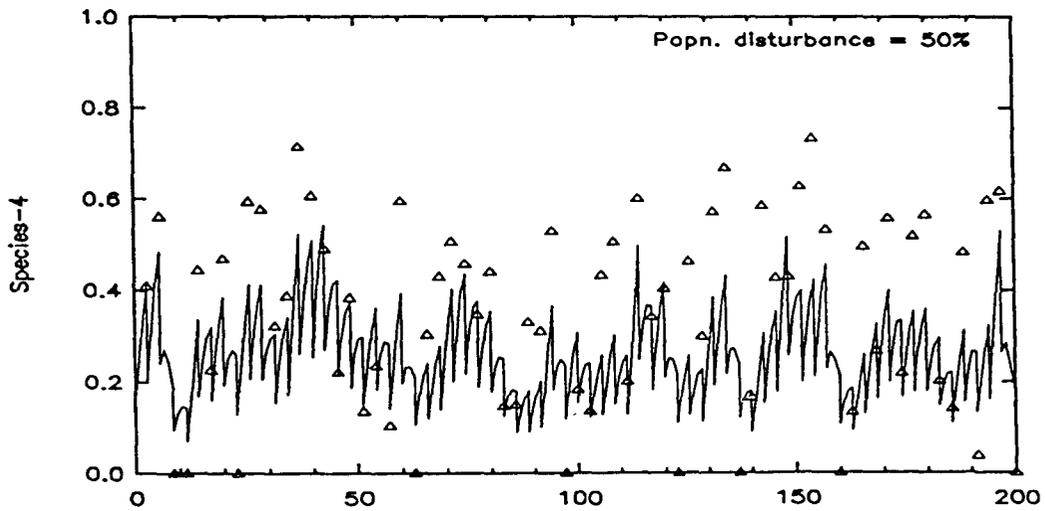
Figure 10b.   RDR = 5.0

Figure 10c.   RDR = 8.0
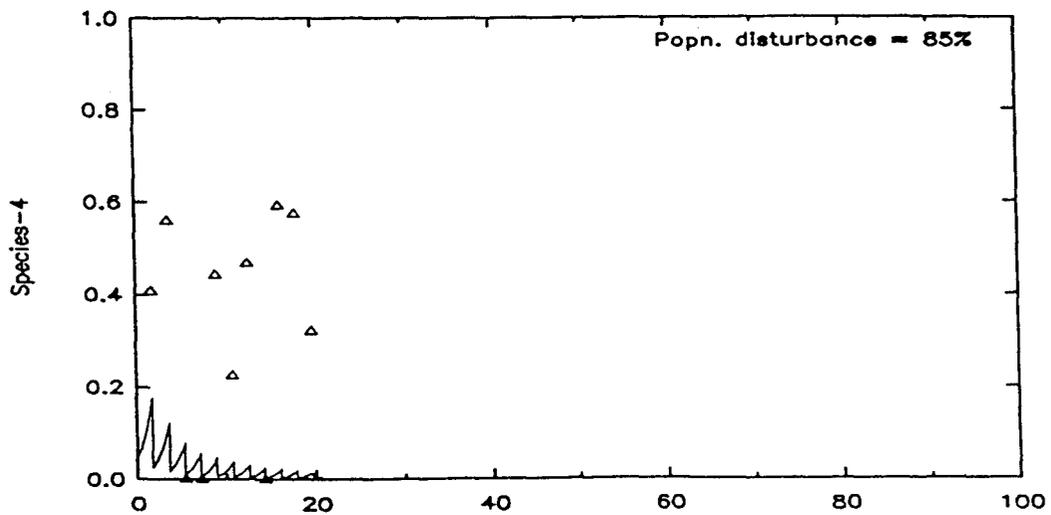
10-species, Gamma = 0.75, C = 0.25
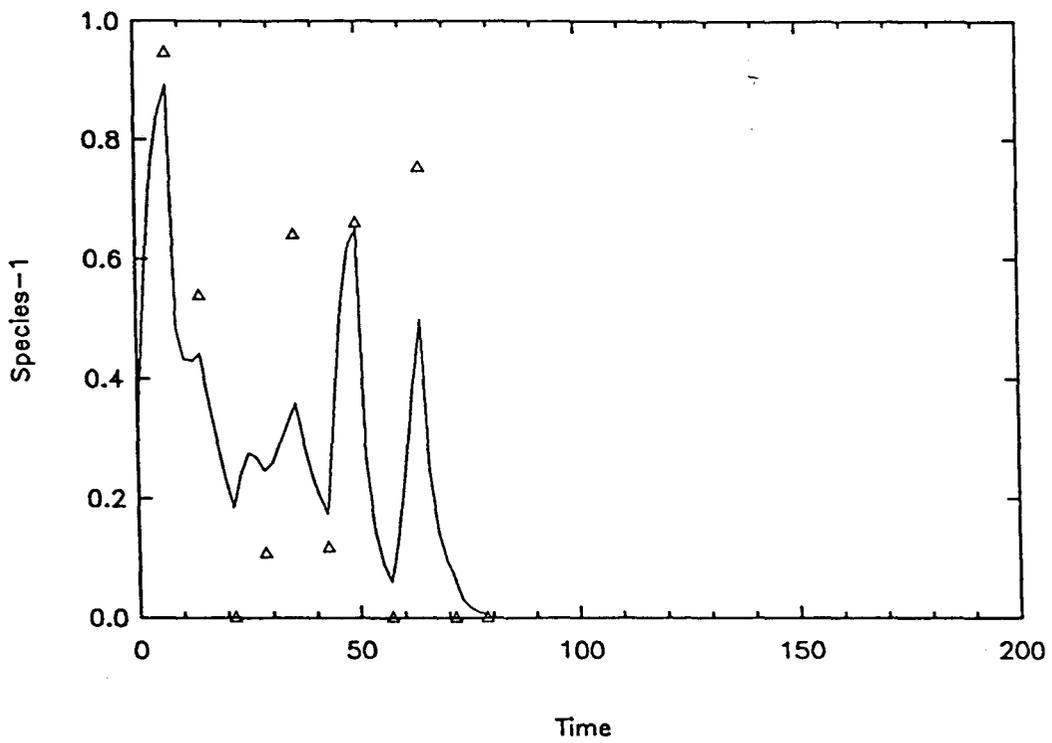
Figure 11a.   RDR = 2.0
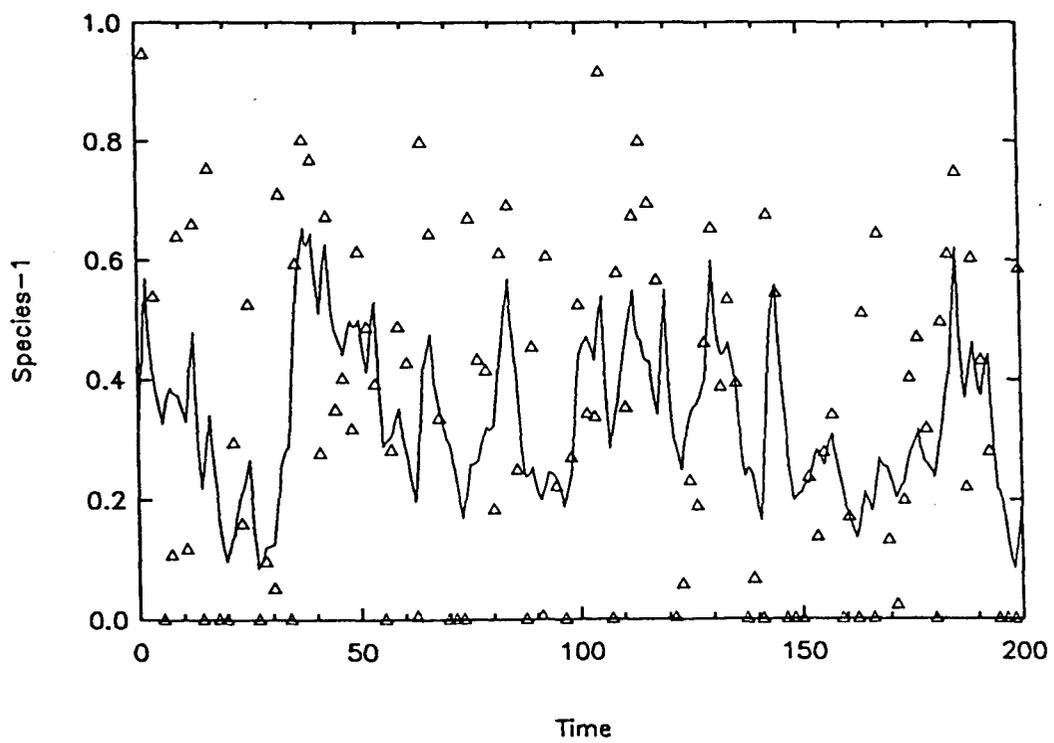
Figure 11b.   RDR = 8.0

10-species, Gamma = 0.9, C = 0.25

Chapter 4

Coexistence in Multi-species Communities

§1 Coexistence is Attained From a Multiplicity of Factors

A central question lying at the core of much ecological theory is: what is it that decides whether an assemblage of species can coexist? As discussed in Chapter 1, competition has frequently and sometimes uncritically been pointed to as an answer, if not the answer. Its basic premise, the competitive-exclusion principle, became in a somewhat paradoxical manner the foundation of a theory to explain coexistence. Competition came to be seen as a source of stabilizing negative feedback, and so appeared as an attractive theory of coexistence to those trained to think in terms of a "systems approach".

However, the stabilizing negative feedback provided by competition is by no means the only mechanism that might account for coexistence. Jurgen Jacobs (1979) made this clear when attempting to explain how two species of waterfleas could have coexisted for at least fifty years. Jacobs found ten factors, all of which seemed to be contributing in some way to the maintenance of long-term coexistence. These included environmental conditions, longevity of individuals, ability to spread risks, colonization patterns, evolutionary changes, predation, dispersal, and indirect effects. "None of them needs to be permanently effective but each may be important under certain circumstances" (p.404). This led him to realize that, rather than a single explanation, what is needed are "general theories about the coaction of many basic principles" (p.403).

The task of modelling or theorizing on the simultaneous effects of multiple-coaction principles would be enormously difficult. Instead, the model outlined in Chapters 2 and 3 is used to provide insight into - not just competition, but a variety of coexistence mechanisms. The

simplicity of the model, and the generality of the results obtained, make this methodology seem promising. It appears to lay the framework for an integrated approach as suggested by Jacobs.

§2 Temporal Variation may aid Coexistence

§2.1 The Non-equilibrium View

Conventional competition/equilibrium theory accounts for species diversity by way of niche differentiation - i.e., each coexisting species avoids competitive interactions by virtue of its differences in niche. More recently, however, there has been a renewed interest in the belief that environmental variability is a major factor governing community diversity (Chesson and Case 1986, Connell 1978, Huston 1979).

Hutchinson (1961), in his study of "The Paradox of the Plankton", posed the problem of "how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials" (p.137). He believed that in the plankton communities he observed, competition was "likely to be extremely severe", since there were sufficient periods "of striking nutrient deficiency" (p.137). If the principle of competitive exclusion operated, it would be expected that only the best competitor survive, outcompeting all others. The paradox then, was why such large species diversity occurred in the plankton community. Hutchinson argued that a species-rich community could be achieved when external environmental variations interrupted the exclusion process and altered competitive rankings amongst species. If these environmental interruptions occurred within the time required for competitive elimination of a species, exclusion would be prevented and diversity maintained.

Hutchinson's explanation was designated the "gradual change hypothesis" by Connell (1978). In the example of the plankton lake communities discussed by Hutchinson, seasonal variations in light and temperature constantly alter the intensity of competitive interactions. These variations, which are usually only gradual, may never allow any particular competitor to dominate the community, and thus they act to prevent competitive exclusion. Even though these disturbances are not of great intensity, they appear to be of major importance for the achievement of long term coexistence.

Eddison and Ollason (1978) confirmed Hutchinson's conjecture under laboratory conditions. A control community of freshwater ciliate protozoa kept at constant temperature was compared to another community under fluctuating temperature conditions. The results indicated that higher species the diversity was achieved in the latter community experiencing the greater environmental variability.

Connell (1978) extended Hutchinson's theory and put forward "the intermediate disturbance hypothesis". The hypothesis suggests:

a) that when the disturbance rate is not appreciable, diversity will be minimal. This is because the community's superior competitor, or the species that has proven to be most resistant to ongoing perturbations, will gradually exclude all other organisms and reduce diversity.

b) that at slightly higher (or intermediate) frequencies and intensities of disturbances, greater diversity should result. "Disturbances interrupt and set back the process of competitive elimination, remove occupants that are competitively excluding further invaders" (p.1303). New species will find it possible to invade and establish themselves, thereby conserving the composition and maintaining the diversity of the community.

c) that those disturbances at the extreme end of the frequency and intensity scale can reduce community diversity considerably. These disturbances severely damage or kill organisms, depress population levels, and deplete resources. At this end of the scale, some species might be eliminated.

Pieced together, the hypothesis predicts diversity to be maximal at intermediate scales of disturbance (see Figure 1a).

Connell (1978) provides a fascinating account of coral reef communities at Heron Island, Queensland. In 1967 and 1972 hurricanes destroyed a good deal of live coral. The amount destroyed depended on the coral's exposure to the storms. The percentage coral cover over an area was taken to be an indicator of disturbance. Connell plotted this against species diversity, as reproduced in Figure 1b. The graph displays the "humped" species diversity curve that is so characteristic of the "intermediate disturbance hypothesis".

Connell found the "intermediate disturbance hypothesis" a better explanation for the high species diversity of tropical rain forests and coral reefs, than the usual equilibrium arguments invoked so often (particularly for tropical communities). He argued that environmental calamities such as windstorms, lightning strikes, floods or herds of predators play major roles in maintaining these complex communities.

§2.2 Tilman's Equilibrium Approach

Tilman (1982), on the other hand devised a competitive-equilibrial model that accounts for diversity in variable environments. Rather than viewing disturbance as a process which periodically interrupts competition by continually depressing populations below equilibrium, he considered it as one that controls the availability of resources being competed for. The hypothesis is most appropriate for space-limited

communities as found for example in marine intertidal zones and amongst stream invertebrates.

Because of their immobility, sessile organisms are often required to compete for space. Although space is not actually consumed it has many properties similar to a limiting resource, if only by providing the necessary "home" essential for continued growth. As well, space indirectly provides access to light, nutrients and water. Disturbances have the capability to open up new sites previously inaccessible to species. Tilman cites examples of this phenomenon in the works of:

- Dayton (1971) who describes wave-caused disturbances;

- Horn (1971), Sprugel and Bormann (1981) who describe wind-caused tree falls;

- Garwood, Janos, and Brokaw (1979) concerning landslides.

In all the above examples, disturbance was the mechanism whereby new sites were opened up. Since disturbance rate appeared a good indicator of the supply rate of space, Tilman found it plausible to construct an equilibrium model in the following way:

a) Suppose a community experiences environmental variation only on a small scale, and the competitive rankings are such that the strongest competitors for light and space exclude all others. Diversity would then be at a minimum.

b) Upon greater disturbance, those competitors inferior in getting open space and light, but superior in obtaining some other resource, have a better chance of establishing themselves - as openings previously unused become available. In these new sites, they maintain their superiority for the particular resource they are best suited to, and become firmly established there. Moderate disturbances, by opening up resources previously unobtainable, can in this way allow a highly diverse community as a direct result of competitive equilibrium in a

heterogeneous environment.

c) With further increases in disturbance, those competitors that have managed to establish themselves on a patch, can monopolize a particular resource - one that the strong space-and-light competitors can now only weakly compete for. Once this resource is reduced below the level required for the survival of the latter organisms, then they will be excluded and diversity reduced.

The above equilibrium outlook of Tilman utilizes competition theory as an alternative to Connell's non-equilibrium approach. Effectively, intermediate disturbances give rise to spatial heterogeneity and create optimal division of resources amongst species so that coexistence may be attained. The approach is based on the differential requirements of competitors which may be best fulfilled under heterogeneous conditions. Importantly, like the non-equilibrium view, it predicts maximum species diversity at an intermediate level of disturbance.

The above discussion has centred upon communities in which open space acts as a limiting resource. Such is not the case for terrestial plant communities - yet, as Tilman shows, the conclusions of the model are equally applicable. Plant communities depend greatly on the limiting resource of light. Disturbances indirectly supply light whenever individual plants are destroyed or removed, since new sites, and thus areas in which light can be procured, are opened up. In the same way extra nutrient supplies become available. Since, in plant communities, disturbances can indirectly create heterogeneity in resources, the characteristic species-diversity hump should be expected.

Tilman suggests that the resource-based equilibrium theory is generally applicable to communities in which disturbances create heterogeneity in any types of resource, and not just space. It also

explains the "paradox of enrichment" discussed by Rosenzweig (1971). By studying six different model-communities, Rosenzweig described how coexistence was only possible, when available nutrients were at particular optimal levels. Paradoxically, schemes that attempt to enrich an ecosystem, by increasing certain nutrients beyond these optimal levels, were predicted to end in catastrophe.

If predation is taken to be a form of disturbance, Tilman finds his theory of relevance to the work of Connell (1978) and Lubchenco (1978). Both of the latter ecologists found species richness to be highest at intermediate levels of disturbance. Connell observed this in coral communities, whilst Lubchenco identified the phenomenon in algae communities.

Not only are disturbances capable of indirectly increasing availability of resources, they are able to introduce them directly. For example, Sousa (1984) documents cases where nutrient-rich ash becomes available because of forest fires. Nutrients also become available when they are leached from rotting trees that have fallen. In both these cases, disturbance is responsible for introducing the nutrients.

Strong (see Pianka 1978, pp.298-299) pointed out that some organisms may themselves introduce disturbances, and thereby open up new sites. One example of this phenomenon is the epiphyte loading of trees in the Tropics. Epiphyte loads can build up to such an extent that they cause tree falls, which in turn may open up patches. Organisms that can so create spatial heterogeneity promote community diversity.

§2.3 Gradation of Competitive Abilities

Both the equilibrium and the non-equilibrium views above suggest that the competitive interactions of species within a community change considerably with environmental variation. Species that persist in relatively unperturbed habitats are predicted to be stronger competitors than those in harsher, or more heterogeneous environments, that reduce and slow down the exclusion process.

Wilson and Keddy (1986) made a study of plant "Species Competitive Ability and Position Along a Natural Stress/Disturbance Gradient". In their experiment, the amount of exposure to wave action was taken to be the environmental disturbance gradient. The exposure gradient was characterized "at one end by wave-washed, sparsely vegetated, nutrient-poor beaches and at the other by sheltered, densely vegetated, nutrient-rich bays" (p.1236).

Competitive ability was found to be significantly correlated with position along the environmental gradient. Species in low disturbance habitats were found to have high competitive abilities whilst those in stressful and exposed environments had low competitive abilities. Wilson and Keddy note that their study is the only one they known of, which tests this proposed relationship in multi-species communities. Given that stress and disturbance are similarly manifested in other environments, they suggest that their findings would be equally applicable in other communities.

§2.4 The Model

In real situations, the state of a community experiencing environmental variations, undoubtedly lies somewhere between the two extremes of Tilman's equilibrial community and Connell's randomly interrupted competitive community. The ensemble model presented in

Chapters 2 and 3 is appropriate for most circumstances anywhere along this gradient.

The model can represent those situations in which:

a) disturbances, either by creating spatial heterogeneity or depressing populations below their carrying capacities, weaken the exclusion process and therefore lower the average level of competition. The ensemble model expresses increasing disturbance by a reduction in the magnitude of c, the average intensity of competition. This accords with the study of Wilson and Keddy (1986);

b) at high disturbance rates, where communities usually have a mean stength of interaction that is weak, overall, differences in the competitive abilities of species can be a critical factor. For example, under conditions of heavy disturbance, chance events might deplete certain resources and induce severe competition between particular species that normally had little effect on one another. This might result in one or more species extinctions. To model these situations of high disturbances, the variation v in competition coefficients is taken to be large, indicating that some interactions can be intense while others comparatively negligible.

c) communities track environmental changes more slowly when the frequency of disturbance increases (see Chapter 3).

Frequency of Disturbance:	Low	Intermediate	High
Mean interaction strength - c:	High----------------------------------Low (species exclusions)		
Variation in interactions - v:	Slight--------------------------------Large (species exclusions)		
γ:	Maximum --------→ Minimum ---------→ Maximum		

Table 1:

The variation in the last entries (γ) of Table 1 can be understood as follows. Recall that (cf. Chapter 2, §2.4):

$$\gamma = \frac{\sqrt{(m-1)}\,\sigma}{1-c} \qquad \text{and} \qquad \sigma = \frac{cv}{\sqrt{3}} \ .$$

Making use of points a) and b) above, Table 1 shows how γ varies with the frequency of disturbance as a result of changes in c and v. The parameter γ will be considerably large at very low frequencies (because the community's mean strength of interaction competition can be high and $\gamma \sim c/(1-c)$) and at very high rates of disturbance (where, although c is small, the variation in interactions can be outstanding and $\gamma \sim v$). It is at intermediate frequencies when γ achieves its minimum value (because of moderate values in both c and v).

Consider first, those ecosystems that tend to remain nearly always close to equilibrium, because they possess a relatively fast recovery rate at most frequencies of disturbance. We saw in Chapter 3 that the persistence of these communities depends mainly on their ability to survive structural disturbances. In terms of the model's parameters, this constrained γ to be less than the critical value $\gamma = 0.4$. According to Table 1, γ is small only at intermediate disturbance rates. Hence it is at these rates where coexistence will be most likely, just as the intermediate disturbance hypothesis argues.

For communities that do not possess fast recovery rates (and may therefore be rarely observed at an equilibrium), allowance must also be made for the variable tracking rates expected when the frequency of disturbance changes. In Chapter 3 it was found that the slower the tracking rate a community had, the better it was able to average out and thus ameliorate dangerous disturbances. It was also shown that tracking rates become slower as the frequency of disturbance increased. Taken together, these effects predict that the higher the frequency of

disturbance, the slower the tracking rates will be, and the more likely populations will be able to survive. However, at very high disturbance levels, populations can be severely depressed to such an extent, and feasible states can be so rare, that extinctions are bound to occur. This means a community will have the best chances of survival at intermediate rates of disturbance. We saw this in Chapter 3 (§7.2) where the model (in such a non-equilibrium setting) was shown to confirm the intermediate disturbance hypothesis because of these reasons.

§3 Environmental Variability Limits Niche Overlap.

§3.1 The Conjecture.

Ecologists have often attempted to deduce how "similar" or "identical" competing species can be, and still coexist stably. The similarity of two species is often specified by niche overlap - i.e., the degree to which a common set of resources is shared between them. High overlap is likely for a pair of species that have almost identical requirements. The ratio d/w between interspecific niche separation (d) and intraspecific niche breadth (w), has been used as a measure of niche overlap, since it can indicate the degree two species share a common set of resources (see May 1974). If niche overlap is small (i.e., d/w is very large), then the two species are taken as dissimilar and predicted to compete only weakly. When there is almost complete overlap between two species (i.e., $d/w \rightarrow 0$) and resources are limiting, then intense competition would be predicted to occur.

For species that are too alike, and competition is strong, the Gause competitive-exclusion principle states that coexistence is impossible. The term "limit to similarity" has been used to denote the maximum similarity possible for species to maintain stable coexistence. One controversial question arising concerned the influence environmental disturbances had, if any, on this limit.

Klopfer and MacArthur (1961), amongst others, believed that comparing the species-rich tropics with the less diverse temperate regions, might shed light on the matter. It appeared to them from examining data on avian communities that an increase in the similarity of coexisting species, and a greater niche overlap, was to be found when going from the temperate zone to the tropics. This increase in niche overlap could only occur, they maintained, if "climatic stability is such as to assure a fair degree of stability in the availability of the required food and perch sites" (p.225) - i.e., in climates similar to the tropics. They defined stability to be high whenever there was an absence of frost, and the ranges in temperature and rainfall were suitably low. If the tropics permitted greater niche overlap, as observed data indicated, then this might explain the region's high species diversity.

Simpson (1964) reviewed Klopfer and MacArthur's work and found their results inconclusive. Moreover, Simpson's own studies, on the species densities of mammals in North America, indicated that the degree of niche overlap was a relatively unimportant factor in determining the apparent species-diversity gradient. However, the conjecture reappeared again in the work of Miller (1967) and MacArthur (1971), who deduced that "in the real world environmental fluctuations will put a limit to the closeness of species packing compatible with an enduring community, and that species will be packed closer or wider as the environmental variations are smaller or larger" (quoted from May and MacArthur 1972 p.1109).

In order to get to the bottom of these conflicting opinions, MacArthur (1972), and May and MacArthur (1972) reviewed the many estimates of d/w reported in the literature. They noticed that for many different species, over a wide range of environments (as long as they

were not extreme like, e.g., the Arctic), d/w remained roughly in the interval 1 - 2. This suggested that there was a limit to niche overlap in the natural world which is insensitive to the degree of variation so long as it is not too severe.

§3.2 The May and MacArthur Models

One-Dimensional Continuum of Resources

May and MacArthur (1972) then constructed a GLV competition model in order to simulate the effect. Initially the model was based on species all having a one-dimensional continuum of resources with Gaussian utilization functions. The interaction matrix $\underline{A}$ was shown to have entries

$$\alpha_{ij} = -c^{(i-j)^2} \qquad \text{with} \qquad c = \exp(-d^2/4w^2) \ . \qquad (2)$$

A stability analysis of the model indicated that there is a significant limit to niche overlap in variable environments, which is insensitive to the degree of environmental fluctuations as long as they are not too severe. May (1974) found the results of the model quite robust, and appropriate for a wide range of resource-spectrum shapes as well as a variety of shapes for the resource-utilization functions. In contrast, the model in a deterministic setting showed no indication of a limiting similarity.

McMurtrie (1976) extended the May and MacArthur model by allowing for non-uniform niches. The constraint that all niches have the same overlap ratio d/w was relaxed so that the disparity of niches normally found within a community could be incorporated. In order to do this, McMurtrie added a stochastic component to the model's interaction coefficients, in much the same way as done in the ensemble model of Chapter 2. He showed that: "The substance of the conclusions set forth by May and MacArthur stands firm" (p.96).

m-dimensional Continuum of Resources

In order to model a community in which each species competes equally for the same resources in an m-dimensional resource space, May (1974) took the interaction matrix to have all entries:

$$\alpha_{ij} = -c \text{ (for } i \neq j) \quad \text{and} \quad \alpha_{ii} = -1.$$

This is none other than the uniform competition model described in Chapter 2. May found that for this model-community, where the resource partitioning is multi-dimensional, the limit of niche overlap was no longer independent of environmental fluctuation (as parametrized by σ). Instead the limit d/w ~ σ, so that a greater limit to niche overlap would be expected in regions of greater constancy. He noted that this was contrary to the result obtained from a one dimensional resource spectrum, where niche overlap was limited, and largely independent of environmental fluctuation.

Schoener (1974) drew attention to the point that resource partitioning generally occurs along several dimensions. This, together with the above finding of May's for models with multi-dimensional resource partitioning, led Abrams (1975) to assert that the May and MacArthur result was "in most cases.....not applicable" (p.370), and that environmental fluctuations might not set a limit to niche overlap. By using the feasibility results of Chapter 3, I will explore this particular problem in depth below.

§3.3 Limiting Similarity Derived by Feasibility Studies.

Fast-Tracking Communities - RDR < 1

As explained in Chapter 3, a community with a low Relative Disturbance Rate (RDR < 1) is fast-tracking and spends much of its lifetime close to equilibrium. Hence the existence of such a community depends crucially on whether it always possesses a feasible equilibrium point. May (1974) and Abrams (1975) attempted to find a limiting

similarity in models of competition systems by calculating feasibility requirements, but because of the tedious algebra involved, they were not able to do so for communities with more than three species. An understanding of larger systems was instead obtained by stability analyses.

It was shown in Chapter 2 that feasibility was a more crucial factor than stability. Thus any limits to similarity found by a stability analysis, might well be improved upon by a study of feasibility. Armed with the analytic feasibility predictions formulated in Chapter 3, which were shown to be accurate for large model-communities, it is now possible to methodically determine whether (on the basis of feasibility) the model is limited by niche overlap. A neat theoretical and affirmative solution will now be provided.

To begin, it is worth re-examining the lifetime curves in Chapter 3 (Figures 4 and 5). One sees that there is a critical value of γ, at which the probability that an m-species community will persist, abruptly changes from 1 to 0. This critical value was termed γ_{crit} and approximated as $\gamma_{crit} \simeq 0.4$.

Following Turelli (1978), I will begin by taking the "degree of niche overlap" to be a synonym for intensity of competition. May and MacArthur's result may now be obtained qualitatively. High niche overlap means that $c \simeq 1$. But upon examining the definition of γ (Chapter 2, Equation 12), one sees that $\gamma \rightarrow \infty$ as $c \rightarrow 1$. Thus for models in which species have high niche overlap, the critical value of γ is greatly exceeded, and no system will be feasible. Hence γ_{crit} sets a limit to niche overlap.

The limiting similarity can be calculated by noting that feasible systems are only possible if $\gamma < \gamma_{crit} \simeq 0.4$.

This gives $\gamma = \dfrac{\sqrt{(m-1)}\ vc}{\sqrt{3}(1-c)} < \gamma_{crit}$ as the criterion of feasibility,

or upon rearrangement, $v < \dfrac{\sqrt{3}\ \gamma_{crit}}{\sqrt{(m-1)}}\ (\dfrac{1}{c} - 1)$. $\qquad$ (3)

Here v is the maximum possible fractional change in a species' interaction coefficient from its mean c (as discussed in Chapter 2, §2.3).

By using inequality (3), and by making use of the formula for the competition coefficient given in (2), the limiting value of d/w can be found for any given variation v. Figure 2a plots graphs of v versus the limiting value of d/w, for systems of size m = 8, 14, 20. From these graphs, the results of May and MacArthur can be recovered since d/w is always greater than 0.5 even if variations are as small as 2% .

Being realistic, it would hardly be plausible, to suppose an ecosystem whose species interactions stayed rigidly constant over time. It is thus quite conservative to take the minimum value of v as 5% . In the Table below the estimated values of d/w are given when v = 5% and v = 80% .

m	v = 5% Limiting d/w	v = 80% Limiting d/w
8	0.8	2.4
14	1.0	2.6
20	1.0	2.7

Table 2

The model demonstrates that feasibility does set a limit to the degree of niche overlap. It predicts that no feasible system will be found when d/w is any less than the limiting value. As Table 2 makes

clear, the limiting value of niche overlap for these fast-tracking communities lies in the interval 0.8 - 2.7 (when interactions vary from 5% to 80%).

Slow-Tracking Communities - RDR > 1

Suppose now, that disturbance rates are relatively high so that the Relative Disturbance Rate RDR > 1 (see Chapter 3). A community in these conditions would be "slow-tracking". The conventional view is that environmental disturbances do not permit niche overlap to be large, or species to be too similar. We will now see that this is not the case when RDR > 1. It turns out that a higher disturbance rate can permit greater niche overlap.

To understand this, recall from Chapter 3 that slow-tracking communities are able to average out traumatic disturbances so that species extinctions are much less likely to occur. Figure 10b of Chapter 3, for example, displays a community with $\gamma = 0.9$; this is well above γ_{crit}, yet the community manages to persist because it is slow-tracking. Thus, when RDR > 1, one can no longer take $\gamma_{crit} \simeq 0.4$. Instead, γ_{crit} will increase with the rate of disturbance, and permit greater niche overlap (smaller d/w). Figure 2b displays the limiting values of v against d/w, when γ_{crit} is taken as $\gamma_{crit} = 1$. Table 3 below gives the estimated values of d/w when v = 5% and v = 80% (as obtained from the graphs of Figure 2b).

m	v = 5% Limiting d/w	v = 80% Limiting d/w
8	0.6	1.8
14	0.6	2.0
20	0.7	2.1

Table 3

One sees that for this model of a slow-tracking community, d/w is confined to the interval 0.6 - 2.1 (when interactions vary from 5% to 80%).

Discussion

Both Figures 2a and 2b display how the ensemble model is affected by environmental changes. It shows that limiting similarity is only weakly dependent on environmental fluctuations as long as they are not too severe, which is exactly what May and MacArthur (1972) concluded. In the case of slow-tracking communities, the model predicts that the limiting similarity will lie in the interval 0.6 - 2.1, unless environmental conditions are particularly harsh (v > 80%), or particularly stable (v < 5%). This agrees with the range that May and MacArthur offered after a review of field data (but see Abram's (1975) criticisms).

For fast-tracking communities, the model predicts that the limiting value of d/w lies in the interval 0.8 - 2.9 . Although May and MacArthur have not reported observed values of d/w as high as the upper estimates given by the fast-tracking model, this might be because:

a) few communities are fast-tracking and it is likely that the observed data is representative of slow-tracking communities,

and

b) the variation in competition coefficients, after structural disturbances in communities which have relatively low disturbance rates, is rarely as high as 80%. It may be, that in these stable communities, structural disturbances have minimum effect. Suppose, for example, they achieved a limit of v = 40% rather than 80%. In this case d/w would lie in the interval 0.8 - 2.2 .

The Form of the Competition Coefficient

In Tables 2 and 3 above, the limiting value of d/w has been calculated by making use of the formula for the competition coefficient given by Equation 2. Abrams (1975) argued that the limiting values so obtained are an artifact of the form of this formula. When he used other formulae for the coefficient (that have application when the GLV equations are used to approximate other models), no obvious limits to similarity emerged. However, Abrams' analyses were for small communities only (m = 3, 4, 8), with the restrictive assumption that interaction matrices were all symmetric. Further, all communities with more than three species were investigated on the basis of stability and not feasibility.

Nevertheless, when assessing the degree of applicability of the ensemble-model, it is important to keep in mind that the form of the competition coefficient may be an important factor.

The Importance of Global Stability

In MacArthur and Levins' (1967) original investigation of limiting similarity, conditions were derived that predicted when a rare invader may increase. Turelli (1978) correctly pointed out that the May and MacArthur stochastic analysis is a linear approximation of a near equilibrium competition community. As such, it "can be reconciled with the invasion paradigm only if the local stability properties of the model reflect its global behaviour." Thus since the model of May and MacArthur was not shown to possess global stability, their results may lack validity. For the model analysed in this dissertation, we have seen that it is almost certain to be globally stable whenever it is feasible. Hence rare invaders with low populations can increase to their respective equilibria. For this reason, Turelli's criticism becomes inapplicable.

§3.4 Conclusion

The results obtained by examining the feasibility of the m-dimensional resource model coincide with the general result of May and MacArthur. The model predicts limiting values of niche overlap that are similar to those May and MacArthur have interpreted real observations as showing. These limiting values of d/w predicted from the model do not have a wide range, typically falling within the interval 0.6 - 2.1 for slow-tracking communities, or 0.8 - 2.9 for fast-tracking communities, when the environmental variation varies from v = 5% to v = 80%. Although the limit to similarity, as given by the parameter d/w, is dependent upon the magnitude of environmental disturbance (v), the dependence is only weak. Thus the model gives little indication that environmental fluctuations account for species diversity gradients.

A significant contribution to the study of stability in the tropics, was made by Wolda (1978) upon examining the abundances and fluctuations of insects (see also the review by May 1979). Wolda concluded that "the wet but seasonal tropics are physically no more stable than the wet temperate zone" (p.1039), and that "hypotheses which predict greater stability..... must be rejected, even for insects in a tropical forest" (p.1038). This suggests that it would indeed be difficult to attribute the gradient in species diversity (when going from the temperate zones to the tropics) to a stability gradient which may not exist. Various field studies (e.g., Connell 1978, Hubbell and Foster 1986) have found that the high diversity of some tropical communities is dependent upon ongoing environmental disturbances - i.e., upon instability.

There are other hypotheses for gradients in species diversity. For example, the high diversity of the tropics could well be greater than that of temperate regions simply because the tropics have more habitats

available. Another possibility is that the tropics, more than other regions, have had greater evolutionary time for species to adapt, giving the region comparatively higher diversity (see Pianka (1978) for a review of these factors).

What the model does suggest is the extraordinary effect environmental disturbances may have on ecosystems. A deterministic setting without any environmental fluctuations at all $(v = 0)$, would impose no limit on similarity. However, even only a small amount of perturbation will significantly alter these circumstances, so that niche overlap will be confined to a relatively small interval. In the m-dimensional resource model, stability was not a strong enough test to elicit this effect, which became patently obvious upon examining feasibility.

The model shows how, even if the world is to some extent governed by competition, environmental factors tend to set a limit to niche overlap (or intensity of interactions). It is predicted that environmental disturbances can prevent the formation of intensely competitive systems because of the stringent criteria of feasibility. That this holds for quite small levels of environmental fluctuations suggests the vital influence and role of stochastic factors.

§4 Coexistence in Patchy Environments - The Theory of Spreading the Risk

Andrewartha and Birch (1984) outlined a "Theory of the Distribution and Abundance of Animals" in which the "natural population" of a species was shown to be multipartite. This recognizes that environments are inhomogeneous and patchy, and therefore the natural population may be considered to be divisible into a set of k component local populations. All of these local populations fluctuate in number, sometimes quite considerably and perhaps dangerously from the point of

view of survival. den Boer (1981) maintains that local populations live only for short periods. He suggests that the short time scale of most field studies, or for that matter the relatively short active life of field ecologists themselves, often leave the misleading impression that populations have a relatively lengthy lifetime.

den Boer argues that "in nature populations - taken as 'interaction groups' ....do not persist, but die out and are (re)founded more or less frequently" (den Boer 1980 p.279). "Although 'populations' taken as 'interaction groups' cannot be expected to survive very long..., populations that are composed of large numbers of highly interconnected 'interaction groups' (subpopulations) may show an impressive survival time, if the risk of extinction is sufficiently spread over a great part of these subpopulations..." (1981 p.49).

The theory of "spreading the risk", envisaged by Andrewartha and Birch (1954) and named by den Boer (1968), has much in common with the principles of insurance risks. den Boer (1968) gave the analogy of an industry which produces only one specialized product. Such an industry runs far greater risks than one which manufactures a number of goods and thus spreads its risks or chances of survival. In much the same way, heterogeneity in natural populations endows them with a multipartite structure. The greater the number of local populations, the smaller is the probability that all of them will synchronously reduce to extinction, wiping out the species completely.

den Boer found this to be the case in his study of carabid beetles. He summarized his results, writing that the "survival time of small and isolated populations will often be relatively low, by which the survival of species living in such a way will depend on powers of dispersal sufficiently high to result in a rate of population foundings that about compensates the rate of population extinctions. The survival

time of composite populations uninterruptedly inhabiting large and heterogeneous areas, highly depends on the extent to which the numbers fluctuate unequally in the different subpopulations" (den Boer 1981 p.39).

Andrewartha and Birch as well as den Boer have emphasised that asynchrony in the variation of local populations and the "unequal fluctuations" of populations are a means of spreading risk. When this is the situation the local fluctuations tend to cancel out one another leaving the total population relatively unchanged. den Boer (1981) confirmed this result by an analysis based on field data of the carabid beetle species <u>Pterostichus versicolor</u> and <u>Calathus melanocephalus</u> collected over a 19-year period. He observed that the former species spread its risks since it had unequally fluctuating subpopulations, whilst the latter species, whose subpopulations fluctuated in parallel, did not. Most interestingly, it appeared that "the former species can be expected to survive more than ten times better than the latter..." (p.39).

The model shows why the spreading of risks may be so advantageous to community coexistence. If risks are spread, then the variances of the natural populations will be reduced. Thus at a given disturbance rate, any reduction in a population's variance will mean simply that the population is perturbed less. As such it provides populations with a greater inertia to disturbance so that environmental changes are tracked more slowly. In Chapter 3 I outlined the benefits conferred on a community that manages to respond slowly to disturbances. What often occurs is that dangerous fluctuations tend to average or cancel themselves out. A community that "spreads its risks" will in this way protect itself because destructive environmental effects are ameliorated.

§5 Relative Competitive Ability and Coexistence

Lonnie Aarssen (1983,1984) has suggested that coexistence between competing species may be explained, in certain situations, by the organisms' similarities in competitive abilities. This contrasts with the usual emphasis on species differences in ecological niche space as a means of attaining coexistence.

Aarssen's viewpoint may be understood if one recalls the two essential conditions required for competitive exclusion to take place between two species, when resources are limiting. These are:

a) niche overlap must be greater than a certain critical level;

b) one species must be a superior competitor for the shared resources.

Aarssen points out that exclusion between competitors is usually attributed to (a). Very rarely is anything mentioned with reference to the competitive abilities of the species. However requirement (b) points out that exclusion may depend on the ability of one species to outcompete another. Conversely, coexistence will be greatly aided if two species are comparable in their competitive abilities, so that the exclusion process is slowed down or stopped. Coexistence then could conceivably hinge on competitive similarity or "competitive combining ability".

There are many situations where the concept of coexistence through differences in niche appears inapplicable. The higher plants, for example, "are relatively immobile, lack any real choice in energy supply, and by and large make demands on essentially the same resources (light, water, and nutrients..)... This has raised serious doubts concerning any predominant or widespread importance of niche differentiation as a mechanism for coexistence of plants" (Aarssen 1983 p.708).

By focussing on (b), Aarssen arrived at a possible mechanism that could explain coexistence in circumstances such as those for the higher plants described above. The argument was basically an evolutionary one, proposing that species' competitive abilities are selected for, so that species cannot differ too greatly in these abilities. It "implies a balance between competitors for the same resources and that this balance is maintained by natural selection" (1983 p.716).

Aarssen summarizes six other balancing mechanisms that have been suggested previously in the literature, but do not incorporate evolutionary arguments:

1. Relative competitive abilities are ameliorated by environmental conditions. This has been developed in §2.1 .

2. Predators or pathogens may suppress a potentially superior competitor which would otherwise competitively exclude other species. Paine (1966,1974) has studied such communities and developed the theory of the "keystone predator". Nassios (1984) has extended the model used here to analyse this effect.

3. Competitive abilities vary unevenly with age amongst species. Thus competitive ability has a temporally varying component.

4. Coexistence may be possible in heterogeneous systems where each competitor is superior in a different subregion of niche space. This theme is developed also in §2.2 .

5. Coexistence may result from dispersing seeds in the vicinity of interspecific competitors rather than close to the parent plant. This could occur for example, when there is seed-predation in the locality of the parent plant.

6. Coexistence may be permitted in systems in which circular networks of competitive abilities operate. For instance, species A may be a superior competitor to B which in turn is superior to C. However, species C may

be a better competitor than A.

The ensemble model has already simulated many of the above effects.

As well as the balance Aarssen describes, some of the points examined above could in fact have the effect of making interaction coefficients attain an equality that would not otherwise be expected. Any tendency towards balance, which Aarssen suggests is so important for coexistence, would decrease the spread or variation v in species interaction coefficients. If we could plausibly suggest that this resulted in all species having the same competitive ability, then, and only then, would the Gause competitive-exclusion principle predict community coexistence. However, all species can have the same competition coefficient only in the mathematical imagination and such a possibility completely lacks any field confirmation.

But, if we consider that some of the points raised may reduce considerably the variation v in interaction coefficients, then the ensemble model confirms the theory Aarssen advances. Contrary to the competitive-exclusion principle, the model showed coexistence to be possible provided that differences in competitive abilities are small, and this is indeed just as Aarssen argues.

[In terms of the models parameters, a decrease in v signals that the competitive differences between species have become smaller. For communities with a fixed number of species and constant mean interaction strength, if there is a decrease in v, then there must be a corresponding decrease in γ. It was shown that if γ was below the critical level γ_{crit}, coexistence was always possible. (In fast-tracking communities $\gamma_{crit} \simeq 0.4$ while in slow tracking communities it can be somewhat larger in value.)]

§6 Effect of Species Invasions on Community Coexistence

§6.1 Species Invasions and Extinctions

An understanding of extinction processes helps in formulating an overview of community organization. If a clear picture is secured, then ecologists may be more able to devise the policies needed to maintain and control natural diversity. For example, pest introductions have well-known catastrophic consequences. Understanding of community structure may yield clues as to how to correct or eradicate any destructive introductions. Also it may provide predictions as to which species may be successful invaders, which might become extinct and which will be of detriment to the community. Diamond and Case (1986b), in their detailed discussion of introductions, extinctions, exterminations and invasions, believe that the study of these processes have to date been "unjustly neglected".

Data sets required for any serious analysis need to be fairly elaborate and to have been collected over a sufficiently long time-span. Unfortunately, available data is usually inadequate for any extensive analysis. A review of evidence concerning the "Community Effects of Introduced Species" was undertaken by Simberloff (1981). He concluded that "the most striking result is that in so many instances.... an introduced species has no effect whatever on species in the resident community, or on the structure and function of that community. Perhaps the second most striking result is the scarcity of extinctions apparently attendant on introductions" (p.66).

Herbold and Moyle (1986) found this remark rather puzzling since all the reviews Simberloff based his analysis on were of the opposite conviction. According to Herbold and Moyle, the sources themselves make clear that "successful introductions have either altered the structure and function of natural communities or have occurred in habitats highly

modified by humans" (p.751). Moyle's (1986) own reviews and experiments on North American fish demonstrated that introduced species can and do replace native species. Evidence of "no effect" upon introduction was not found.

Recently Moulton and Pimm (1983,1986) examined perhaps the largest source of extinction data, the introduced Hawaiian avifauna, to determine whether competition is operative. By examining the extinction rate of passerines that were introduced between 1860 and 1980 they obtained the graph of Figure 3a.

If competition was not a significant factor, the probability of extinction would be constant and there would be a linear relationship between extinctions and the number of species present. However if competition operates, then Moulton and Pimm expected a non-linear relation, since the probability of extinction should rise with more competitors in the community.

Moulton and Pimm examined other possibilities before they felt sure that competition was responsible for the non-linear extinction rate. Perhaps the simplest alternative hypothesis is that species were introduced to inappropriate habitats. The majority of these cases were removed from the analysis. It was also noted that many introduced species survived for long periods, sometimes ten years or more, and then subsequently become extinct. In these cases, Moulton and Pimm found it doubtful that disappearances could have come about because of species initially colonizing an inappropriate habitat some ten years previous.

Moulton and Pimm had little difficulty in establishing anecdotal evidence for the existence of competition. They observed a number of examples where it appeared that one species competitively excluded another. Their observations also indicated:

a) a relationship between the extinction rate and morphological similarity;

b) a relationship between the extinction rate and taxonomic similarity;

c) variation in species abundance patterns.

All of these were suggestive of competition. However, there was no firm evidence that the process occurred on a community scale.

Two other possibilities were examined. One involved determining whether habitat alteration over time correlated with the extinction rate. The other checked if species introduced earliest were more likely to survive than those introduced later. Both of these possibilities were rejected as implausible, after a careful study of the appropriate ecological field data.

§6.2 The Extinction Rate Curve.

What is most noticable upon examining Moulton and Pimm's data, presented in Figure 3a, is the distinctive flat plateau where no extinctions occur, which suddenly, when the number of species increases, is characterized by a particularly high extinction rate. The plateau accords with Elton's (1950) remark that "the number of different kinds of animals that can live together in an area of uniform type rapidly reaches a saturation point" (as quoted in Terborgh and Faarborg (1980)). The latter authors examined and demonstrated "saturation" in bird communities in the West Indies. They found that when islands are not "saturated", resources or "empty niches" permit accommodation of further species. What normally occurs is that invaders fill whatever empty niches are available until no further species can be supported.

Previous studies of extinction curves (see Gilpin and Diamond 1976) have not predicted this unusually flat plateau. Gilpin and Diamond (1976) put forward the hypothesis that the curve is concave, and constructed a model predicting it to be nearly parabolic in shape. They found:

$$\text{Pr(Extinction)} = k_1 \, m^{2.37} \, .$$

Moulton and Pimm found $\text{Pr(Extinction)} = k_2 \, m^{1.85} \, .$

It became difficult to reconcile rounded curves like these with the sharp transition portrayed in Figure 3a.

Gilpin and Diamond (1981) developed a new model of island biogeography based on conditional probabilities of species occurrences. With lognormal probability distributions assumed, some of their computer results indicated the presence of plateaus, but no comment was made concerning their occurrence.

In what follows the extinction rate is derived by examining the competition model under simulated invasions, and the presence of the plateau regions will be confirmed. Suppose an invading species enters a fast-tracking community that can be represented by the ensemble (m, c, γ). To determine the chance of coexistence after this event, I will assume that the invasion does not change the community's mean strength of competition, or the variation v in interaction strengths. Thus the community after invasion can be described by the ensemble $(m+1, c, \mu\gamma)$ where $\mu = \sqrt{m}/\sqrt{(m-1)}$. Because the community is assumed fast-tracking, the effects of invasion may be understood by comparing the feasibility characteristics of the two different ensembles.

Extinctions may only occur in a fast-tracking community if it has an unfeasible equilibrium point. The probability of extinction after one structural disturbance is given by $Pr(E) = [1 - Pr(F)]$, where $Pr(F)$ is the probability of feasibility. Over a period of time that spans k structural disturbances, the probability that an extinction occurs is given by:

$$\sum_{j=0}^{k-1} [Pr(F)]^j \, Pr(E) = 1 - Pr(F)^k \, . \tag{3}$$

Figures 4a, b and c plot this probability versus m (the number of species present), for k = 1, 10, 50 respectively. Each figure consists of four graphs with c = .25, .3, .35, .4 . (Note that for purposes of making comparisons, Figure 3b is a reproduction of Figure 4b.) Environmental variation was set at a level of v = 30% and the theoretical feasibility predictions of Chapter 3 were then used to obtain these graphs. For each particular combination of k and c, the probability of feasibility was calculated for communities of 1, 2, ..., 30 species. This probability was inserted into Equation 3, which then gave the probability that an extinction would occur over a time that spanned k structural disturbances.

Comparing these graphs (eg., Figure 3b) with the empirical data for extinctions on the Hawaiian Isles (Figure 3a), similar overall characteristics stand out. Perhaps most noticeable is the distinctive flat plateau discussed above. The sharp transition in extinction rate is due to the increase in the parameter γ as species are added to the ecosystem, until the critical value of $\gamma = 0.4$ is reached, at which point the probability of extinction rapidly approaches one. Notice how the transition becomes sharper as k, the number of disturbances experienced, increases (see Figures 4a, b and c).

For reasons as those given in §2.4, slow-tracking communities will display a similar, though not as critical, step-like transiton in extinction rate. The transition will not have the same sharpness because of the way slow-tracking communities average over disturbances. This latter property allows the community to survive at higher levels of disturbance and so increases γ_{crit}. The higher the critical value of γ, the greater the number of species that can be added to the community.

After examining the empirical data of the Hawaiian avifauna, Moulton and Pimm maintained that there was "no escaping the inherently nonlinear nature of the data". They concluded that competition was the only reasonable explanation that would account for its nonlinearity. Such a nonlinearity is strikingly apparent in Figure 3a, which gives the relation between extinction and the number of coexisting species. We see there that the relation is not at all linear, but more like a sharp step-transition, with a flat plateau before "saturation". This plateau, so prominent in Moulton and Pimm's data, is an essential feature of the model's predictions.
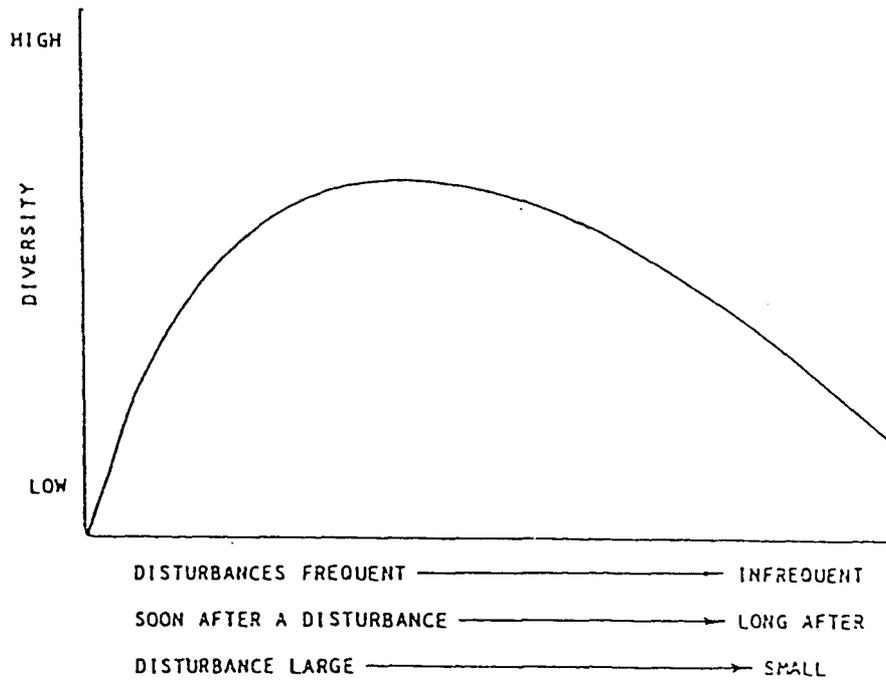
Figure 1a. The "intermediate disturbance" hypothesis displaying the "humped" diversity versus disturbance relation. (Reproduced from Connell 1978, p.1303)
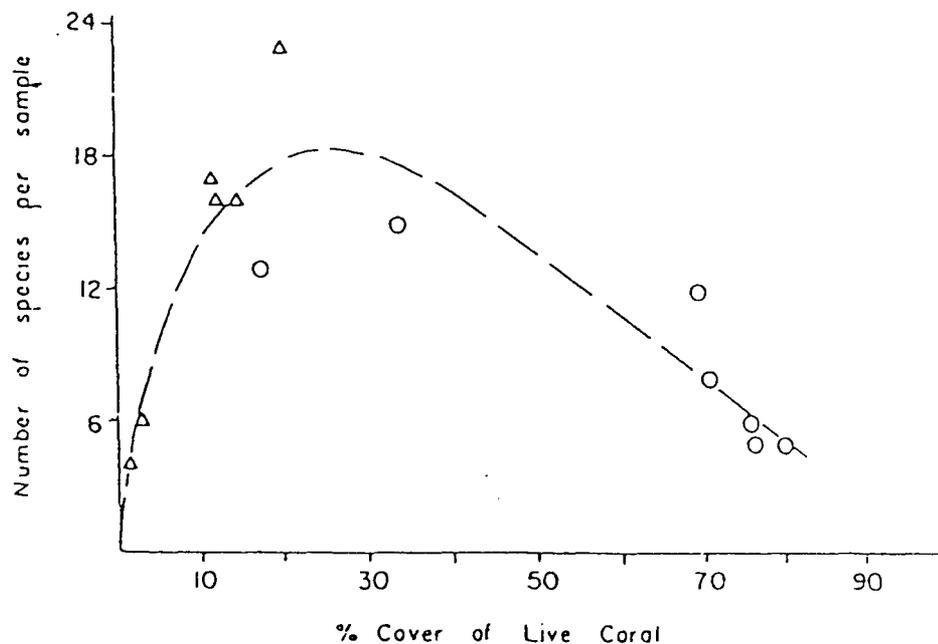
Figure 1b. Species diversity of corals in the subtidal outer reef slopes at Heron Island, Queensland. (△) Data from the heavily damaged north slopes; (O) data from the undamaged south slope; the line drawn by eye. (Reproduced from Connell 1978, p.1305)
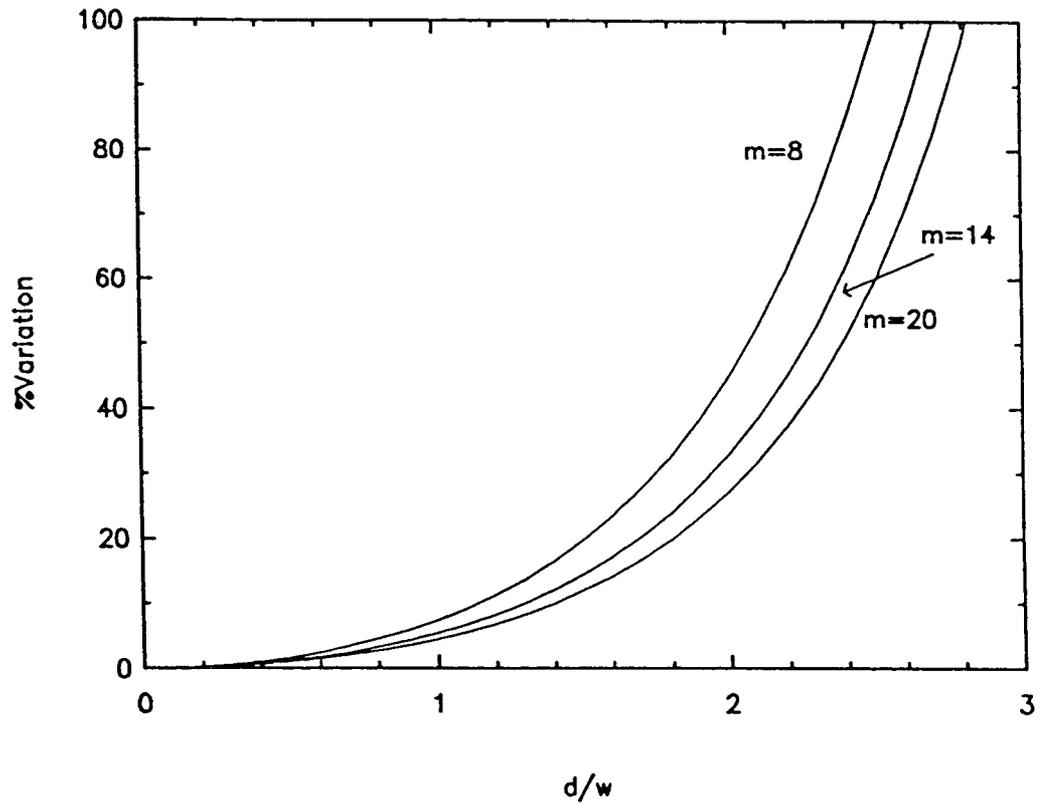
Figure 2a. $\gamma_{crit} = 0.4$
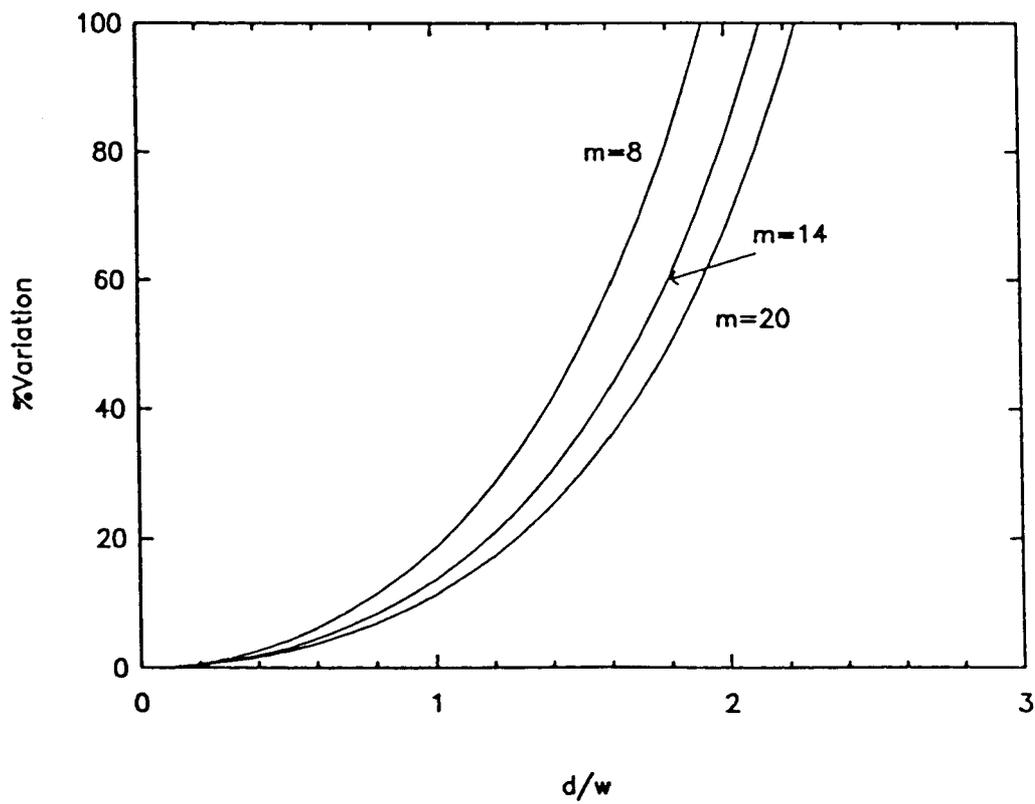
Figure 2b. $\gamma_{crit} = 1.0$
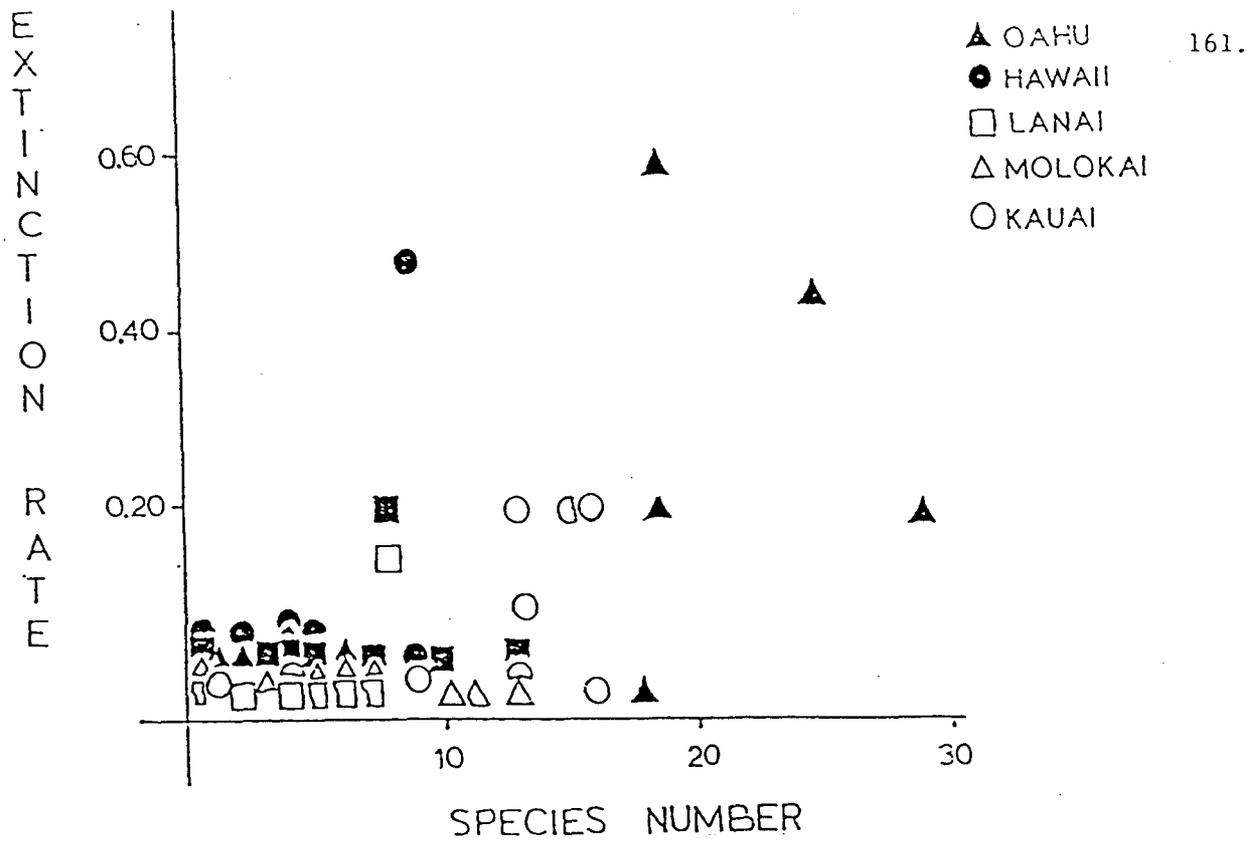
Figure 3a. Extinction rate for the period 1860 to 1980 expressed as the number of extinctions per year, averaged over 10-year periods, against the number of passerine species surviving on each island at the end of the 10-year period. (Reproduced from Moulton and Pimm 1986.)
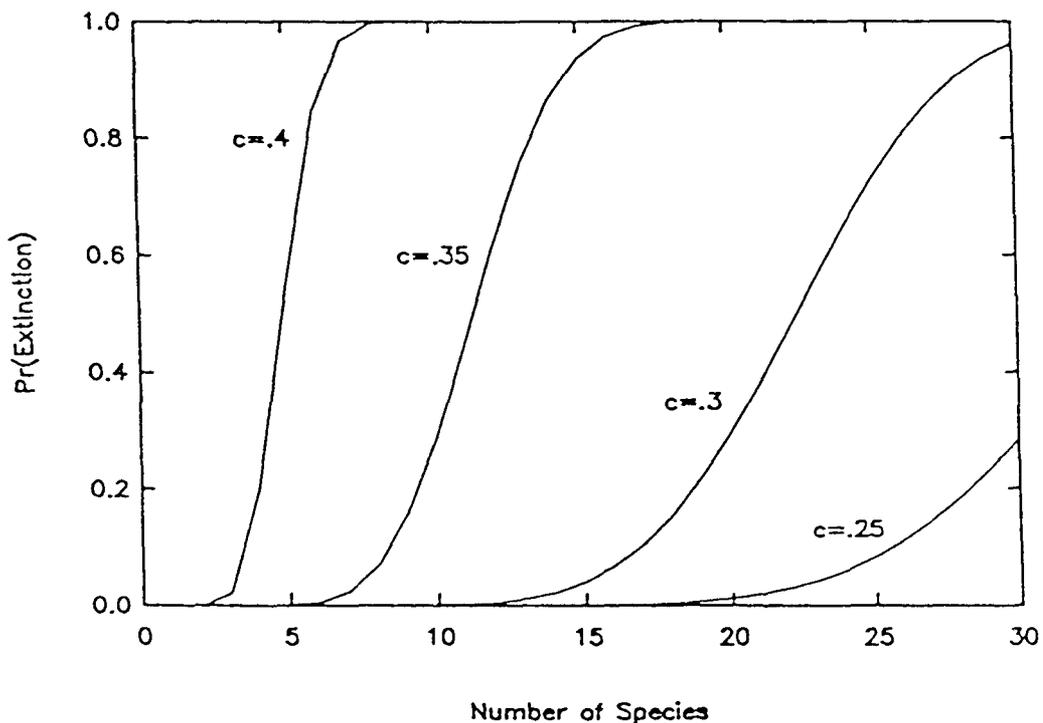
Figure 3b. The probability of an extinction occuring over a time-scale that spans ten structural disturbances. This probability is plotted against m - the number of species present.
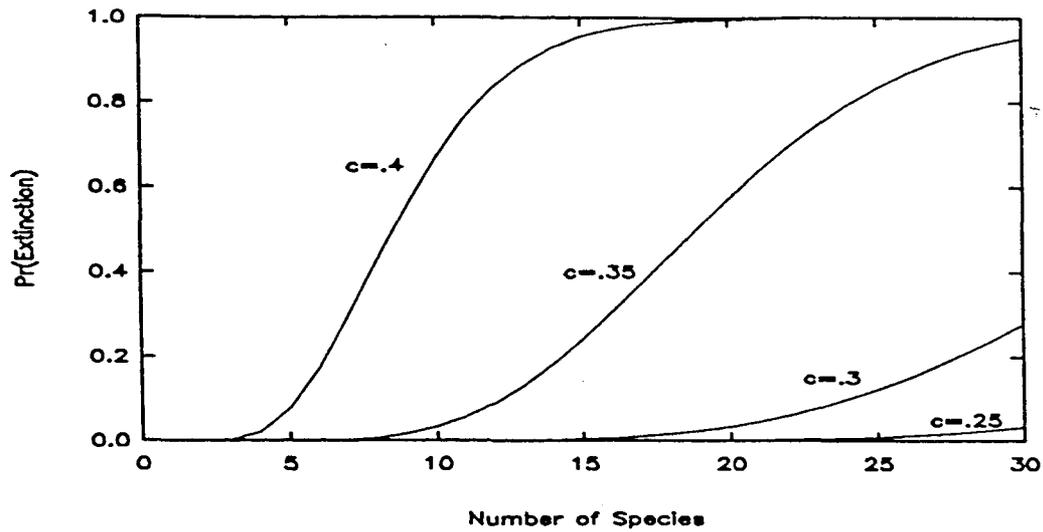
Figure 4a. $k = 1$
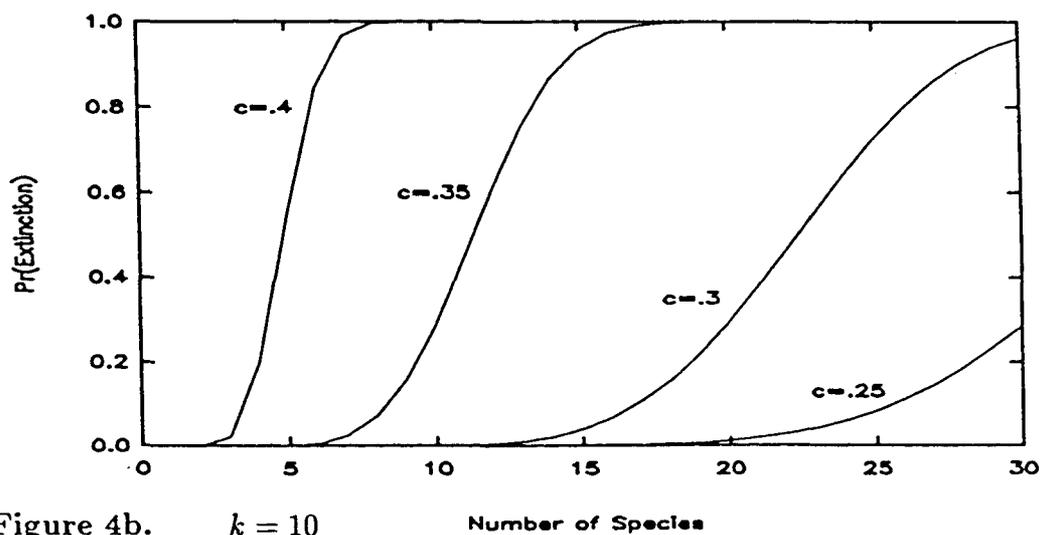
Figure 4b. $k = 10$
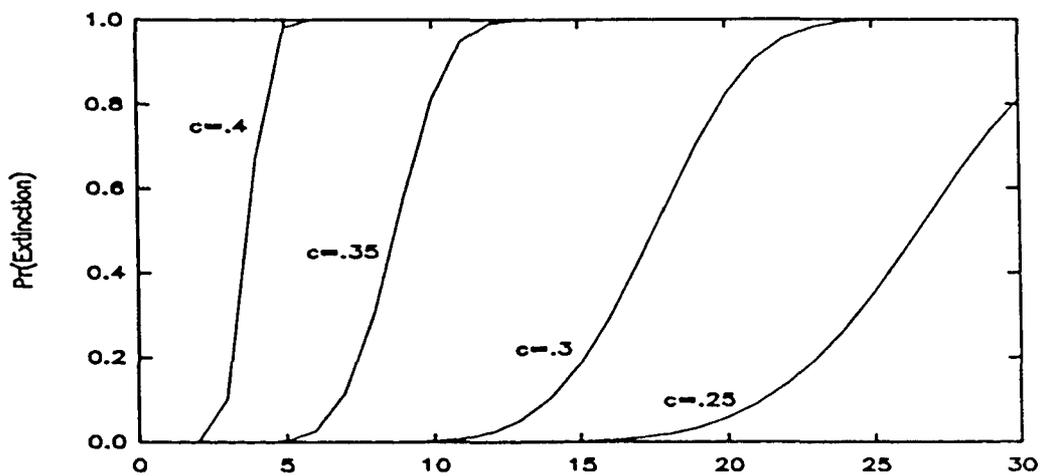
Figure 4c. $k = 50$

The probability of an extinction occuring over a time-scale that spans k-structural disturbances. This probability is plotted against m - the number of species present.

Chapter 5

Indirect Interactions and Competition Communities

§1 Introduction

Competition communities, in which each species suffers directly from the presence of every other, have been the basis of many ecological models this century (Volterra 1926, MacArthur 1969, 1970, Strobeck 1973, Gilpin and Case 1981). A theoretical framework was put forward by Levine (1976) indicating how two consumers that might be strong competitors in isolation could, when put in the context of a community, have a mutualistic association. Thus a full understanding of community processes cannot be obtained by studying how each pair of species directly interacts, but requires acknowledgement of hidden, underlying, "indirect" community-effects.

It is instructive to recall once again Haeckel's (1870) visionary definition of ecology. He described it as "the total relations of the animal .... to its .... environment; including above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact" (Translated in Allee et al 1949:frontispiece). Unfortunately, it is only in the last decade that the indirect effects to which Haeckel referred have been given serious attention.

Field evidence of indirect interactions, particularly those of facilitation and mutualism, have only recently begun to be documented (eg., Atsatt and O'Dowd 1976, Boucher et al 1982, Cluett and Boucher 1983, Connell 1983b, Davidson 1980,1985, Dethier and Duggins 1984). Culver (1982), for example, found that indirect facilitative interactions occurred amongst isopods in the small cave communities he was studying. The isopod Caecidotae recurvata and the

amphipod <u>Crangonyx antennatus</u> were positively associated when the isopod <u>Lirceus usdagalum</u> was present, but negatively associated in its absence.

The general prominence of these effects indicates the need to review and revise accepted ideas concerning systems of many competitors. MacArthur's (1972) theory of "diffuse competition" in multi-species communities treats competitive interactions in a simple additive manner, so that each species suffers from the presence of every other. However, we will see that from a community-wide perspective, these same interactions may result in some species actually benefitting from the presence of others.

For competition communities, three interacting competitors are all that are required for an indirect facilitation to arise. Figure 1 gives a schematic representation of a three-species competition community. The direct effect of species j on species i is given by the coefficient α_{ij}, and is taken to be negative in communities of competition. Here species 2 has a negative effect on species 3 which in turn has a negative effect on species 1 (via the interactions α_{32} and α_{13}). Indirectly then, species 2 (via the pathway of the two negative interactions) exerts a positive effect on species 1. Boucher <u>et al</u> (1982) have aptly described this sort of mutualism as due to a species' "enemies' enemies."

In many circumstances the positive indirect facilitation can be of greater magnitude than the losses species 1 suffers from its direct competitive association with species 2. Levine (1976) showed that if

$$|\alpha_{13}||\alpha_{32}| > |\alpha_{12}| \quad \text{and} \quad \alpha_{ij} \leqslant 0, \tag{1}$$

then the net effect of species 2 on 1 becomes facilitative. I will refer to this interaction as being Facilitative in a Community Context or more simply (in abbreviated form) - FCC.

§2 Determining the Effects of Indirect Interactions

§2.1 The Community Effects Matrix

Indirect effects can be found by the following technique. Recall once again that the GLV equations (see Chapter 2, Equation 3) when solved at equilibrium give:

$$k_i + \sum_j \alpha_{ij} N_j^* = 0 \ ,$$

so that in matrix form
$$\underline{N}^* = -\underline{\underline{A}}^{-1} \underline{k} \ . \tag{2}$$

Note that here and in the remainder of this chapter, $\underline{\underline{A}}$ is not taken to be normalized, but is the real interaction matrix - i.e., $\underline{\underline{A}} = (\alpha_{ij})$.

If we put $\underline{\underline{E}} = -\underline{\underline{A}}^{-1} = (e_{ij})$, then $N_i^* = \sum_q e_{iq} k_q .$ (3)

Our object is to determine the effect species j has on the equilibrium value of species i, in the context of the whole community. Now if the interaction matrix remains fixed, Equation 3 shows that the only way species j may modify the equilibrium value N_i^*, is by a change in its carrying capacity k_j. As we are interested in determining the behaviour of N_i^* as species j's equilibrium population is modified, then this is equivalent to monitoring ΔN_i^* (the change in N_i^*) after changing k_j by an amount Δk_j. If all the other carrying capacities remain constant, Equation 3 gives:

$$\Delta N_i^* = e_{ij} \Delta k_j \qquad \text{and} \qquad \Delta N_j^* = e_{jj} \Delta k_j \ .$$

Thus
$$\frac{\Delta N_i^*}{\Delta k_j} = e_{ij} \qquad \text{and} \qquad \frac{\Delta N_i^*}{\Delta N_j^*} = \frac{e_{ij}}{e_{jj}} \ . \tag{4}$$

Because the entries of the matrix $\underline{\underline{E}}$ indicate the behaviour of the interaction in the context of the whole community, it will be called the "community-effects" matrix[†].

For the uniform model (see Appendix 1):

a) $e_{ii} > 0$ so that N_i^* rises/drops when its birthrate rises/drops;

b) $e_{ij}/e_{jj} < 0$ so that N_i^* rises/drops when N_j^* drops/rises.

Thus the uniform model depicts a community in which each species suffers from the presence of every other. I define communities with this property as hyper-competitive. Further on (see §3), it will be shown that hyper-competitive communities are unusual and found only in models that are very similar to the uniform model.

§2.2 Similarities With Lawlor's Method and Levins' Loop Analysis

Lawlor (1979) presented a technique that was designed to analyse indirect interactions in an m-species competitive community. Appendix 2 shows that the formula he obtained for community effects is equivalent to the matrix inversion method described here.

To account for interactions in the context of a community, Levins (1973,1975) developed the theory of loop analysis. Since then, the method has been utilized extensively (eg., Briand and McCauley 1978, Lane 1975, 1985, 1986, Lane and Levins 1977, Puccia and Levins 1985).

[†] Levine (1976), Bender et al (1984), and Davidson (1980, 1985) have all made use of the inverse interaction matrix to elicit information concerning indirect effects, though not proceeding to the generalization presented here.

By determining all possible feedback loops the analysis examines "a two-species direct effect as it becomes embedded in increasingly more complex ecological networks" (Lane, 1985 p.347). Once all the indirect pathways to a specific interaction are found, then the total community-effect can be ascertained.

In loop analysis all interactions are described by their sign only. Interaction intensities are completely neglected. If species j directly competes with species i, then loop analysis takes $\alpha_{ij} = -1$. If on the other hand species j facilitates species i, then the interaction would be set at $\alpha_{ij} = +1$. No interaction at all would be described by $\alpha_{ij} = 0$. Although this representation of the community matrix provides a useful first approximation, care must be taken. As Levins (1973) warns, it is quite possible to get the wrong or ambiguous results when the magnitudes of interactions are neglected.

To analyse a community by loop analysis, it is necessary to enumerate the number of feedback loops of various "lengths" and "levels", embedded in the community matrix. Because, in this method, all entries of the community matrix are assigned values +1,-1 and 0, the task is greatly simplified. Even so, for large communities, loop analysis becomes tedious and usually necessitates the use of a computer (and a specialized computer program) to enumerate the loops, of each particular "length" and "level", within a matrix. In contrast, the method presented here requires the use only of generally available computer software for inverting matrices. It also has the added advantage that interaction intensities are allowed for.

If one allows for the way that the interaction matrix has been simplified, it turns out that loop analysis is almost identical to the matrix inversion method. An examination of the underlying mathematics (Levins 1973, p.131, Equation 23), reveals that the loop analysis

process for obtaining community-effects is nothing more than computing the inverse of the interaction matrix. Calculating loops is, after all, the process entailed when expanding the determinants of cofactors required for inverting a matrix. To confirm the equivalence, I compared the "community-effects" matrices of both Lane (1986), and Briand and McCauley (1978) as calculated by loop analysis, to those obtained by the inverse method. In both cases identical results were obtained, as shown below where I detail the work of Briand and McCauley (1978).

§2.3 Planktonic Food Web Example

Toxic algae in lakes and ponds, if unchecked, are ecological hazards. These algae can fatally poison livestock or impart dermititis to humans. In an attempt to find a means of controlling these toxic algae, Briand and McCauley (1978) took advantage of the system' features they believed evident in plankton communities. They designed a model with six variables: nutrients (N), inedible (undesirable) algae (A1), edible algae (A2), herbivores (A3), carnivores (C) and planktivorous predators (P).

After they constructed a loop diagram of the planktonic food web (reproduced in Figure 2a), and an interaction matrix (reproduced in Figure 2b) based on the signs of the interactions, the community-effects matrix was calculated by loop analysis (reproduced in Figure 3a). As a check I reconstructed the community-effects matrix by inverting the given interaction matrix.* When the entries of the matrix so obtained (Figure 3b), were compared to the loop analysis predictions of Briand and McCauley, one entry was found to differ. This entry was also found inconsistent by Puccia and Levins (1985 p.128) when they performed a loop analysis of the matrix.

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* However it should be repeated that the inverse method, like loop analysis, can give ambiguous results when the magnitude of interactions are ignored.

Briand and McCauley proceeded to investigate whether the system features of the real system matched the prediction given by the community-effects matrix. In their experiments, the planktonic systems were perturbed to check the predictions, and the literature was surveyed for previous experiments along these lines. Their findings are reproduced in Figure 3a and concur with the predictions given by the community-effects matrix.

The community-effects matrix indicates that Al, the undesirable algae, may be reduced by:

a) reducing nutrient supply (N);

b) increasing carnivore level (C);

c) reducing predators (P);

d) reducing herbivores (H);

The above predictions led Briand and McCauley to suggest biological manipulations that would help in reducing the level of algae (eg., introducing herbivore-specific disease or adding primary carnivores).

§3 Facilitative Interactions in a Stochastic Competition Community

§3.1 Empirical Results Using the GLV Model

It will be shown that there are many cases when species j directly competes with species i in isolation, but in the context of the whole community, the net interaction is facilitative - i.e.,

$$\alpha_{ij} < 0 \qquad \text{while} \qquad e_{ij}/e_{jj} > 0.$$

In order to determine the extent of these facilitations, an ensemble of competitive interaction matrices specified by (m, c, γ) were analysed, where the elements of the matrix $\underline{\underline{A}}$ were again taken as:

$$\alpha_{ij} = -(c + b_{ij}) \quad i \neq j, \qquad \alpha_{ii} = -1 .$$

In this investigation, the b_{ij} were taken to be normally distributed.

Appendix 1 found that the uniform model (where $b_{ij} = 0$ for all i,j) was hyper-competitive - i.e., none of its interactions are Facilitative in a Community Context (FCC). Surprisingly, upon introducing perturbations (i.e., the b_{ij}), the community exhibited a large proportion of these facilitative interactions. Table 1 indicates the percentage of interactions that were FCC upon perturbing the uniform model. These interactions were found to make up from 0 to nearly 50% of the total possible, depending upon the magnitude of γ.

```
.........................................
: 20-species, c = 0.25, samples = 200 :
:.......................................:
```

γ	%FCC	%FCC Predicted
0.00	0.0	0.0
0.10	2.3	3.0
0.20	16.4	17.6
0.30	26.0	27.3
0.40	32.2	33.0
0.50	36.1	36.7
0.60	39.1	39.3
0.70	41.3	41.2
0.80	42.9	42.7
0.90	44.6	43.8
1.00	46.0	44.7
1.10	47.1	45.4
1.20	47.9	46.0

Table 1

%FCC = The average % of interactions that were Facilitative in a Community Context from an analysis of 200 computer generated community matrices.

%FCC Predicted = The % of interactions analytically predicted to be FCC (see §3.2).

§3.2 Predicting Facilitation Within Models of Competition Communities

It is possible to estimate the extent of indirect facilitation in the stochastic competition community. Appendix 1 approximates $\underline{E} = -\underline{A}^{-1}$ by a perturbation technique and finds that it has as entries:

$$e_{jj} > 0 \quad \text{for all } j \ ,$$

$$e_{ij} = -(\underline{A}^{-1})_{ij} \simeq \frac{-1}{1-c} \left(\frac{c}{1 + [m-1]c} + b'_{ij} - \sum_{k=1}^{m} b'_{ik} b'_{kj} \right) \qquad i \neq j \ ,$$

$$\langle e_{ij} \rangle = \frac{-c}{(1-c)(1 + [m-1]c)} \qquad i \neq j \ ,$$

$$\text{Var}(e_{ij}) \simeq \frac{1}{m-1} (\gamma^2 + \gamma^4)/(1-c)^2 \qquad i \neq j \ .$$

$$\text{Then} \quad Z = \frac{e_{ij} - \langle e_{ij} \rangle}{\sqrt{(\text{Var}(e_{ij}))}} \qquad i \neq j,$$

is a normal variate with $\langle Z \rangle = 0$ and $\text{Var}(Z) = 1$.

(Note that again the notation ' indicates a general division by $(1-c)$.) Because $e_{jj} > 0$, the probability of an interaction being FCC is:

$$\Pr(\text{FCC}) = \Pr(e_{ij} > 0) = \Pr(Z > 0) \ . \tag{5}$$

Column-3 of Table 1 gives the probability calculated by Equation 5 . Comparing this with the actual Monte Carlo runs it appears to be a reliable predictor. These results show that there is a remarkable amount of facilitation in model competition communities where each species supposedly "suffers" from the presence of every other.

§3.3 Hyper-competitive Communities

In Appendix 1, it was pointed out that the uniform competition model has no interactions that are Facilitative in a Community Context. Accordingly, it can be said that each species suffers from each of the others – i.e., the community is "hyper-competitive". Because a strictly uniform system must be considered to be a mathematical fiction, we might wonder if hyper-competitive communities are just as ficticious.

To attempt to answer this question, the conditions are found under which these FCC interactions arise in the ensemble model. When γ is small, Appendix 1 approximates the elements of the community matrix $\underline{\underline{E}}$ as:

$$e_{ij} \simeq \frac{-1}{1-c} \left(b'_{ij} + \frac{c}{1 + (m-1)c} \right) \qquad i \neq j \ .$$

Hence hyper-competition is assured if, for all i,j:

$$b_{ij} < \frac{-c(1-c)}{1 + (m-1)c} \quad .$$

A sufficient condition would thus be $\quad |b_{ij}| < \frac{1-c}{m} \quad$ for all i,j . $\qquad$ (6)

This would be fulfilled if γ was less than $O(1/\sqrt{m})$. $\qquad\qquad\qquad$ (7)

In practical terms, (6) suggests that large systems can be hyper-competitive when no interaction varies from its mean value c by as much as m^{-1}. It would be quite implausible to suggest that coexisting species within ecosystems have interaction strengths that remain almost identical over time, as the above condition requires. Recall also that (for slow-tracking communities) persistence requires $\gamma < 0.4$. This is a factor of order $\sqrt{m}$ greater than the condition given in (7), and so implies that there are a large number of feasible systems which are not hyper-competitive. It would appear then, that hyper-competitive systems are unlikely to be found and that indirect interactions should figure

prominently in community structure. This suggests that we would do well to discard the usual notion of a competitive community being one in which each species suffers from the presence of every other.

§4 Community-Effects in Some "Real" Ecosystems

To make sure that the above findings are not just mathematical artifacts of the ensemble model, I have analysed field-data for various real systems believed to be purely competitive; they are discussed below.

Bird Communities

When Lawlor (1979) examined Cody's data for eight avian communities, he found that, of the elements in the community-effects matrix, between 30% and 40% were facilitations. Unfortunately, Cody's data was in the form of symmetric overlap matrices, and it is not clear how reliably they estimate the α-interaction matrices essential for this analysis. Thus, although the results Lawlor found agree with the predictions given by the stochastic model, they are not necessarily a reliable confirmation.

Ant Communities

Davidson (1980,1985) made studies of granivorous ants in the Chiuahuan Desert near Rodeo, New Mexico, over a five year period. Initially, there was indirect evidence to support the belief that exploitative competition for seeds was common amongst the ant species.

Simberloff (1983b) applied a null test to Davidson's data, but could not infer any exclusive distribution patterns in the communities. He believed that more direct evidence was necessary to demonstrate competition, and suggested (Simberloff 1982) performing experiments such

as food augmentation or individual species removals. When such tests were later carried out by Davidson (1985), her earlier results were confirmed.

She constructed the α-interaction matrix, based on the dietary overlaps of six ant species, and made careful allowance for any interference competition. The community-effects matrix was then determined by matrix inversion. After performing manipulatory experiments and then examining correlations between populations, Davidson corroborated that the community-effects matrix gave realistic predictions.

Eleven of the thirty off-diagonal coefficients within the community-effects matrix were found to be of positive sign, showing that 34% of interactions were facilitative. This high proportion supports the predictions of the stochastic model, namely, that interactions which are Facilitative in a Community Context are quite common in systems usually designated as competitive.

Plankton Communities

Lane (1975) examined four zooplankton communities in which she assumed that interspecific competition was a predominant community force. She documented this assumption with seven supportive arguments based on field evidence from the literature. Lane suggested that habitat selection, where species occur in different "place-times", was the predominant mechanism that alleviated competition and allowed species to coexist. This contrasts with the usual explanation of coexistence by resource allocation, whereby species occur together but partition available resources.

Using the GLV model, Lane calculated eleven interaction matrices from data on four lakes at differing times. She derived the entries α_{ij} from equations (based on resource turnovers) developed by Richard

Levins. By inverting the interaction matrices provided by Lane, I obtained the community-effects matrices (see Appendix 3), and tabulated the percentage of interactions that were Facilitative in a Community Context in Table 2.

Lake	Michigan			Gull				Cranberry		George	
Cruise	1	2	3	4	5	6	7	8	9	10	11
Size	8	3	8	8	9	8	8	5	5	7	7
C	.27	.86	.27	.37	.29	.36	.44	.61	.64	.64	.66
%FCC	42.8	0.0	35.7	50.0	41.7	28.6	44.6	20.0	20.0	23.8	23.8

Table 2

Again, what stands out, in this study of communities that are taken to be purely competitive, is the large proportion of interactions that are Facilitative in a Community Context. This supports the predictions of the ensemble model.

§5 Interpreting Indirect Effects in Multi-species Competition Communities

In the uniform model (as Appendix 1 shows) the community effect associated with competitor j's interaction with competitor i is given by:

$$e_{ij} = \frac{-c'}{1 + [m-1]c} \qquad (8)$$

Examine now the ensemble model for which the community effects can be approximated by (Appendix 1):

$$e_{ij} \simeq -\frac{c'}{1 + [m-1]c} - b''_{ij} + \theta_{ij} \qquad (9)$$

where $\theta_{ij} = \sum_{k} b''_{ik} b'_{kj}$.

(Here the notation '' indicates a division by $(1-c)^2$.)

The three components of e_{ij} can be understood as follows:

1) The term $-c'/(1 + [m-1]c)$ is the community effect exactly as in the uniform model (see Equation 8).

2) The term $-b_{ij}''$ arises because of competitor j's direct interaction with competitor i.

3) θ_{ij} expresses the first-order indirect effects of the community that arise because of the non-uniformity of the interaction coefficients. (The higher order interactions are of relatively smaller magnitude and are here neglected.)

As an aid to understanding how the indirect effects θ_{ij} come into play, it is useful to redefine a "friend" and "enemy" in these competition communities as follows:

i) Competitor j is an "enemy" of competitor i, if the strength of its interaction α_{ij} is greater in magnitude than the community's mean c. Since $\alpha_{ij} = -(c + b_{ij})$, then competitor j is an "enemy" of competitor i when $b_{ij} > 0$.

ii) Competitor j is said to be a "friend" of competitor i if the strength of its interaction is less in magnitude than the community's mean c. This translates to the condition that $b_{ij} < 0$.

For the interaction of, say, competitor 2 with competitor 1, the indirect effects θ_{12} would be:

$$\theta_{12} = \sum_k b_{1k}'' b_{k2}' \quad .\tag{10}$$

Consider any one of the terms in the summation given in the right hand side of (10), for example, $b_{13}'' b_{32}'$. Now competitor 1 will be facilitated whenever $b_{13}'' b_{32}' > 0$. This can occur only if either:

a) Competitor 2 is an "enemy" of competitor 3 which is an "enemy" of competitor 1;

or

177.

b) Competitor 2 is a "friend" of competitor 3 which is a "friend" of competitor 1.

Thus a competitor is facilitated by its "enemies' enemies" or its "friends' friends".

The above representation elucidates an unusual aspect of indirect effects in competition communities. It seems that the community takes careful account of species' relative competitive strengths with respect to the overall mean interaction strength c. The community discerns whether a species is competing weakly or strongly with another, relative to this mean. In simplified terms, the community determines its own picture of relationships between competitors, deciding which interactions are relatively "friendly" or "unfriendly". Indirect effects are then passed on according to this evaluation - i.e., via a competitor's relative "enemies' enemies" or "friends' friends".

Diffuse Competition and Indirect Facilitation

The approximation for e_{ij} (Equation 9) makes it evident that interactions which are Facilitative in a Community Context are more prevalent (percentage-wise) in communities of larger size. To see this, note that:

$$\frac{c}{1 + (m-1)c} < \frac{1}{m} \quad ;$$

now take the limit for large m so that (9) becomes:

$$e_{ij} \simeq -b''_{ij} + \sum b''_{ik} b'_{kj} \quad \text{and} \quad \langle e_{ij} \rangle = 0 \quad \text{(for large m)}.$$

Because $\langle e_{ij} \rangle = 0$, the community effects are equally likely to be positive or negative. Thus the proportion of interactions that are Facilitative in a Community Context can be of the order of 50% in these circumstances.

However, for smaller community sizes, the term $c'/(1 + [m-1]c)$ has the effect of reducing the amount of FCC interactions to somewhere below 50% . Nevertheless, even for moderate values of m there can still be a significant proportion of these interactions. As Table 1 shows, when $m = 20$ and $\gamma = .4$, 32.2% of interactions were found FCC.

It seems that increasing the number of competitors can induce many community-effects that are facilitative. This contrasts sharply with the usual notion of diffuse competition which predicts that a species should suffer more if the number of its competitors increases (see Pianka 1974). One further implication of this prediction is that it would be rare to find big "competition" systems without a large number of these facilitative interactions. This is quite contrary to the results of the uniform model which is so misleading in this - as in so many other effects - simply because it ignores variation in species interactions.

§6 Indirect Interactions in Multi-trophic Communities

The benefits conferred by indirect effects have been best documented for systems with more than one trophic level. One well-known example is the "keystone-predator" effect, exhaustively studied by Paine (1966,1974), and modelled by Nassios (1984). In the intertidal zones of Mukkaw Bay, Washington, the predator starfish Pisaster preys on the mollusc Mytilus, the community's superior competitor. By suppressing Mytilus, a high species diversity is attained. However, when the predator is not present, the diversity drops rapidly as Mytilus competitively excludes all other species. Thus the predator provides an overall positive contribution to the community as a whole.

Plant defences provide a very interesting demonstration of how competitors may have strong positive effects on one another. Mark Hay (1986) recently observed such a situation in his study of a seaweed community. Along similar lines to Atsatt and O'Dowd (1976), he explained that a weak competitor may advantageously associate (competitively) with a stronger one, if the latter reduces the probability of the weaker being preyed upon. For the seaweed community, the most abundant competitors, were relatively unpalatable, and acted as "decoys" to the local herbivores. Thus for the less abundant, but palatable species, the competitive costs of associating with the "decoys" are much less than the costs of increased herbivory in the absence of these "decoys". He concluded that "increases in the most abundant competitor can lead to increases, instead of decreases, in the number of other species present" (p.618). In other words the (facilitative) indirect interaction here outweighs the (competitive) direct interaction.

§7 Conclusion

The importance of indirect interactions has yet to be fully appreciated. Connell (1983a) surveyed 72 studies of interspecific competition. Of these 14 (19%) demonstrated facilitation, usually of an indirect nature. Vandermeer et al (1985) make the point that this is indeed impressive, since only 32% successfully demonstrated competition as they were designed to show.

The study of indirect effects within competition communities, as presented here, raises some basic and important questions normally overlooked simply because of the non-intuitive nature of "community-effects". It was found that one should expect a good proportion of interactions to be facilitative, even in a community where each species is supposed to be working to the detriment of every other.

This adds an element of contradiction to the usual meaning of "competition." Modellers may benefit from investigating all types of interactions, both direct and indirect, if only to be sure that their models bear a true relation to the processes they try to portray.

Because of the unusual way in which these interactions are so commonly embedded within communities and hidden, and because of their significance, Vandermeer (1980) has the view that a full evaluation will reveal that indirect interactions "may eventually challenge the apparent general acceptance of competition theory as the received theory of community structure" (p.442).

Appendix 1

Approximating the Community Effects Matrix

In this Appendix, the elements of the "community effects" matrix are approximated by a perturbation method.

The interaction matrix $\underline{A}$ was defined in Chapter 2 as:

$\underline{A} = \underline{A}_o + \underline{B}$ where $\underline{B} = (-b_{ij})$ is a matrix of small perturbations,

and $\underline{A}_o$ is the interaction matrix for the uniform model. Specifically,

$\underline{A}_o = -[(1-c)\underline{I} + c\underline{U}]$ where $\underline{U}$ has all its elements $u_{ij} = 1$.

1. The Uniform Model

For the uniform model - i.e., with no perturbations,

$\underline{B} = \underline{O}$ and thus $\underline{A}^{-1} = \underline{A}_o^{-1}$.

Matrix multiplication will confirm that:

$$(\underline{A}_o^{-1})_{ii} = g_1 = - \frac{1 + (m-2)c}{(1-c)(1 + [m-1]c)} ,$$

$$(\underline{A}_o^{-1})_{ij} = g_2 = \frac{c}{(1-c)(1 + [m-1]c)} .$$

Define $g = g_2/g_1 = \frac{-c}{1 + [m-2]c}$. Note that $|g| < \frac{1}{m-1}$.

$\underline{A}_o^{-1}$ may now be represented as:

$\underline{A}_o^{-1} = g_1(\underline{I} + \underline{G})$ where $\underline{G} = (g_{ij})$ has elements $g_{ii} = 0$ and $g_{ij} = g$ for $i \neq j$.

Since $e_{ii} = -g_1 > 0$, and $e_{ij} = -g_2 < 0$,

then the uniform model is hyper-competitive.

2. The Ensemble Model

The inverse of $\underline{A}$ is approximated here by making use of the following expansion:

$$\underline{A}^{-1} = -(e_{ij}) = (\underline{A}_o + \underline{B})^{-1} = \underline{A}_o^{-1}(\underline{I} - \underline{B}\underline{A}_o^{-1} + (\underline{B}\underline{A}_o^{-1})^2 - \ldots\ldots) .$$

The above expansion is valid when $\rho(\underline{B}\underline{A}o^{-1}) < 1$.

Below I examine the second term in the expansion.

Let $X = [\underline{A}_o^{-1} \underline{B} \underline{A}_o^{-1}]_{ij} = g_1^2[(\underline{I} + \underline{G}) \underline{B} (\underline{I} + \underline{G})]_{ij}$

$$= g_1 [\underline{B} + \underline{G} \underline{B} + \underline{B} \underline{G} + \underline{G} \underline{B} \underline{G}]_{ij}$$

When taking into account that $|g| < \frac{1}{m-1}$ and after calculating X above, one finds that: $\langle X \rangle = 0$,

and $\text{Var}(X) = \text{Var}(g_1^2 b_{ij}) + 0(\sigma^2/m)$

$$\simeq \text{Var}(g_1^2 b_{ij}) = g_1^4 \sigma^2 \quad \text{for large m.}$$

For this reason I have made the approximation that $\underline{A}_o^{-1} = g_1\underline{I}$, whenever it is multiplied with the matrix of small perturbations $\underline{B}$.

Hence $\rho(\underline{B}\underline{A}_o^{-1}) \simeq \rho(g_1\underline{B}) \simeq \rho(\underline{B})/(1-c) \simeq \gamma$ so that the above expansion is valid when $\gamma < 1$, i.e., for all feasible and stable systems.

The expansion becomes $\underline{A}^{-1} = \underline{A}_o^{-1} - g_1^2 \underline{B} + g_1^3 \underline{B}^2 - \ldots\ldots$ so that:

$$e_{ij} = (-\underline{A}^{-1})_{ij} \simeq \frac{-1}{1-c}\left(\frac{c}{1 + (m-1)c} + b'_{ij} - \sum_{k=1}^{m} b'_{ik}b'_{kj} \right) + 0(g) \qquad i \neq j$$

which, when γ is small, can be approximated as:

$$e_{ij} = \frac{-c'}{1 + [m-1]c} \quad .$$

(Again I have used the symbol ' to represent a general division by 1-c.)

$$e_{ii} = (-\underline{A}^{-1})_{ii} \simeq \frac{1}{1-c} \quad .$$

The computer simulations made use of in this chapter selected the b_{ij} from a Normal statistical distribution. Thus the above approximation shows the e_{ij} to be Normally distributed.

Appendix 2

Lawlor's Formulation

Lawlor (1979) calculated the net per capita effect of manipulating

the equilibrium of species 2, on the equilibrium density of species 1 as

T_{12}. Here it is shown that $T_{12} = e_{12}/e_{11}$.

$$T_{12} = \frac{\alpha_{12} - [\alpha_{13} \cdots \alpha_{1m}] \ \underline{B}^{-1} \begin{bmatrix} \alpha_{32} \\ \vdots \\ \alpha_{m2} \end{bmatrix}}{1 - [\alpha_{13} \cdots \alpha_{1m}] \ \underline{B}^{-1} \begin{bmatrix} \alpha_{31} \\ \vdots \\ \alpha_{m1} \end{bmatrix}}$$

where $\underline{B}$ here, is the $(m-2)$-x-$(m-2)$ matrix obtained from the community

matrix $\underline{A}$ by deleting rows 1 and 2 as well as columns 1 and 2. It is

shown here that $T_{12} = e_{12}/e_{22}$.

Using matrix theory it is possible to express the inverse of $\underline{A}$ in terms

of its cofactors. Thus:

$$e_{ij} = \frac{|\underline{A}_{ji}|}{|\underline{A}|} \ (-1)^{i+j}$$

where $\underline{A}_{ji}$ is the matrix formed from $\underline{A}$ by deleting row j and column i .

Hence $\qquad \dfrac{e_{ij}}{e_{jj}} = \dfrac{|\underline{A}_{ji}|}{|\underline{A}_{jj}|} \ (-1)^{i+j}$. $\qquad\qquad\qquad$ (11)

The following formula for the determinant of a partitioned matrix now

becomes useful.

If $\underline{M} = \begin{bmatrix} P & Q \\ R & S \end{bmatrix}$ then $\qquad |\underline{M}| = |\underline{S}| \ (|\underline{P}| - |\underline{R} \ \underline{S}^{-1} \underline{Q}|)$.

Applying this to Equation 11 (taking $\underline{P}$ as a 1-x-1 matrix etc.) gives the

result that $e_{12}/e_{11} = T_{12}$.

Appendix 3

Lane Interaction Matrix 1

```
-1.00 -0.25 -0.71 -0.02 -0.55 -0.03 -0.08 -0.12

-0.61 -1.00 -0.39 -0.13 -0.48 -0.03 -0.10 -0.10

-0.60 -0.13 -1.00 -0.01 -0.28 -0.02 -0.07 -0.14

-0.45 -1.32 -0.12 -1.00 -0.36  0.00  0.00 -0.05

-1.03 -0.36 -0.61 -0.03 -1.00 -0.10 -0.10 -0.20

-0.35 -0.14 -0.27  0.00 -0.58 -1.00 -0.18 -0.10

-0.49 -0.22 -0.44  0.00 -0.30 -0.10 -1.00 -0.05

-0.59 -0.19 -0.80 -0.01 -0.53 -0.05 -0.05 -1.00
```

C = 0.268, Sigma = 0.278, Gamma = 1.006

Community Effects Matrix 1

```
 3.58 -0.17 -1.65  0.01 -1.53  0.08 -0.02  0.12

-0.30  1.49 -0.03 -0.17 -0.46  0.02 -0.08 -0.01

-1.36  0.03  1.93  0.00  0.31 -0.02 -0.05 -0.17

-0.03 -1.78  0.33  1.22  0.30  0.01  0.13  0.01

-2.91 -0.31  0.75  0.01  2.78 -0.18 -0.02 -0.26

 0.85  0.05 -0.25  0.01 -1.03  1.09 -0.15  0.03

-0.33 -0.17 -0.19  0.03  0.02 -0.09  1.07  0.03

 0.55 -0.02 -0.95  0.01 -0.69  0.01  0.03  1.20
```

42.86% of the interactions are Facilitative in a Community Context.

Lane Interaction Matrix 2

```
-1.00 -0.95 -0.81

-0.80 -1.00 -0.81

-0.81 -0.96 -1.00
```

C = 0.857, Sigma = 0.070, Gamma = 0.688

Community Effects Matrix 2

```
 4.30 -3.34 -0.78

-2.78  6.66 -3.13

-0.81 -3.69  4.64
```

0% of the interactions are Facilitative in a Community Context.

Lane Interaction Matrix 3

```
-1.00 -0.36 -0.17 -0.37 -0.54  0.00 -0.41 -0.07

-0.11 -1.00 -0.04 -0.18 -0.61 -0.04 -0.07 -0.17

-0.41 -0.34 -1.00 -0.45 -0.42  0.00 -0.40 -0.02

-0.23 -0.38 -0.11 -1.00 -0.69 -0.02 -0.11 -0.08

-0.15 -0.55 -0.05 -0.30 -1.00 -0.03 -0.08 -0.16

 0.00 -0.65  0.00 -0.14 -0.59 -1.00 -0.01 -0.86

-0.88 -0.52 -0.34 -0.39 -0.59  0.00 -1.00 -0.07

-0.09 -0.64 -0.01 -0.15 -0.67 -0.20 -0.04 -1.00
```

C = 0.267, Sigma = 0.244, Gamma = 0.879

Community Effects Matrix 3

```
 1.67  0.02 -0.03 -0.26 -0.36  0.02 -0.62 -0.01

 0.00  1.57 -0.01  0.01 -0.85 -0.01 -0.03 -0.12

-0.03 -0.09  1.19 -0.36  0.04  0.00 -0.42  0.05

-0.17  0.01 -0.08  1.34 -0.84 -0.01  0.02  0.05

-0.09 -0.76  0.00 -0.36  1.86  0.01 -0.01 -0.14

 0.12 -0.18  0.00 -0.04  0.05  1.21 -0.01 -1.02

-1.33 -0.33 -0.34  0.03  0.02  0.01  1.70  0.03

-0.03 -0.45  0.02  0.07 -0.55 -0.24  0.02  1.37
```

35.7% of the interactions are Facilitative in a Community Context.
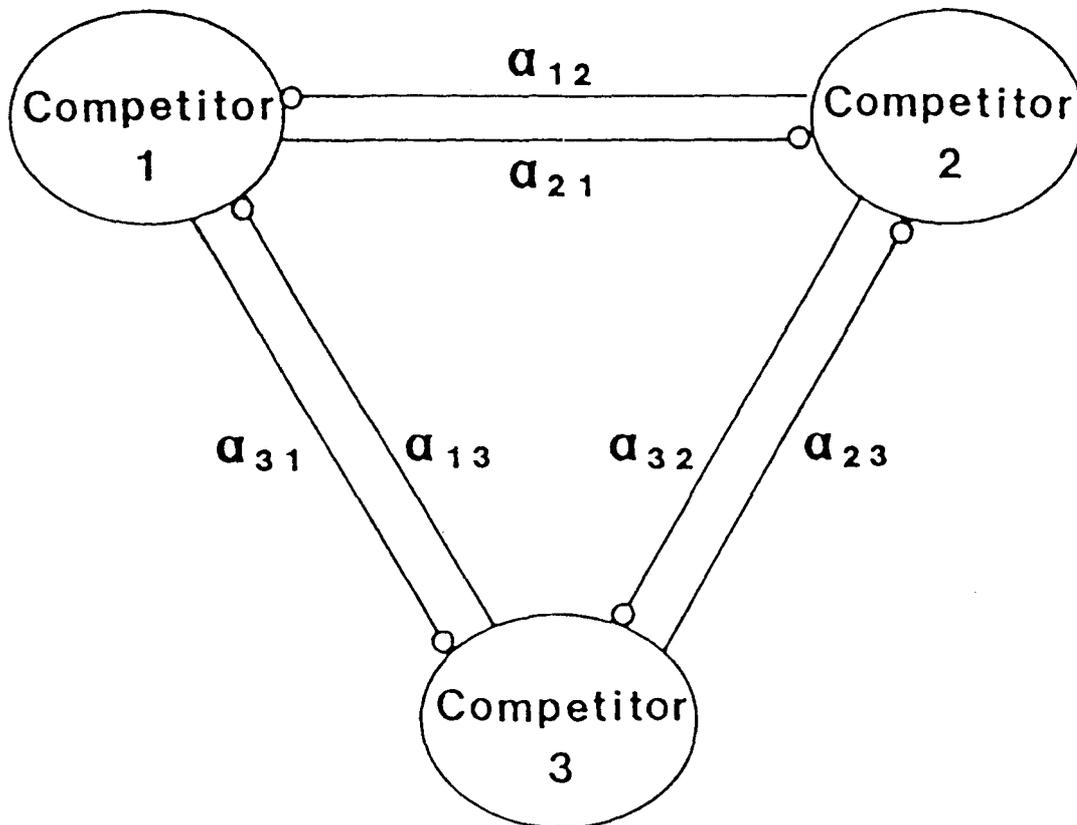
Figure 1. Three interacting competitors (reproduced from Vandermeer *et al* 1985, p.328).
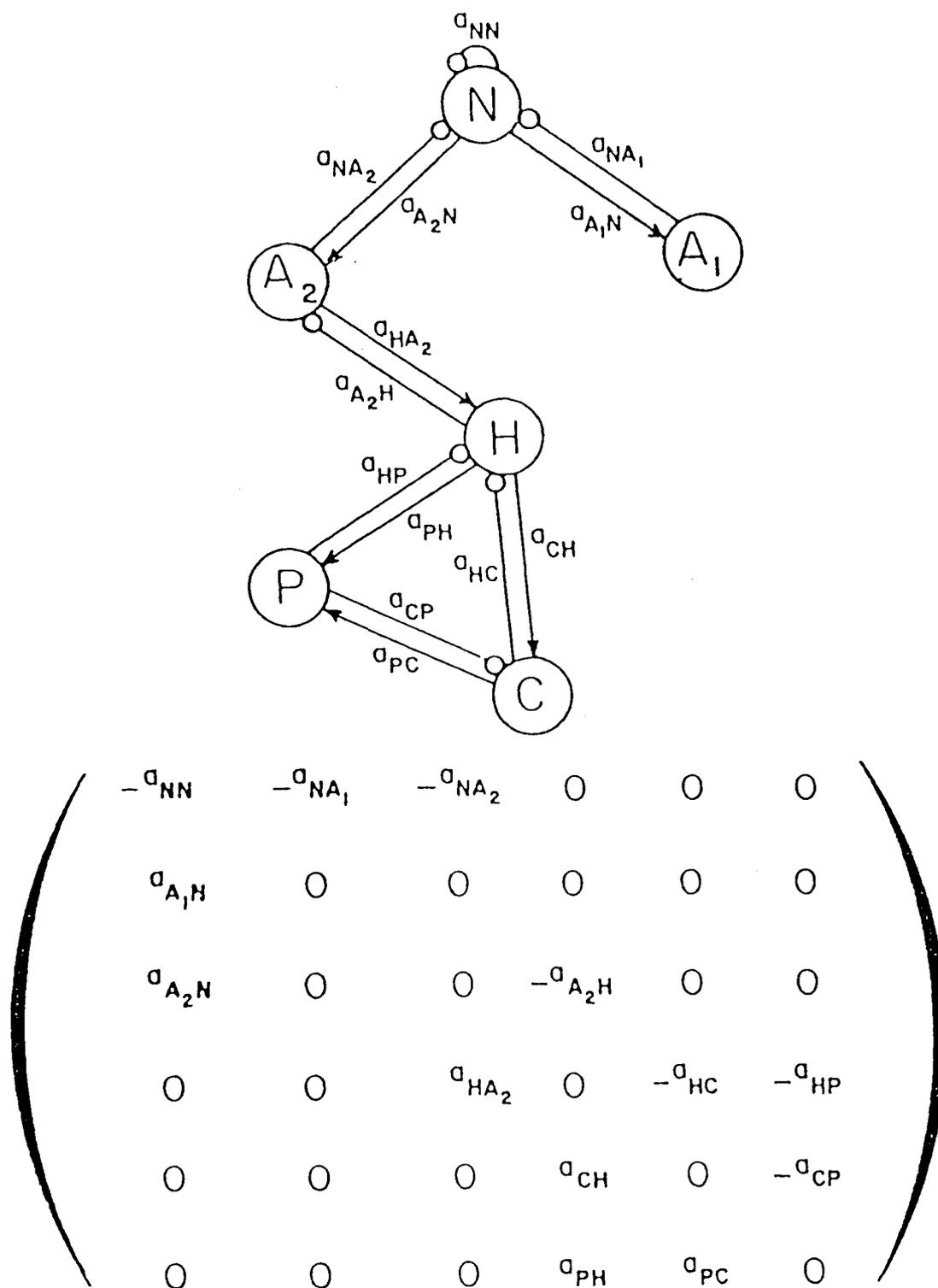
Fig.2 *a*, Loop diagram of the six-variable system. Positive effect of variable *i* on variable *j* is indicated by an arrow going from *i* to *j*. Negative effect is indicated by a circle. Nutrient resources are not self-reproducing and are thus self-damped. *b*, Matrix of the system, taking all the a_{ij} as positive numbers and representing the directions of their effects by the sign in front.

(Reproduced from Briand and McCauley 1978, p.228 .)

Case	Perturba-tion*	N	A_1	A_2	H	C	P	Predictions supported by
1	$+N$	0	+-	0	0	0	0	Fertilisation experiments and evidence from 'cultural' eutrophication (refs 16–18)
2	$+A_1$	—	0	0	—	+	—	(Currently being tested
3	$+A_2$	0	0	0	+	—	+	in long-range experi-
4	$+H$	0	+	—	0	0	0	ments *in situ*)
5	$+C$	0	—	+	0	0	+	
6	$+P$	0	+	—	0	—	0	Lake manipulations (ref. 21)
7	$-N$	0	—	0	0	0	0	Enclosure experiments
8	$-C$	0	+	—	0	0	—	of the authors
9	$-P$	0	—	+	0	+-	0	Lake manipulations (ref. 22)

* Three cases $(-A_1, -A_2, -H)$ have been omitted to avoid redundancy. They can be derived simply by reversing the sign of the effect of $+A_1$, $+A_2$, and $+H$, respectively.
+, Enhancing effect; —, inhibiting effect; 0, no effect.

Figure 3a. Predicted response of plankton systems to perturbations in each variable, as found by loop analysis. (Reproduced from Briand and McCauley 1978, p.229 .)

Perturbation:

Effect on the level of:

	N	A_1	A_2	H	C	P
N	0	1	0	0	0	0
A_1	-1	1	0	-1	1	-1
A_2	0	0	0	1	-1	1
H	0	1	-1	0	0	0
C	0	-1	1	0	0	1
P	0	1	-1	0	-1	0

Figure 3b. Predicted response of plankton systems as found by matrix inversion method. (The matrix presented is the transpose of the Community Effects matrix.)

Chapter 6

Checkerboard Distributions and Species Co-occurrence Patterns

Within Communities

§1 Introduction

The distributions and patterns of species combinations on island archipelagos have received much attention by ecologists, as a means of determining the presence of community processes. In this chapter a straightforward method is presented that tests for exclusive species patterns as well as co-occurrence patterns in biogeographic data. The test is used to re-examine the controversial conclusions reached by Diamond (1975) concerning the "Assembly of Species Communities". Diamond deduced seven assembly rules in his study of birds in the Bismarck Archipelago near New Guinea. These rules assert the existence of certain patterns and "permissible combinations" of species within bird communities. Further, it was suggested that these patterns were chiefly determined by the operation of competition.

Connor and Simberloff (abbreviated C&S) (1979), by constructing random communities incorporating biological constraints they believed appropriate, contested these conclusions: They argued that the observed patterns of the archipelagos examined would, for the most part, be expected had species been randomly distributed on the islands. Gilpin and Diamond (abbreviated G&D) (1982) and Diamond and Gilpin (abbreviated D&G) (1982) criticized the Monte Carlo method employed by C&S, claiming that it had "many fatal weaknesses." Instead they offered a "new" method that "lets one ... examine whether a whole fauna is non-randomly structured" (G&D, p.75). The problem has been an issue of major controversy ever since (see for example C&S 1983, 1984, G&D 1984, Hastings 1987, S&C 1984, Wilson 1987, Wright and Biehl 1984).

The C-test described below (§3), resolves many of the problems inherent in the above approaches. It is used to analyse complete avifaunas and to detect patterns found at the family level.

§2 The Null Hypothesis Proposed by C&S

For the analysis of biogeographic data, presence/absence (or "incidence") matrices are employed to depict which species are present and where. In the case of the matrices examined here, each column represents a known island, and each row a particular species. A "1" appearing as the (i,j)'th entry denotes that species i (S_i) is on island j (I_j), whilst a "0" indicates its absence. For example, Appendix 1 displays the presence/absence matrix of birds in the New Hebrides as synthesised by Diamond and Marshall (1976).

Diamond's (1975) rules for the assembly of species communities predicted certain patterns to be found within such an incidence matrix. Two of the rules state (p.423):

a) "If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature."

b) "Some pairs of species never coexist, either by themselves or as a part of a larger combination."

Rules like these led Diamond to argue that competition predominantly shaped species distributions on the islands. For example, in another study Diamond and Marshall (1977) asserted: "The distributions of most New Hebridean species are limited more proximately by competition than by species' adaptations to the physical environment itself" (p.705).

In order to test these assembly rules C&S (1979) randomly generated "possible worlds" of biogeographic patterns so that a null hypothesis of random colonization could be made. They felt it reasonable to incorporate the following three constraints (p.1133):

"(i) For each island, there is a fixed number of species, namely, that which is observed.

(ii) For each species, there is a fixed number of occurrences, namely, that which is observed.

(iii) Each species is placed only on islands with species numbers in the range for islands which that species is, in fact, observed to inhabit. That is, the "incidence" range convention is maintained."

Constraint (i) requires that, in the incidence matrices representing these "random" worlds, the column sums have values fixed to the same as that observed. The motivation here is that islands do have a species/area relationship which must be taken into account. The larger the island, the more species it will accommodate (see the review in Connor and McCoy 1979).

Constraint (ii) acknowledges that certain species colonize better than others. Species vary in their ability to disperse, invade and persist on islands. For the New Hebrides avifauna, some species even lose their inter-island dispersal ability after invading an island, preventing any further inter-island colonizations (Diamond and Marshall 1976). The row sums are taken to be representative of dispersal ability and thus all "possible worlds" are given the observed values of these sums.

Constraint (iii) requires that a particular species will never appear on an island with fewer species than the minimum value of the islands it is observed on. Neither can it occur on islands with more than the maximum of that which it is observed on. This serves to simulate the incidence functions described by Diamond (1975).

By incorporating these constraints a null hypothesis can be made which filters out their associated ecological effects. In this way, the null hypothesis tests for patterns in the biogeographic data making full

allowance for those ever-present patterns induced naturally by:

a) the island species-area relationships;

b) species colonization abilities;

c) incidence functions;

- all of which may tell us little about biological interactions.

How successfully the above constraints allow us to estimate reliably the distribution of colonists, in the absence of interspecific associations, is a problematical issue. Grant and Abbot (1980), D&G (1982), Harvey et al (1983), and Quinn and Dunham (1983), suggest that the procedure of fixing marginal constraints to observed values has a degree of circularity. If relative species abundances and incidence functions are in fact shaped by such community structures as competition, then, by incorporating the constraints, hidden structures are automatically built in.

Whether or not competition does shape the above-mentioned constraints is controversial. For example, doubt has been cast on the hypothesis that the species-area relation has any causal basis - from competitive processes or otherwise (Connor and McCoy 1979). One might expect a species-area relation to be apparent had the islands been colonized randomly, simply because large islands accomodate more species than smaller islands.

What we witness here, is the extreme difficulty investigators face when trying to construct a correctly posed null hypothesis. Graves and Gotelli (1983) and Quinn and Dunham (1983) pointedly elaborate on the need for investigators to make their null hypotheses more convincing; to pay more "attention to the "underlying quality of the data" (Graves and Gotelli 1983, p.323). Because of the high sensitivity of techniques employed in testing ecological hypotheses, Graves and Gotelli believe the constraints of C&S to be hazardous approximations. It was suggested

that for these tests one needs to:

(a) construct source pools realistically;

(b) explicitly incorporate habitat preferences;

(c) use adequate estimates of colonization potential.

However, all of these features may never properly be estimated, and it is only very recently that explicit data along the lines mentioned have begun to be documented. For this reason alone one must applaud the studies of C&S, and their attempt to assess the validity of Diamond's assembly rules. Certainly C&S drove their point home to all ecologists - that the basic testing procedures and the quality of reference data need to be improved, in order to deduce patterns in ecological processes.

The aim of this chapter is to elaborate further a means of ascertaining structure in biogeographic data. The test provided here, lacks some fundamental flaws, which appeared in the methods used previously.

§3 A Test for Checkerboardedness

§3.1 Checkerboard Distributions

Diamond (1975) argued: "[T]he simplest distributional pattern that might be sought as possible evidence for competitive exclusion is a checkerboard distribution. In such a pattern, two or more ecologically similar species have mutually exclusive but interdigitating distributions in an archipelago, each island supporting only one species" (pp.387-388). Further: "Checkerboard distributions are of great interest in demonstrating the existence of competitive exclusion" (p.392). D&G (1982) also agree that the "simplest and clearest pattern that might be produced by competition is a checkerboard distribution" (p.65). However, we will see below that checkerboard distributions may

emerge for a variety of reasons.

The checkerboard pattern between species S_i and S_j displayed in M1a and M1b, will be used as the basic unit of exclusiveness.

	I_p	I_q
S_i	....1.........0...	
S_j	....0.........1...	

M1a

	I_p	I_q
S_i	....0.........1...	
S_j	.....1.........0...	

M1b

The configuration portrayed in M1a(/M1b) is referred to as a "latent interchange," since it can always be "flipped" (i.e., interchanged) to the state displayed in M1b(/M1a), whilst maintaining the row and column constraints of the data matrix.

It is helpful to examine the following simple examples.

	I_1	I_2	I_3	I_4	· ·	
S_1	1	1	0	0		2
S_2	1	1	1	0		3

M2a

	I_1	I_2	I_3	I_4	· ·	
S_1	1	1	0	0		2
S_2	1	0	1	1		3

M2b

Nowhere in M2a will one find a unit of exclusiveness between species S_1 and S_2. It might be argued that the pattern on island I_3, where S_1 and S_2 might be said to "snub" each other, indicates exclusiveness. However, a closer examination reveals that given the two co-occurrences on I_1 and I_2, there is no other possibility but a "snub", on either I_3 or I_4. The "snub" is an artifact of the given row sums and co-occurrence scheme, and not indicative of exclusiveness. In fact, Appendix 2 shows that the number of "snubs" in _any_ incidence matrix having the same row and column constraints is a fixed constant. Hence a tally of the number of "snubs" within an incidence matrix cannot be used as a measure of

"exclusiveness".

On the other hand, consider M2b which is obtained from M2a after several interchanges. In this matrix, two checkerboard units are to be found between S_1 and S_2, on islands:

a) I_2 and I_4

b) I_2 and I_3.

In matrix M2b, species S_1 and S_2 appear to be more exclusively arranged than in matrix M2a, where they have no checkerboard units at all.

§3.2 The C-score

Below I present a method to calculate the number of checkerboard units (i.e., the C-score) between any two species S_i and S_j, embedded in a presence/absence matrix. Suppose the entries are as in M3a;

$$
\begin{array}{c|cccccccccc|c}
 & I_1 & & & & & & & & & I_{10} & \\
\hline
S_i & 1 & 0 & 0 & 0 & 1 & 1 & 0 & 1 & 0 & 1 & 5 \\
S_j & 1 & 1 & 1 & 0 & 1 & 0 & 1 & 1 & 1 & 0 & 7 \\
\end{array}
$$

M3a

Simply re-arrange the pattern putting the co-occurrences and co-absences at the beginning so as to obtain:

$$
\begin{array}{c|cccccccccc|c}
S_i & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 5 \\
S_j & 1 & 1 & 1 & 0 & 1 & 1 & 1 & 1 & 0 & 0 & 7 \\
\end{array}
$$

M3b

Then drop the co-occurrences and co-absences to obtain:

$$
\begin{array}{c|cccccc|c}
S_i & 0 & 0 & 0 & 0 & 1 & 1 & 2 \\
S_j & 1 & 1 & 1 & 1 & 0 & 0 & 4 \\
\end{array}
$$

M3c

which has 2x4 = 8 checkerboard units.

The number of checkerboard units C_{ij}, between S_i and S_j, can be calculated for the general case as follows. Let S_{ij} be the number of co-occurrences between S_i and S_j (i.e., the number of islands upon which the two species Share). Taking r_i to be the i'th row sum, then

$$C_{ij} = (r_i - S_{ij})(r_j - S_{ij}) . \qquad (1)$$

The C-score statistic will be defined to be the mean number of checkerboard units per species-pair of the community. For M species, there are $P = M(M-1)/2$ species-pairs, and hence the C-score is:

$$C = \sum_{i<j} \sum C_{ij} / P . \qquad (2)$$

A Simple Example

I will now examine all 4-x-4 presence/absence matrices whose row and column sums are 2. Matrices $\underline{A}$ and $\underline{B}$ (below) are typical representatives.

$$\underline{A} = \begin{matrix} 1100 \\ 1100 \\ 0011 \\ 0011 \end{matrix} \qquad \underline{B} = \begin{matrix} 1100 \\ 1010 \\ 0101 \\ 0011 \end{matrix}$$

M4

The C-scores are respectively,

$$C(\underline{A}) = 16/6 = 2.67;$$

$$C(\underline{B}) = 12/6 = 2 .$$

Matrix $\underline{A}$ is thus taken to be more exclusive than $\underline{B}$.

§3.3 Equivalent Matrices

Two matrices will be said to be equivalent if they can be derived from each other merely by interchanging (i.e., swapping) rows or columns. Matrices $\underline{A}$ and $\underline{B}$ (in M4 above) are therefore non-equivalent, while matrices $\underline{A}$, $\underline{D}$ and $\underline{E}$ (in M5 below), are all equivalent.

$$\underline{D} = \begin{matrix} 1010 \\ 0101 \\ 1010 \\ 0101 \end{matrix} \qquad \underline{E} = \begin{matrix} 1001 \\ 1001 \\ 0110 \\ 0110 \end{matrix}$$

M5

One can confirm these equivalences by simple manipulation. For example, by interchanging column-2 with column-4 in matrix $\underline{A}$, one obtains $\underline{E}$. Biologically swapping rows or columns describes the relabelling of species or islands. Thus if one examines co-occurrence statistics - such as the number of species-pairs, -trios, etc. that share x islands - all equivalent matrices must have the same co-occurrence patterns (as C&S have pointed out).

The ensemble of allowable matrices may be divided up into a set of equivalence classes. Two matrices from distinct classes will be non-equivalent, while members of the same class will all be equivalent. The C-score can be shown to be invariant to row or column interchanging, so that members of the same equivalence class all have the same C-score. To see this, let C be the score of a given incidence matrix and suppose after swapping row-f with row-g that its new score is C'.

Thus $C' = \sum_{i<j} \sum C'_{ij} / P$ where P is the number of species-pairs.

After the row swap $C'_{fj} = C_{gj}$ and $C'_{gj} = C_{fj}$ for all j;

otherwise $C'_{ij} = C_{ij}$ for i,j ≠ f,g.

Hence
$$C' = \sum_{i<j} \sum C_{ij}/P = C \ ,$$

which proves the invariance of C after row interchanges. (An identical argument shows the C-score to be invariant to column interchanges.) From this invariance property it follows that equivalent matrices (or matrices in the same equivalence class) must necessarily have the same C-score.

By examining only non-equivalent matrices, Connor and Simberloff (1979) imply that, in the ensemble of allowable matrices, each distinct equivalence class should be given equal weight. For example, the highly exclusive equivalence class represented by matrix $\underline{A}$, would be given the same weight as the class of which matrix $\underline{B}$ is a member. In an attempt to justify this, I examined all 90 possible different 4-x-4 matrices of row and column sum two. It was found that there are only two equivalence classes to be found amongst the 90 possible distinct matrices (with matrices $\underline{A}$ and $\underline{B}$ belonging to different classes). There were

a) 18 distinct matrices equivalent to $\underline{A}$;

b) 72 distinct matrices equivalent to $\underline{B}$.

Thus matrices equivalent to $\underline{B}$ are four times commoner than the extreme checkerboards equivalent to matrix $\underline{A}$.

Recall that each matrix is supposed to represent a particular pattern produced by random colonization, whereas each equivalence class represents a particular co-occurrence pattern. In our case, the null hypothesis is that species colonize islands completely independent of interactions and therefore of any species co-occurrence preferences. There is no reason why one matrix or colonization pattern should be more probable than another. Thus distinct matrices (not equivalence classes) must be given equal probability measure, contrary to the procedure of

C&S, who weight each non-equivalent matrix (and therefore class or co-occurrence pattern) equally.

§4 Constructing Random Matrices

For constrained matrices larger than 4-x-4, it is extremely difficult to generate the full ensemble or even enumerate its size. To overcome this problem an attempt was made to construct a representative random sample from the ensemble with the aid of a computer. Two methods were employed and both ultimately yielded the same conclusions.

§4.1 The Method of Random Interchanges

Ryser (1957) in his study of the "Combinatorial properties of matrices of zeros and ones" proved that it is always possible to transform one matrix into any other, within the ensemble of matrices having the same row- and column-constraints, by a sequence of unit interchanges. Thus to generate a random sample of matrices from the ensemble, the computer constructed a sequence of allowable matrices, in which each successive matrix was obtained by implementing 100 random interchanges to its predecessor. In each of the cases described below, one thousand sample matrices were produced in this manner. The observed presence/absence matrix was used to initiate the sequence.

A "random interchange" was made as follows. Two different species, S_i and S_j, were chosen at random. All possible "latent interchanges" between these species were listed and their total number C_{ij} determined. A random integer r, between 1 and C_{ij}, was selected. The computer then implemented the r'th interchange on the list by performing the "flip" described in §3.1 .

Generating allowable matrices thus, by the method of random interchanges, is rather similar to Diamond's (1975) description of how

species are shuffled throughout the archipelago: "Combinations of colonists might be reshuffled through invasion and extinction until the best-suited groups of colonists had been assembled, and these would then persist" (p.440).

§4.2 The Milne Method

C&S (1979) attempted to generate a random sample of allowable matrices, in a manner that in some respects resembled the colonizing process (under the null hypothesis of random colonization). Thus species were (randomly) picked one at a time, and placed on a randomly chosen available island (subject to the three constraints). This continued until either the presence/absence matrix was filled, or a "hang-up" situation arose.

"Hang-ups" occur when, after inserting a number of 1's within the matrix, it becomes impossible to fill the matrix any further without breaking the given constraints. For example, the partially filled matrix M6a (below) can never be completed and has thus "hung up." M6b shows an allowable matrix subject to the same constraints as M6a .

$$
\begin{array}{cccc|c}
0 & 1 & 1 & 1 & 3 \\
0 & 1 & 1 & 0 & 2 \\
? & 0 & 0 & 0 & 2 \\
1 & 0 & 0 & 0 & 1 \\
\hline
3 & 2 & 2 & 1 &
\end{array}
$$
M6a

$$
\begin{array}{cccc|c}
1 & 1 & 1 & 0 & 3 \\
1 & 1 & 0 & 0 & 2 \\
1 & 0 & 1 & 0 & 2 \\
0 & 0 & 0 & 1 & 1 \\
\hline
3 & 2 & 2 & 1 &
\end{array}
$$
M6b

C&S found that "hang-up" situations occurred with great frequency when attempting to generate large and tightly structured matrices, by this matrix "filling" method. The problem leads to a large amount of computer time being required to produce a single allowable member of the ensemble. However, B. Milne recently developed a technique of randomly filling a constrained matrix so that a large number of allowable

matrices can be generated rapidly. The computer program made use of a look-ahead technique, whereby a "1" would be inserted in the matrix only if it would not produce a "hang-up" situation. Using this program there was little difficulty in quickly generating 1000 sample matrices for each data set that was examined.

§4.3 Analysing an Ensemble

To help explain the procedure employed, a simple example of 20-x-20 matrices with all row and column sums equal to ten (after G&D 1982) will be analysed. (This would portray an archipelago in which each of the twenty islands was inhabited by ten birds, and each of the twenty bird species present inhabited ten islands.) One thousand such matrices were generated randomly by the Milne method so that a frequency histogram for the C-score could be constructed (Figure 1a). The distribution was characterized by:

$<C> = 29.01$ and $\sigma(C) = .12$. (Sample size = 1000 .)

Random interchanging produced a similar histogram (Figure 1b) with
$<C> = 29.02$ and $\sigma(C) = .14$. (Sample size = 1000 .)

Note that the two methods give almost identical statistics.

In the given ensemble the most exclusive matrix would be equivalent to the matrix $\underline{U}$ given below.

```
     11111111110000000000        00101011110100001110
     11111111110000000000        11010100001011110001
     11111111110000000000        00101111001001001110
     11111111110000000000        11010000110110110001
     11111111110000000000        10110000000011111011
     11111111110000000000        01001111111100000100
     11111111110000000000        10011101011001001100
     11111111110000000000        01100010100110110011
     11111111110000000000        00101011100100110110
U =  11111111110000000000   V =  11010100011011001001
     00000000001111111111        11010111100001011000
     00000000001111111111        00101000011110100111
     00000000001111111111        10000111100011001110
     00000000001111111111        01111000011100110001
     00000000001111111111        11001100100111000110
     00000000001111111111        00110011011000111001
     00000000001111111111        00010101101011101010
     00000000001111111111        11101010010100010101
     00000000001111111111        01101101010001010101
     00000000001111111111        10010010101110101010
```

$$C(U) = 52.6 \qquad\qquad C(V) = 30.3$$

M7

Matrix U has a C-score of $C(U) = 52.6$, almost 200σ to the extreme right of the mean. Not one of the 1000 randomly generated matrices had a C-score so extreme. Thus the C-test easily picks high levels of exclusiveness.

D&G (1982) examined the matrix V given in M7 (their Figure 4), where ten out of the possible 190 pairs are in a "perfect checkerboard" arrangement. They reported that although the "inference of exclusion was very strong" in this matrix, the C&S test could not distinguish anything unusual. But upon evaluating the C-score for the matrix, it was found $C(V) = 30.3$. Using the Monte Carlo estimates for the distribution parameters (see above), this value exceeds the mean by more than ten standard deviations. To confirm the rarity thus indicated, of the 1000 randomly generated allowable matrices I examined, not one was found to be so highly exclusive. Thus the C-test finds V to be significantly exclusive.

§5 Analysis of Field-Data

§5.1 The New Hebrides Birds (NHB)

The presence/absence matrix for the NHB birds (56 bird species on 28 islands), presented in Appendix 1, was constructed from data in Diamond and Marshall (1976). Because the matrix appears to be so highly aggregated, it would be difficult to imagine how this pattern could be anything but "non-random". However, C&S argue that given the marginal distributions of the row and column sums as well as incidence ranges, the observed data is strikingly close to what one would expect, had the birds colonized randomly.

The NHB data examined by C&S (1979) will now be re-analysed using Milne's program outlined above, and making use of the C-test. Upon randomly filling 1000 matrices, subject to the constraints derived from the actual NHB community (i.e., row and column sums as well as incidence ranges), the histogram of Figure 2a was obtained, giving:

$<C> = 9.13$ and $\sigma(C) = .07$.   (Sample size = 1000.)

The same test was performed again using the method of random interchanges and the statistics found (see the histogram in Figure 2b) were similar to those obtained by the Milne method. The method of interchanges gave:

$<C> = 9.12$ and $\sigma(C) = .07$.   (Sample size = 1000.)

Yet the observed matrix had the score $C(NHB) = 9.53$, almost 6σ above the mean. In both methods, not one of the sample of 1000 matrices had a C-score larger than that of the observed NHB data. The NHB community is thus highly exclusive, far out of the range one would expect from a null hypothesis of random colonization.

These results conflict sharply with those obtained by C&S, whose test produced a very close matching between the observed and expected

matrix, with χ^2 = 16.34 (27 d.f.) giving .95 > P > .90 . An explanation for this difference will be given in §6.

§5.2 The Antillean Bats (AB)

The above analysis was repeated for the AB data (59 bird species on 25 islands) given in Baker and Genoways (1978). The ensemble's distribution (see Figure 3a) as found by the Milne method gave:

<C> = 3.44,   and   σ (C)= .05   (Sample size = 1000.)

or by the method of random interchanges (see Figure 3b):

<C> = 3.45,   and   σ (C)= 0.06 .   (Samples size = 1000.)

The observed matrix had the score C(AB) = 3.57 , which (by the Milne method) was found to be 2.6 standard deviations above the mean (or 2σ, by the method of random interchanges). To confirm the rarity of the observed matrix, of the 1000 allowable matrices randomly generated by the Milne method, only 20 (2%) were found to be so highly exclusive. By the "method of interchanges", 42 (4%) of a sample of 1000 allowable random matrices were as exclusive.

§6 Correcting R-Mode Analyses

C&S (1979) tested the null hypothesis of random colonization by what they termed R-mode analysis (see Simberloff and Connor 1979 for developmental details of the analysis). The test examined the statistics P_j, the number of pairs of species sharing j = 0,1,2,.....N islands. By Monte Carlo techniques each of the variables P_j were analysed and their expected values and variances estimated. These were then compared to the observed values of the real biogeographic data. A Chi-square (χ^2) test was performed on the (N+1) statistics to see if the observed data differed significantly from that expected. For the NHB community, they obtained an excellent fit, χ^2 =16.34 (27 d.f.), .9 < P < .95 so that the

observed matrix seemed no different to that expected had the islands been colonized randomly.

D&G criticized the C&S test on the grounds that it was based on only 10 sample matrices. Because each sample matrix differed from the other only by a "few interchanges", it was unlikely that they were independent samples. When they repeated the C&S test, using 50 sample matrices, each differing from the other by 500 interchanges, their χ^2 test gave $.1 < P < .25$. However this result still does not give sufficient grounds to reject the null hypothesis.

We repeated the same analysis, utilizing the "method of random interchanges". On our first test, 10 random matrices were generated, each differing from the other by 10 interchanges, and giving a similar result to C&S, i.e., $\chi^2 = 17.55$ (27 d.f.), $.90 < P < .92$. Figure 4a displays the expected distribution of the P_j, and superimposed upon it is the observed P_j for the NHB data. Even when a more extensive investigation was performed, with 1000 sample matrices each differing by 100 interchanges, the hypothesis of random colonization could still not be rejected $(\chi^2 = 20.19$ (27 d.f.), $.78 < P < .83$ - see Figure 4b.). To a great extent this result concurs with that of C&S as given above. The question remains then: Why does the C-score find the observed data so particularly unusual whilst R-mode analysis does not?

A partial answer to the above question may be obtained by a closer examination of the statistics P_j. All the above R-mode analyses make the assumption that the (N+1) variables P_j, have N degrees of freedom. For the NHB community of 28 islands, C&S assumed that (after lumping together two variables) there were in fact 27 degrees of freedom. However, because of the effects of row and column constraints, one must also expect the P_j to be considerably dependent (as shown in Appendix 4). To accurately estimate the degrees of freedom of the P_j,

1000 matrices were generated by the "method of random interchanges" and the distribution of their χ^2 values was obtained (after previously determining the expected value for each of the P_j statistics for these same matrices) and plotted in Figure 5. One sees from Figure 5 that the distribution has a mean $\mu = 12.63$. Since the mean of a χ^2 distribution also corresponds to the number of degrees of freedom, then the P_j must have approximately 13 degrees of freedom; not the 27 assumed by C&S.

Because of the critical nature of the χ^2 test, a poor estimation of the degrees of freedom can give misleading results. If C&S had allowed for 13 degrees of freedom, their results would be far less spectacular ($\chi^2 = 16.34$ (13 d.f.), $.22 < P < .25$). The results of our 1000 sample R-mode analysis were even less convincing ($\chi^2 = 20.19$ (13 d.f.), $.07 < P < .1$).

R-Mode analyses have the potential to be a very important tool for ecological research, but to obtain meaningful results, extreme care is required. The effects of constrained variables can unwittingly be neglected, leading to biased conclusions. The method given above is one possible way of eliminating these biases. However, even after determining the degrees of freedom empirically, it still appears that the C-score test for checkerboardedness is a more sensitive and more powerful test than R-mode analysis.

§7 Coexistence or Exclusion?

§7.1 The Relation Between Checkerboard Patterns and Aggregation

Both the NHB and AB data sets possess significantly high C-scores when compared with ensembles of allowable matrices each obeying the observed incidence constraints. If checkerboard patterns could arise only from competitive exclusion, then one could conclude from the C-test that the process of competition is significant in these archipelagos.

There are, however, quite plausible alternative explanations for these checkerboard patterns - for example:

1) As C&S (1979) point out, checkerboard distributions could well arise from allopatric speciation, where formerly conspecific populations geographically speciate without subsequent reinvasion. The checkerboard distributions that are created are thus independent of present competition.

2) The C-score is intimately linked with species co-occurrences so that as C&S (1983) point out: "many exclusive patterns are expected for non-competitive reasons" (p.457). To see this, return once more to the matrix $\underline{U}$ in M7, which possesses an extremely high C-score when compared to that expected under a hypothesis of random colonization. Despite the high checkerboardedness of $\underline{U}$, it appears that aggregation, or the sharing of islands by species-pairs, is also extreme.

To examine this apparent contradiction in more depth, consider the sub-matrix presented in M8, where S_i and S_j co-occur on island p but are both absent from island q.

$$
\begin{array}{c|cc}
 & I_p & I_q \\
\hline
S_i & \dots\dots1\dots\dots\dots & \dots\dots0\dots \\
S_j & \dots\dots1\dots\dots\dots & \dots\dots0\dots \\
\end{array}
$$

M8

Let T_{ij} be the number of such submatrices in which the species-pair S_i and S_j are together on an island but both missing from another. Further, let T be the mean number of such submatrices per species-pair. If there are P species-pairs, then

$$ T = \sum_{i<j} \sum T_{ij}/P \quad . $$

Appendix 1 shows that for all matrices with the same row and column constraints, the C-score and the above T-score differ only by a fixed

constant i.e.,   C = T + constant.

This identity confirms that the extremely checkerboarded matrix U̲ also possesses a significantly large T-score, so that the aggregation of species-pairs on islands is far greater than that expected had the islands been colonized randomly.

Although competition might be responsible for the disjoint aggregations seen in U̲, many other processes could equally well be the cause - for example:

a) Suppose there are two different colonization routes, so that species 1 to 10 colonize islands 1 to 10 while species 11 to 20 colonize islands 11 to 20. If we assume that all islands have suitable habitat conditions to support its inhabitants and that there is only a small amount of inter-island dispersion, then the presence/absence matrix U̲ will result. In these circumstances, with absolutely no competition occurring at all, the C-score would be extreme - and so too would aggregation. In fact, for the New Hebrides avifauna, Diamond and Marshall (1976) claim that there are likely to be five different colonization routes. They also reported that some species do lose their inter-island dispersal ability upon invading an island (Diamond and Marshall 1976);

b) Suppose islands 1 to 10 had suitable habitats only for species 1 to 10, while the remaining species, because of their habitat requirements, could only survive on islands 11 to 20. Again, in the complete absence of competitive processes, the presence/absence matrix U̲, with its extreme C-score, would result. Diamond and Marshall (1976) noted that "certain specialized habitats are absent or scarce on many New Hebridean islands and occur extensively only on certain islands, generally larger islands..." (p.712). This factor alone could well bring about unusual aggregation of species, and would arise independently of the

species/area relationship or of competition.

For reasons as those given above, any row- and column-constrained presence/absence matrix in which checkerboardedness is extreme, will be found to have significant aggregations of species. As a result, checkerboardedness cannot be the "simplest and clearest pattern that might be produced by competition" as D&G (1982 p.65) suggested, for if it were, then one would be forced to conclude that the tendency for species to share islands would be the "simplest and clearest pattern that might be produced by competition".

That is not to say that competition must be ruled out as a possible inference in these circumstances. Some patterns of aggregation could be the result of a "well-matched set of related species, and possibly co-evolved local populations, that competitively exclude invaders for long times.." (Diamond and Marshall 1976, p.722). However, as we have seen, aggregations might easily arise from a variety of other factors.

§7.2 The Coexistence Principle

The problem of whether or not ecologically similar species competively exclude one another, or whether they coexist and aggregate together, is an old one. Directly relevant is the work of Williams (1951 p.253) in his study of East African Bird communities. He found:

"(1) That biological competition between closely related species is probably on average greater than that between those less closely related.

(2) That closely related species are probably more suited to similar physical environments, and to similar extra-generic competition.

(3) That the balance of these two major factors, physical and biological, which determine the survival of species in different

habitats, as shown by actual proportional survival in Nature, appears to indicate that the advantages of close relationship are on average greater than the drawbacks."

den Boer (1980) drew on Williams' work when he framed the coexistence principle: "Taxonomically closely related species are also ecologically closely related, and will thus be found coexisting in the same sites more frequently than could be expected by a random distribution of species..." (p.300).

§7.3 Testing at the Family Level

The coexistence principle can be tested by examining species-pairs amongst the New Hebrides birds that are ecologically similar. Since the ecological guilds within the New Hebrides have not as yet been delineated, the test will be conducted on all confamilial bird species. G&D (1982) pointed out that bird families do not necessarily conform with ecological guilds. However, as Graves and Gotelli (1983) conclude after a review, it is difficult to classify these complex avifaunas in any more accurate way than that given by families. Graves and Gotelli "do not believe families represent units of interspecific competition. However, species within a family are usually ecologically and morphologically similar; therefore non-randomness of island avifaunas may be detected at the family level" (p.331).

The 56 bird species were divided up into 16 families as listed in Appendix 3. Their C-score, C_{fam}, was then calculated for the 70 confamilial species-pairs in the observed incidence matrix, and compared to the same confamilial C-score calculated for random colononization. The latter distribution, obtained by the "method of random interchanges", was characterized by:

$<C_{fam}(random)>$ = 7.38 and $\sigma(C_{fam}(random))$ = 0.84 . (1000 samples.)

The observed score was: C_{fam}(Observed) = 5.64 ,

over 2σ below the expected value. In the sample of 1000 randomly constructed matrices, only 21 had a C_{fam}-score less than the observed data. Hence the checkerboard score within families, that Diamond (1975) and G&D (1982) associate with competition, is far less than that expected from random colonization.

Since we are examining a subset of the avifauna (i.e., the confamilial species), which do not have fixed row- and column-constraints, the value of C - T (of Appendix 2) is no longer a constant over the ensemble. Thus we cannot conclude that the exceptionally low observed C_{fam} implies an observed T_{fam} that is likewise exceptionally low. Therefore it is of interest to examine whether aggregations and sharing by confamilial species-pairs (T_{fam}), is greater or less than that expected from random colonization. It was found that:

$$<T_{fam}> = 21.80 \quad \text{and} \quad \sigma(T_{fam}) = 1.36 . \qquad (1000 \text{ samples.})$$

The observed score was: T_{fam}(Observed) = 25.36 ,

approximately 2.6σ greater than the expected value. Of the 1000 randomly constructed matrices, only 9 had an T_{fam}-score greater than the observed data.

Thus, aggregations and sharing are excessive between members of a confamilial pair. So these species which are closely related ecologically, are found coexisting in the same sites significantly more than could be expected by a random distribution of species. Further, the score derived by checkerboard patterns - that is a measure of the strength which species exclude one another (if they do) - is significantly less than that expected from a random distribution of species. These two results, when taken together, go against the

hypothesis of competitive exclusion, and instead give some support to the coexistence principle.

§8 Conclusion

The null hypothesis approach for detecting the presence of non-randomness in ecological communities is becoming an important tool for ecologists (see for example, Case and Cody 1983, Colwell and Winkler 1984, Hopf and Brown 1986, Strong 1980, Van Valen 1985, Harvey et al 1983). We have seen that the complexity involved in carrying out such tests is great, and that results can depend critically upon methods and assumptions employed. Although firm conclusions are difficult to achieve, the analysis presented in this chapter showed that these tests can be particularly useful, acting as a springboard with which to challenge our ideas and preconceptions about island communities.

Using a null model, it was found that both the NHB and AB data sets indicate significant levels of checkerboard distributions when analysed with the C-test. The null hypothesis, that the data is little different from what one would expect, had the islands been randomly colonized, is most unlikely. Although others have reached similar conclusions (Gilpin and Diamond 1982, Wright and Biehl 1982), to our knowledge none have done so in a correctly posed test that allowed for all the constraints assumed by C&S.

If the constraints had incorporated built-in hidden structures such as competition (a possibility that was discussed above) then one would expect this to filter out or reduce the amount of associated checkerboard distributions. However, it was found that even when including all constraints, both the NHB and AB data displayed significant levels of checkerboard distributions. Must we therefore conclude that biological factors exist which tend to keep species apart?

If competition was responsible for these checkerboard distributions, then one would expect such patterns to be most easily observed amongst the confamilial species. However, in the New Hebrides, the checkerboard score between these ecologically similar species was significantly lower than that expected. Surprisingly, the amount of aggregation between confamilial species was unusually high. Thus the New Hebrides avifauna did not appear to display patterns associated with competition. More plausibly, the presence/absence matrix can be taken to exhibit the aggregation associated with the coexistence principle.

Appendix 1

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Incidence matrix of the New Hebrides birds after relabelling rows and columns according to rank. (Data taken from Diamond and Marshall 1976.)

Appendix 2

In this Appendix the relation $C = T + \text{constant}$ is derived.

Let S_{ij} be the number of islands species i and j Share.

Forming the matrix $\underline{A}\,\underline{A}^T$ and one finds:

$$S_{ij} = (\underline{A}\,\underline{A}^T)_{ij} = \sum_k a_{ik}a_{jk} \ .$$

Note that $\sum_i \sum_j S_{ij} = \sum_i \sum_j \sum_k a_{ik}a_{jk} = \sum_k (\sum_i a_{ik})(\sum_j a_{jk}) = \sum_k c_k^2$,

where $c_k =$ the k'th column sum of the incidence matrix $\underline{A}$.

$$\sum_i S_{ii} = \sum_i \sum_j a_{ij}a_{ij} = \sum_i \sum_j a_{ij}^2 = \sum_i \sum_j a_{ij} = \sum_i c_i \ .$$

$$\sum_{i<j} S_{ij} = \frac{1}{2}\left(\sum_i \sum_j S_{ij} - \sum_i S_{ii}\right) = \frac{1}{2}\left(\sum_i c_i^2 - \sum_i c_i\right) = k_1, \text{ a constant.}$$

Define V_{ij} to be the number of snubs between species S_i and S_j, i.e., the total number of islands on which S_i inhabits or S_j inhabits but upon which both species are not found together.

Now $V_{ij} = (r_i - S_{ij}) + (r_j - S_{ij}) = r_i + r_j - 2S_{ij}$,

where r_i represents the number of islands species i inhabits - i.e., the row sums of the incidence matrix.

Because, for any incidence matrix with the same row and column constraints the sum of the row sums is constant and $\sum_{i<j}\sum S_{ij}$ is constant, then the total number of snubs is $\sum_{i<j}\sum V_{ij} = \text{constant}$.

As before, let C_{ij} be the number of Checkerboard submatrices of the form:

$$\begin{matrix}1 & 0 \\ 0 & 1\end{matrix} \quad \text{or} \quad \begin{matrix}0 & 1 \\ 1 & 0\end{matrix} \qquad \text{between species i and j,}$$

and $C = \sum_{i<j}\sum C_{ij} / P$ taken over all P species pairs.

Equation 1 shows that $C_{ij} = (r_i - S_{ij})(r_j - S_{ij})$,

where r_i was the i'th row sum of the incidence matrix $\underline{\underline{A}}$,

and S_{ij} was taken to be the number of islands both species Share.

The number of islands species i and j are both absent from is given by:

$(n - S_{ij}) - (r_i - S_{ij}) - (r_j - S_{ij}) = n - r_i - r_j + S_{ij}$ (since there are n islands

Now let T_{ij} be the number of submatrices of the form:

1 0   or   0 1   in which the two species are Together on one island
1 0   0 1   but not the other.

Let $T = \sum_{i<j} \sum T_{ij} / P$.

Thus $T_{ij} = S_{ij}(n - r_i - r_j + S_{ij})$,

and $C_{ij} - T_{ij} = r_i r_j - n S_{ij}$.

Summing over i and j, $C - T = (\sum_{i<j} \sum r_i r_j - n \sum_{i<j} \sum S_{ij})/P$ = constant,

so that $C = T + \text{constant}$.

Appendix 3

Species	Family
1	Podicipedae
2,3	Ardeidae
4,5,6	Anatidae
7,8	Accipitridae
9	Falconidae
10	Megapodiidae
11,12,13,14	Rallidae
15,16,17,18,19,20,21,22	Columbidae
23,24	Psittacidae
25,26	Cuculidae
27	Tytonidae
28,29,30	Apodidae
31,32	Alcedinidae
33	Hirundinidae
34,35,36	Campephagidae
37	Turdidae
38,39	Sylviidae
40,41,42,43,44,45	Muscicapidae
46	Pachycephalidae
47	Artamidae
48,49	Sturnidae
50,51,52	Meliphagidae
53,54	Zosteropidae
55,56	Ploceidae

Appendix 4

It will be shown here that the P_j are highly dependent.

For demonstration purposes consider a hypothetical arrangement that might arise in some incidence matrix. Suppose S_1 and S_2 are together on 5 islands - i.e., $T_{12} = 5$.

Suppose also that 9 species-pairs share 4 islands and 8 species-pairs share 5 islands. Hence:

$$P_4 = 9 \qquad \text{and} \qquad P_5 = 8.$$

Assuming an interchange can be made that will cause species S_1 and S_2 to be together on one less island so that

$$T_{12} = 4.$$

Because of the interchange, it will nearly always result that the number of species-pairs sharing 4 islands will rise one unit, whilst the number of species-pairs sharing 5 islands will lower by one unit, making

$$P_4 = 10 \qquad \text{and} \qquad P_5 = 7 .$$

On the basis of one interchange alone, this example shows how P_4 and P_5 have large negative correlation. Thus the P_j are highly dependent.

"Test"   (Mean = 29.01, Sigma = .12)

(Milne method)

Figure 1a.

"TEST"   (Mean = 29.02, Sigma = 0.14)

(by interchanges)

Figure 1b.

221.
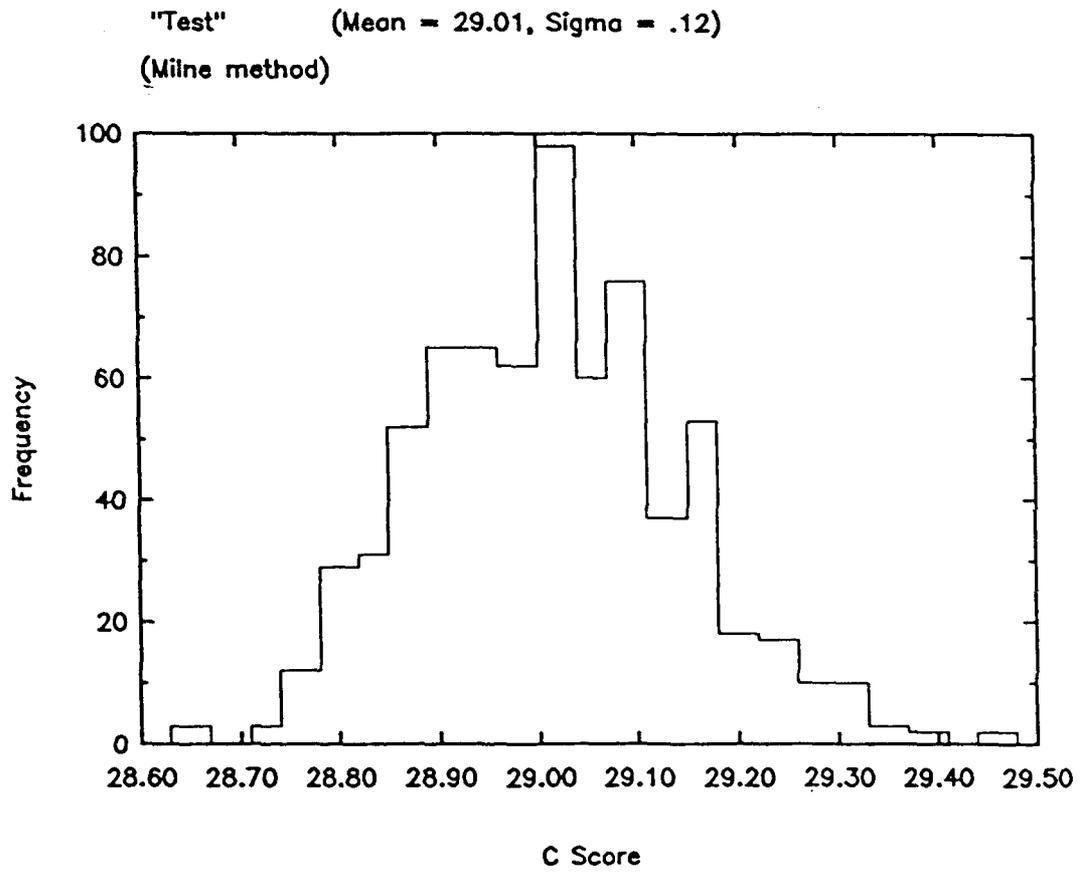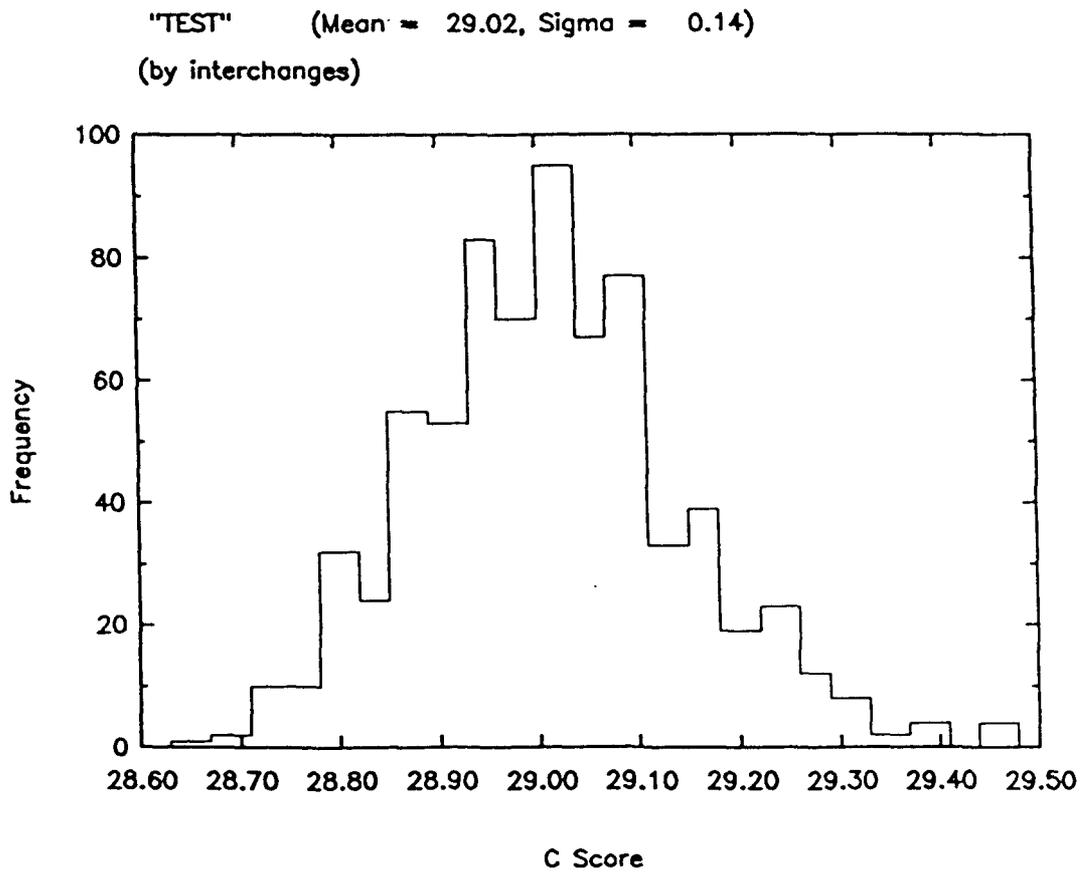
"New Hebrides Birds" (Mean = 9.13, Sigma = .07)

(Milne method)

C Score
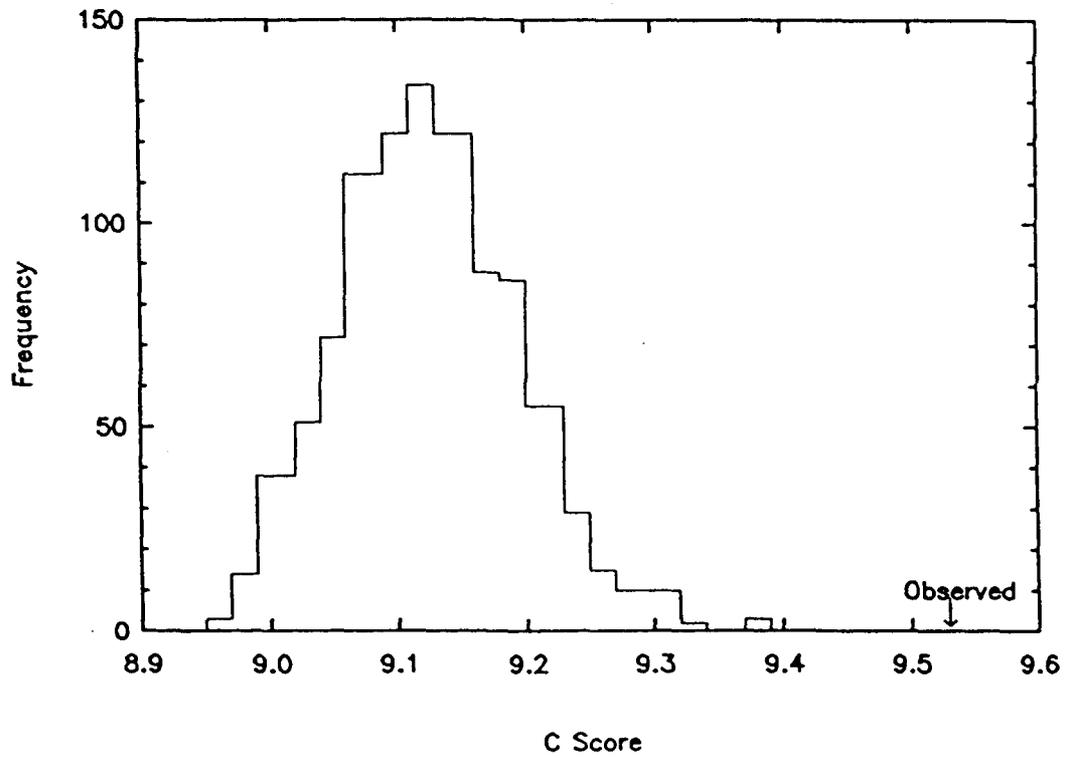
Figure 2a.

"New Hebrides Birds" (Mean = 9.12, Sigma = 0.07)

(by interchanges)

C Score

Figure 2b.

"Antillean Bats" (Mean = 3.44, Sigma = .05)

(Milne method)

Figure 3a.

"Antillean Bats" (Mean = 3.45, Sigma = 0.06)
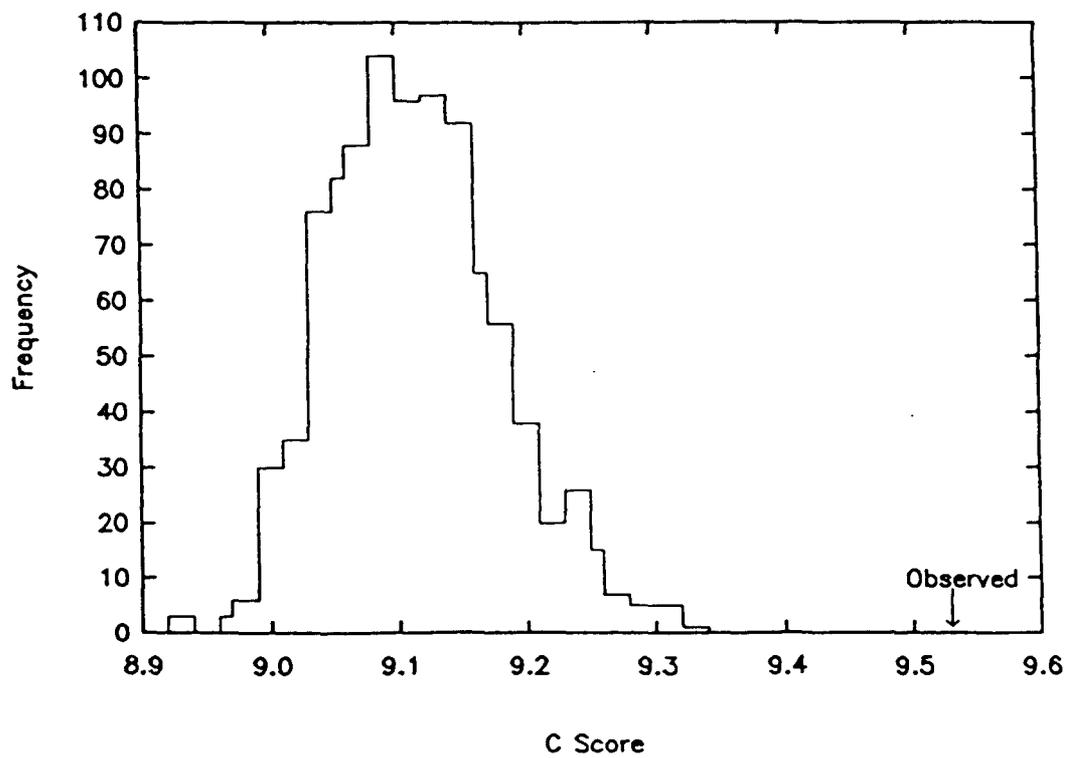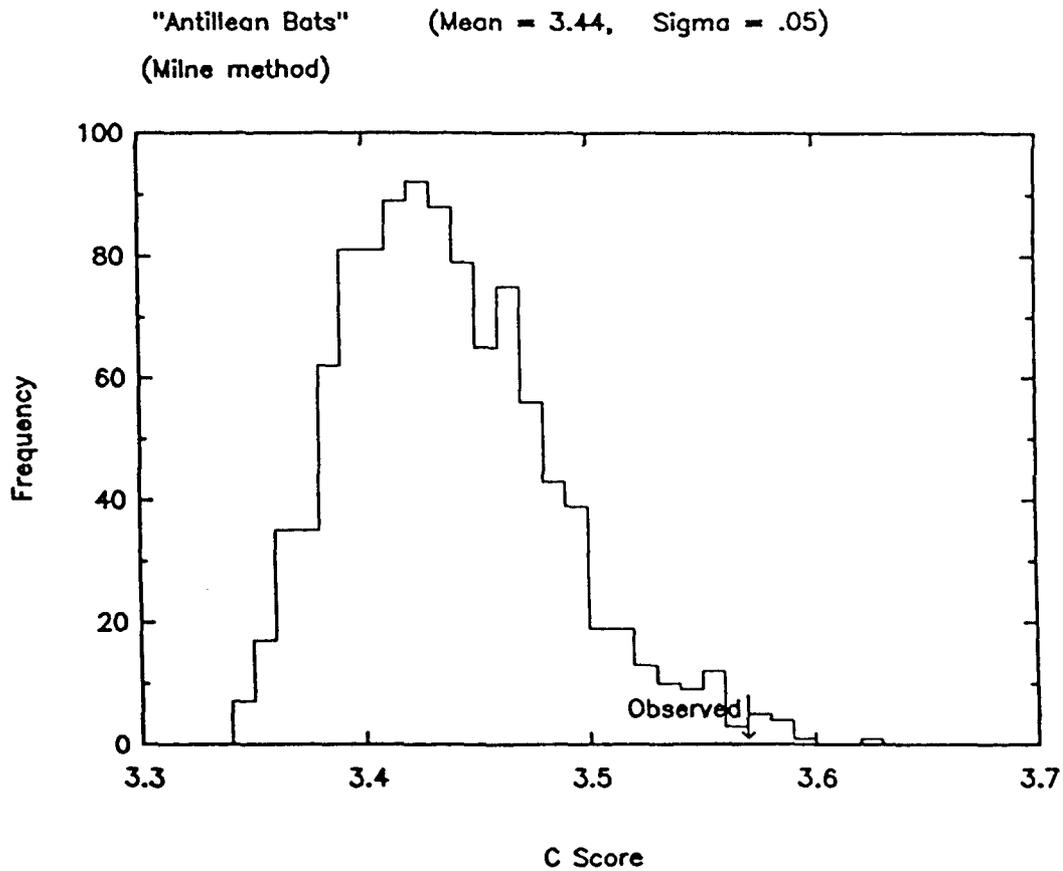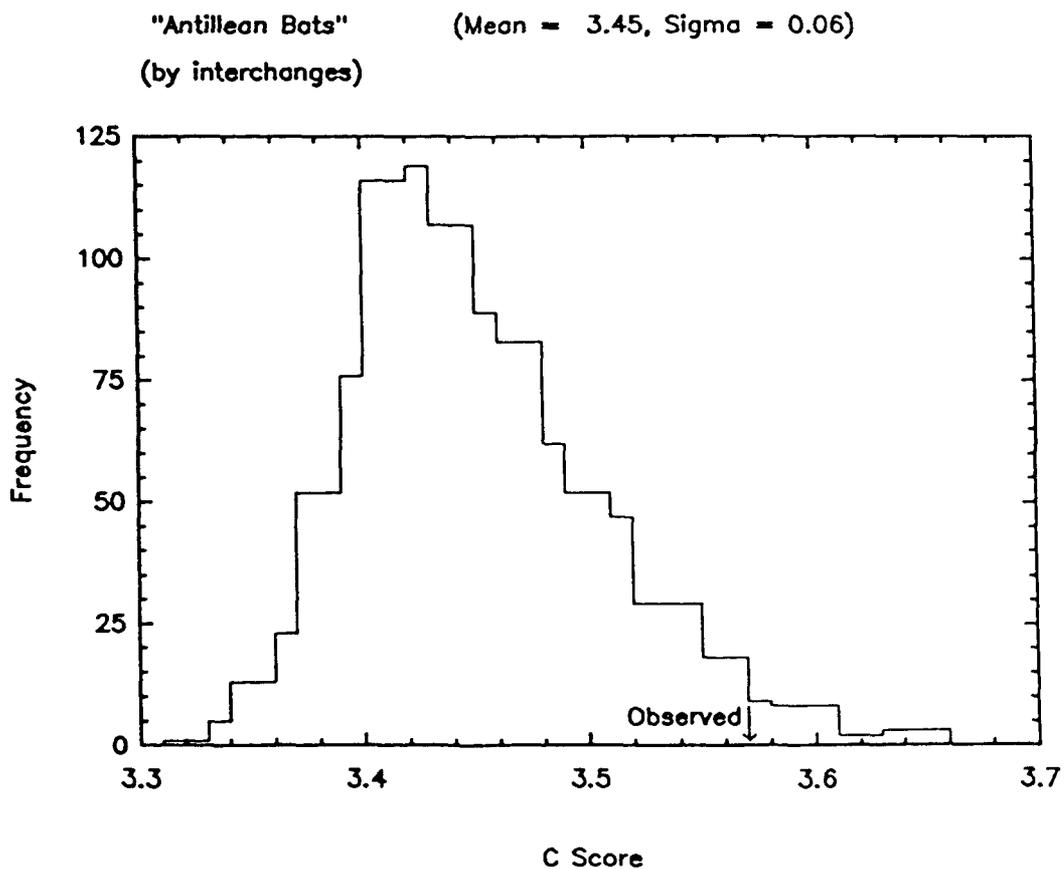
(by interchanges)

Figure 3b.

10 Sample Matrices — each derived from 10 interchanges
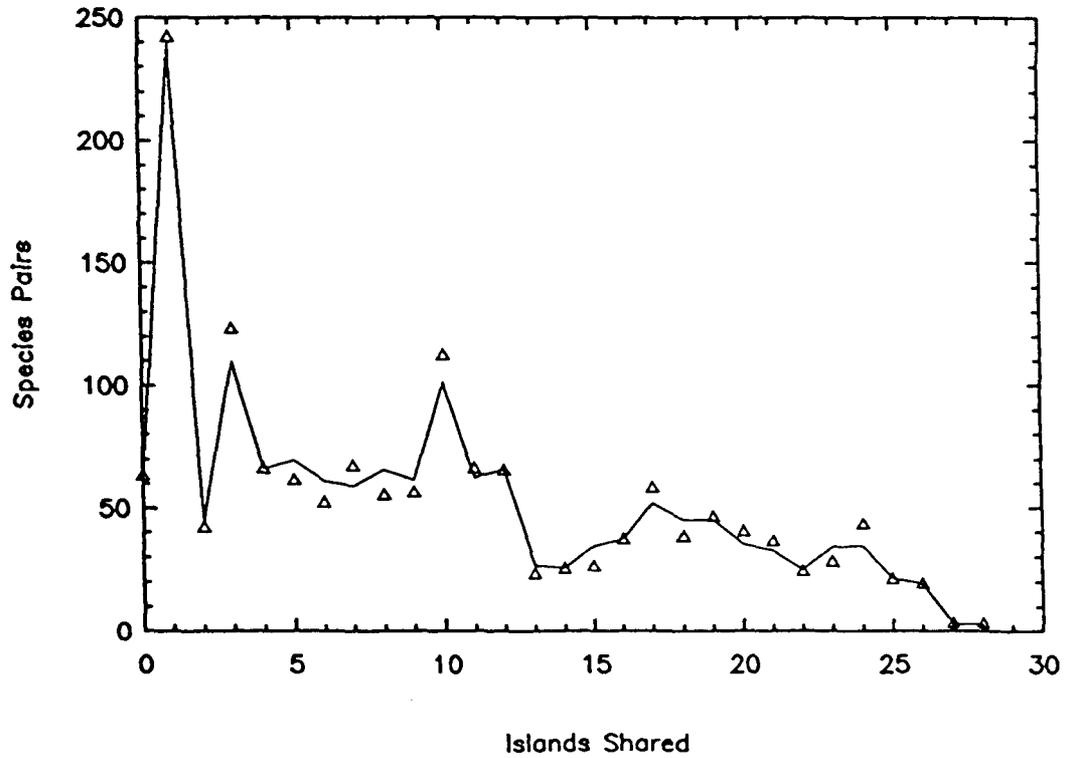

Figure 4a.

1000 Sample Matrices — each derived from 100 interchanges
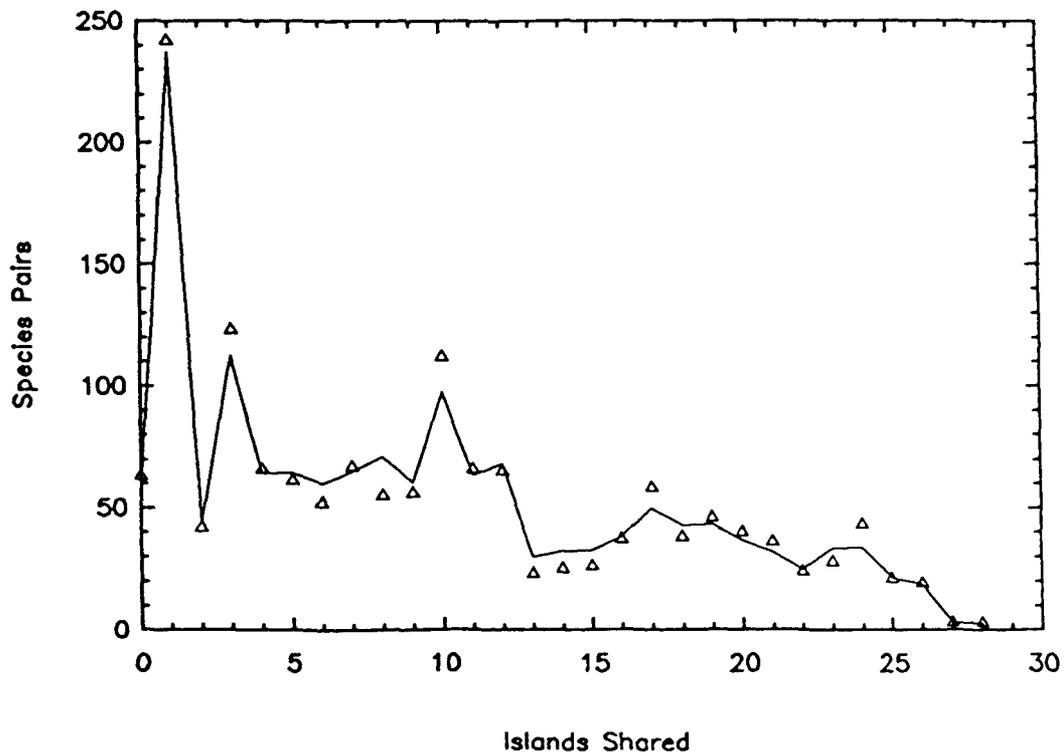
Figure 4b.

New Hebrides Birds — Chi Distribution (1000 samples).

Mean = 12.63, Sigma =4.13, Observed = 20.19
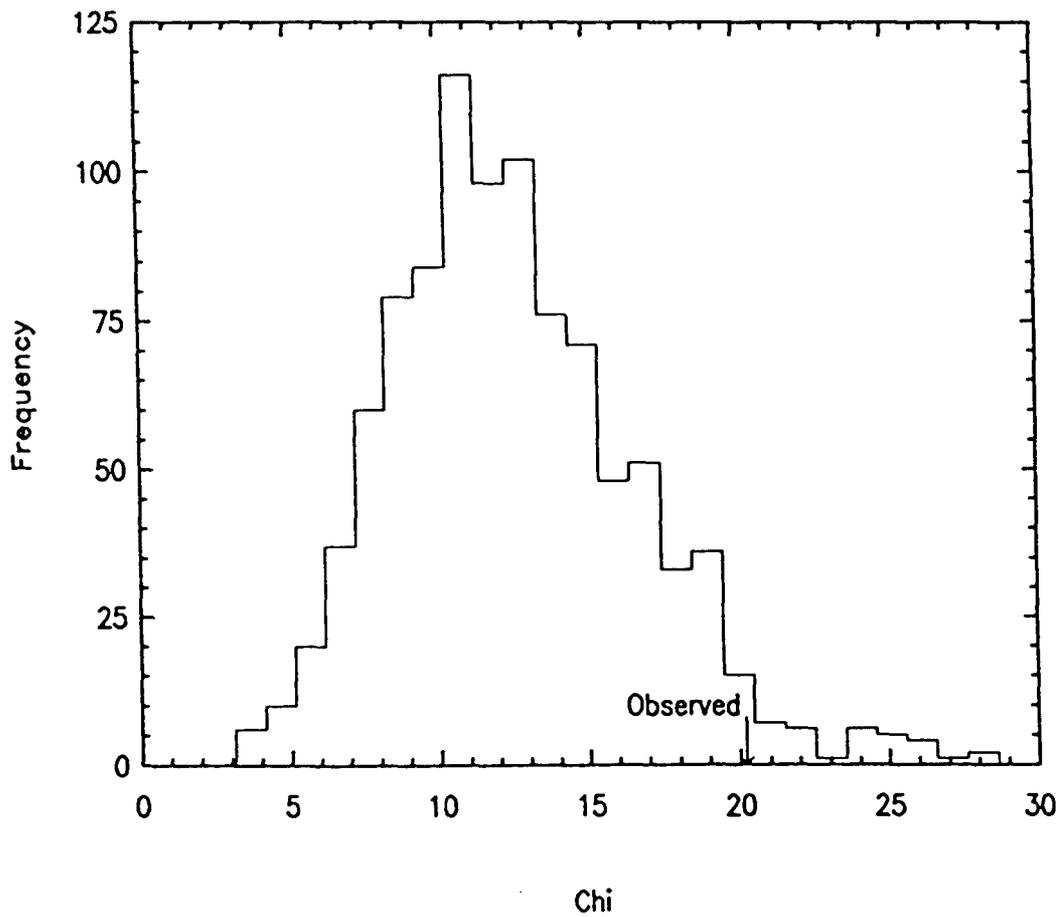
Figure 5.

Bibliography

Aarssen, L.W. 1983.
Ecological combining ability and competitive combining ability in plants:
towards a general evolutionary theory of coexistence in systems of competition.
The American Naturalist 122:707-731.

Aarssen, L.W. 1984.
On the distinction between niche and competitive ability:
Implications for coexistence theory.
Acta Biotheoretica 33:67-83.

Abrams, P. 1975.
Limiting similarity and the form of the competition coefficient.
Theoretical Population Biology 8:356-375.

Abrams, P. 1980.
Are competition coefficients constant? Inductive versus deductive approaches.
The American Naturalist 116:730-735.

Aitken, A.C. 1958.
Determinants and Matrices.
Oliver and Boyd, Edinburgh.

Allee W.C., Emerson A.E., Park O., Park T. and Schmidt K.P. 1949.
Principles of Animal Ecology.
W.B. Saunders Company, Philadelphia.

Andrewartha, H.G. and Birch, L.C. 1954.
The Distribution and Abundance of Animals.
The University of Chicago Press, Chicago, Illinois.

Andrewartha, H.G. and Birch, L.C. 1984.
The Ecological Web.
The University of Chicago Press, Chicago, Illinois.

Aristotle's Physics, Books I and II.
Translated Charlton W.,
Oxford University Press, 1970.

Atsatt, P.R. and O'Dowd, D.J. 1976.
Plant defense guilds.
Science 193:24-29.

Auerbach, M.J. 1979.
Some real communities are unstable.
Nature 279:821-822.

Baker, R.J. and Genoways, H.H. 1978.
Zoogeography of Antillean bats.
Pages 53-97 in F.B. Gill, editor.
Zoogeography in the Carribean: The 1975 Leidy Medal Symposium.
Academy of Natural Sciences of Philadelphia.
Philadelphia. Pennsylvania. USA.

Bender, E.A., Case, T.J. and Gilpin, M.E. 1984.
Perturbation experiments in community ecology: Theory and practice.
Ecology 65:1-13.

Berman, A. and Hershkowitz, D. 1983.
Matrix diagonal stability and its implications.
SIAM J. Alg. Disc. Meth. 4:377-382.

Berman, A. and Plemmons, R.J. 1979.
Nonnegative matrices in the mathematical sciences.
Academic Press, New York.

Birch, L.C. 1979.
The effect of species of animals which share common resources on
one another's distribution and abundance.
Fortschrift Zoology 25:197-221.

Boecklen, W.J. and NeSmith, C. 1985.
Hutchinsonian ratios and log-normal distributions.
Evolution 39:695-698

Bookchin, M. 1982.
The Ecology of Freedom.
Cheshire Books Inc., Palo Alto, California.

Botkin, D.B. and Sobel, M.J. 1975.
Stability in time-varying ecosystems.
The American Naturalist 109:627-646.

Boucher, D.H., editor, 1985a.
The Biology of Mutualism.
Croom Helm, London & Sydney.

Boucher, D.H. 1985b.
The idea of mutualism, past and future.
Pages 1-28 in Boucher, D.H., editor.
The Biology of Mutualism.
Croom Helm, London & Sydney.

Boucher, D.H., James, S. and Keeler, K.H. 1982.
The ecology of mutualism.
Ann. Rev. Ecol. Syst. 13:315-347

Briand, F. and McCauley, E. 1978.
Cybernetic mechanisms in lake plankton systems:
How to control undesirable algae.
Nature 273:228-230.

Brown, J.H. 1981.
Two decades of homage to Santa Rosalia:
Toward a general theory of diversity.
American Zoologist 21:877-888.

Case, T.J. and Casten, R.G. 1979.
Global stability and multiple domains of attraction in ecological systems.
The American Naturalist 113:705-714.

227.

Case, T.J. and Cody, M.L. 1983.
Synthesis: Pattern and processes in island biogeography.
Chapter 12:307-341 in Case, T.J. and Cody, M.L. editors.
Island Biogeography in the Sea of Cortez.

Chesson, P.L. 1986.
Environmental variation and the coexistence of species.
Pages 240-256 in Diamond, J. and Case, T.J., editors.
Community Ecology.
Harper & Row Publishers, New York.

Chesson, P.L. and Case, T.J. 1986.
Overview: Nonequilibrium community theories:
Chance, variability, history, and coexistence
Pages 229-239 in Diamond, J. and Case, T.J., editors.
Community Ecology.
Harper & Row Publishers, New York.

Clements, F.E. 1935.
Experimental Ecology in the Public Service.
Ecology 16:342-363.

Cluett, H.C. and Boucher, D.H. 1983.
Indirect mutualism in the legume- Rhizobium- mycorrhizal fungus interaction.
Oecologia 59:405-408.

Cody, M.L. 1981.
Habitat selection in birds:
The role of vegetation structure, competitors, and productivity.
BioScience 31:107-113.

Cody, M.L. and Diamond, J.M, editors 1975.
Ecology and Evolution of Communities.
Belknap Press, Harvard University.

Cohen, J.E. 1971.
Mathematics as metaphor.
Science 172:674-675.

Colwell, R.K. and Winkler, D.W. 1984.
A null model for null models. Pages 316-331 in
Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., editors.
Ecological Communities: Conceptual Issues and the Evidence.
Princeton University Press.

Connell, J.H. 1975.
Some mechanisms producing structure in natural communities:
A model and evidence from field experiments.
Pages 460-490 in Cody, M.L. and Diamond, J.M, editors.
Ecology and Evolution of Communities.
Belknap Press, Harvard University.

Connell, J.H. 1978.
Diversity in tropical rain forests and coral reefs.
Science 199:1302-1310.

Connell, J.H. 1983a.
On the prevalence and relative importance of interspecific competition:
Evidence from field experiments.
The American Naturalist 122:661-696.

Connell, J.H. 1983b.
Interpreting the results of field experiments:
Effects of indirect interactions.
Oikos 41:290-291.

Connell, J.H. and Sousa, W.P. 1983.
On the evidence needed to judge ecological stability or persistence.
The American Naturalist 121:789-824.

Connor, E.F. and McCoy, E.D. 1979.
The statistics and biology of the species-area relationship.
The American Naturalist 113:791-833.

Connor, E.F. and Simberloff, D. 1979.
The assembly of species communities: Chance or competition?
Ecology 60:1132-1140.

Connor, E.F. and Simberloff, D. 1983.
Interspecific competition and species co-occurrence patterns on islands:
Null models and the evaluation of evidence.
Oikos 41:455-466.

Connor, E.F. and Simberloff, D. 1984.
Neutral models of species' co-occurrence patterns. Pages 316-331 in
Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., editors.
Ecological Communities: Conceptual Issues and the Evidence.
Princeton University Press.

Coste, J., Peyraud J. and Coullet P. 1978.
Does Complexity Favor the Existence of Persistent Ecosystems?
Journal of Theoretical Biology 73:359-362.

Culver, D.C. 1982.
Cave life: Evolution and ecology.
Harvard University Press, Cambridge.

Davidson, D.W. 1980.
Some consequences of diffuse competition in a desert ant community.
The American Naturalist 116:92-105.

Davidson, D.W. 1985.
An experimental study of diffuse competition in harvester ants.
The American Naturalist 125:500-506.

Davis, M.B. 1986.
Climatic instability, time lags, and community disequilibrium.
Pages 269-284 in Diamond, J. and Case, T.J., editors.
Community Ecology.
Harper & Row Publishers, New York.

den Boer, P.J. 1968.
Spreading of risk and stabilization of animal numbers.
Acta Biotheoretica 18:165-194.

den Boer, P.J. 1980.
Exclusion or coexistence and the taxonomic
or ecological relationship between species.
Netherlands Journal of Zoology 30:278-306.

den Boer, P.J. 1981.
On the survival of populations in a heterogeneous and variable environment.
Oecologia 50:39-53.

den Boer, P.J. 1986.
Density dependence and the stabilization of animal numbers.
1. The Winter Moth.
Oecologia 69:507-512.

Dethier, M.N. and Duggins, D.O. 1984.
An indirect commensalism between marine herbivores and
the importance of competitive hierarchies.
The American Naturalist 124:205-219.

Diamond, Jared M. 1975.
Assembly of species communities.
Pages 342-444 in Cody, M.L. and Diamond, J.M, editors.
Ecology and Evolution of Communities.
Belknap Press, Harvard University.

Diamond, J.M. 1978.
Niche shifts and the rediscovery of interspecific competition.
American Scientist 66:323-331.

Diamond, J. and Case, T.J., editors, 1986a.
Community Ecology.
Harper & Row Publishers, New York.

Diamond, J. and Case, T.J. 1986b.
Overview: Introductions, extinctions, exterminations, and invasions.
Pages 65-79 in Diamond, J. and Case, T.J., editors.
Community Ecology.
Harper & Row Publishers, New York.

Diamond, J. and Gilpin, M.E. 1982.
Examination of the null model of Connor and Simberloff
for species co-occurrences on islands.
Oecologia 52:64-74.

Diamond, J.M. and Marshall, A.G. 1976.
Origin of the New Hebridean avifauna.
Emu 76:187-200.

Diamond, J.M. and Marshall, A.G. 1977.
Distributional ecology of New Hebridean birds: A species kaleidoscope.
Journal of Animal Ecology 46:703-727.

Eadie, J.M., Broekhoven, L. and Colgan, P. 1987.
Size ratios and artifacts: Hutchinson's rule revisited.
The American Naturalist 129:1-17.

Eddison, J.C. and Ollason, J.G. 1978.
Diversity in constant and fluctuating environments.
Nature 275:309-310.

Egerton, F.N. 1968.
Ancient sources for animal demography.
Isis 59:175-189.

Egerton, F.N. 1973.
Changing concepts of the Balance of Nature.
Quarterly Review of Biology 48:322-350.

Elton, C.E. 1946.
Competition and the structure of ecological communities.
Journal of Animal Ecology 15:54-68.

Frazer, J.G. 1955.
The Golden Bough Part V: Spirits of the Corn.
Macmillan & Co. Ltd., New York.

Gilpin, M.E. and Case, T.J. 1976.
Multiple domains of attraction in competition communities.
Nature 261:40-42.

Gilpin, M.E., and Case, T.J. 1981.
Diffuse multispecies competition:
Sequence dependent multiple domains and domino collapse.
Differential Equations and Applications in Ecology, Epidemics,
and Population Problems (manuscript) pp.55-64.

Gilpin, M.E. and Diamond, J.M. 1976.
Calculation of immigration and extinction curves
from the species-area-distance relation.
Proc. Nat. Acad. Sci. USA 73:4130-4134.

Gilpin, M.E. and Diamond, J.M. 1981.
Immigration and extinction probabilities for individual species:
Relation to incidence functions and species colonization curves.
Proc. Nat. Acad. Sci. USA 78:392-396.

Gilpin, M.E. and Diamond, J.M. 1982.
Factors contributing to non-randomness in species co-occurrences on islands.
Oecologia 52:75-84.

Gilpin, M.E. and Diamond, J.M. 1984.
Are species co-occurrences on islands non-random,
and are null hypotheses useful in community ecology? Pages 297-315 in
Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., editors.
Ecological Communities: Conceptual Issues and the Evidence.
Princeton University Press.

Goh, B.S. 1977.
Global stability in many-species systems.
The American Naturalist 111:135-143.

Goh, B.S. and Jennings, L.S. 1977.
Feasibility and stability in randomly assembled Lotka-Volterra models.
Ecological Modelling 3:63-71.

Grant, P.R. 1986.
Interspecific competition in fluctuating environments.
Pages 173-191 in Diamond, J. and Case, T.J., editors.
Community Ecology.
Harper & Row Publishers, New York.

Grant, P.R. and Abott, I. 1980.
Interspecific competition, island biogeography and null hypotheses.
Evolution 34:332-341.

Graves, G.R. and Gotelli, N.J. 1983.
Neotropical land-bridge avifaunas:
New approaches to null hypotheses in biogeography.
Oikos 41:322-333.

Haila, Y. 1982.
Hypothetico-deductivism and the competition controversy in ecology.
Ann. Zool. Fennici 19:255-263.

Harrison, G.W. 1979.
Global stability of food chains
The American Naturalist 114:455-457.

Harvey, P.H., Colwell, R.K., Silvertown, J.W. and May, R.M. 1983.
Null models in ecology.
Ann. Rev. Ecol, Syst. 14:189-211.

Harvey, P.H. and May, R.M. 1985.
Competition in imaginary worlds.
Nature 314:228-229.

Hassell, M.P., Lawton, J.H. and May, R.M. 1976.
Patterns of dynamical behaviour in single-species populations.
Journal of Animal Ecology 45:471-486.

Hastings, A. 1987.
Can competition be detected using species co-occurrence data?
Ecology 68:117-123.

Hastings, H.M. 1982.
The May-Wigner stability theorem.
Journal of Theoretical Biology 97:155-166.

Hay, M.E. 1986.
Associational plant defences and the maintenance of species diversity:
Turning competitors into accomplices.
The American Naturalist 128:617-641.

Heinselman, M.L. 1973.
Fire in the virgin forests of the Boundary
Water Canoe Area, Minnesota.
J. Quaternary Res. 3:329-382.

Herbold, B. and Moyle, P.B. 1986.
Introduced species and vacant niches.
The American Naturalist 128:751-760.

Herodotus.
History, translated G. Rawlinson.
John Murray, Abelmarle Street, London, 1862.

Holling, C.S. 1973.
Resilience and stability of ecological systems.
Ann. Rev. Ecol. Syst. 4:1-23.

Hooke, S.H. 1963.
Middle Eastern Mythology.
Penguin, Hazel Watson and Viney Ltd., Aylesbury Bucks.

Hopf, F.A. and Brown, J.H. 1986.
The bull's-eye method for testing randomness in ecological communities.
Ecology,67:1139-1155.

Horn, H.S. and May, R.M. 1977.
Limits to similarity among coexisting competitors.
Nature 270:660-661.

Hubbell, S.P. and Foster, R.B. 1986.
Biology, chance, and history and the structure
of tropical rain forest tree communities.
Pages 314-330 in Diamond, J. and Case, T.J., editors.
Community Ecology.
Harper and Row Publishers, New York.

Huston, M. 1979.
A general hypothesis of species diversity.
The American Naturalist 113:81-101.

Hutchinson, G.E. 1957.
Concluding remarks.
Cold Spring Harbor Symposium on Quantitative Biology 22:415-27.

Hutchinson, G.E. 1959.
Homage to Santa Rosalia, or why are there so many kinds of animals?
The American Naturalist 93:145-59.

Hutchinson, G.E. 1961.
The paradox of the plankton.
The American Naturalist 95:137-145.

Jackson, B.C.J. 1981.
Interspecific competition and species' distributions:
The ghost of theories and data past.
American Zoologist 21:889-901.

Jacobs, J. 1979.
Concluding remarks: On the difficulty to reconcile theories with facts.
Fortschrift Zoology 25:403-409.

Johnson, C.R. 1974.
Sufficient conditions for D-stability.
Journal of Economic Theory 9:53-62.

Klopfer, P.H. and MacArthur, R.H. 1961.
On the causes of tropical species diversity: Niche overlap.
The American Naturalist 95:223-226.

Krebs, C.J. 1985.
Ecology: The Experimental Analysis of Distribution and Abundance
(third edition). Harper and Row, New York.

Kropotkin, P.A. 1902.
Mutual aid: A Factor in Evolution.
W. Heinemann, London.

Lack, D. 1967.
Population Studies of Birds
Camelot Press Ltd., London and Southampton.

Lane, P.A. 1975.
The dynamics of aquatic systems:
A comparative study of the structure of four zooplankton communities.
Ecological Monographs 45:307-336.

Lane, P.A. 1985.
A food web approach to mutualism in lake communities.
Pages 344-374 in Boucher, D.H., editor.
The Biology of Mutualism.
Croom Helm, London & Sydney.

Lane, P.A. 1986.
Symmetry, change, perturbation, and observing mode in natural communities.
Ecology 67:223-239.

Lane, P.A. and Levins, R. 1977.
The dynamics of aquatic systems.
2. The effects of nutrient enrichment on model plankton communities.
Limnology and Oceanography 22:454-471.

Lawlor, L.R. 1978.
A comment on randomly constructed model ecosystems.
The American Naturalist 112:445-447.

Lawlor, L.R. 1979.
Direct and indirect effects of n-species competition.
Oecologia 43:355-364.

Lawlor, L.R. 1980.
Structure and stability in natural and
randomly constructed competitive communities.
The American Naturalist 116:394-408.

Levine, S.H. 1976.
Competitive interactions in ecosystems.
The American Naturalist 110:903-910.

Levins, Richard 1968.
Evolution in Changing Environments.
Princeton, New Jersey, Princeton University Press.

Levins, R.L. 1973.
Discussion paper: The qualitative analysis of partially specified systems.
Ann. NY Acad. Sci. 231:123-138.

Levins, R. 1975.
Evolution in communities near equilibrium.
Pages 16-50 in Cody, M.L. and Diamond, J.M, editors.
Ecology and Evolution of Communities.
Belknap Press, Harvard University.

Lewin, R. 1983a.
Santa Rosalia was a goat.
Science 221:636-639.

Lewin, R. 1983b.
Predators and hurricanes change ecology.
Science 221:737-740.

Lotka, A.J. 1925.
Elements of Physical Biology.
Baltimore, Williams and Wilkins.

Lubchenco, J. 1978.
Plant species diversity in a marine intertidal community:
Importance of herbivore food preference and algal competitive abilities.
The American Naturalist 112:23-29.

MacArthur, R. 1969.
Species packing and what interspecies competition minimizes.
Proc. Nat. Acad. Sci. USA 64:1369-1371.

MacArthur, R. 1970.
Species packing and competitive equilibrium for many species.
Theoretical Population Biology 1:1-11.

MacArthur, R.H. 1971.
Patterns of terrestrial bird communities.
Pages 189-221 in Avian Biology, Vol. 1.
Academic Press, New York.

MacArthur, R.H. 1972.
Geographic Ecology.
Princeton University, Harper & Row, Publishers, New York.

MacArthur, R. and Levins, R. 1967.
The limiting similarity, convergence, and divergence of coexisting species.
The American Naturalist 101:377-385.

Maiorana, V.C. 1978.
An explanation of ecological and developmental constants.
Nature 273:375-377.

May, R.M. 1972.
Will a large complex system be stable?
Nature 238:413-414.

May, R.M. 1973a.
Stability and Complexity in Model Ecosystems.
Princeton, Princeton Univ. Press.

May, R.M. 1973b.
Stability in randomly fluctuating versus deterministic environments.
The American Naturalist 107:621-650.

May, R.M. 1974.
On the theory of niche overlap.
Theoretical Population Biology 5:297-332.

May, R.M. 1975.
Biological populations obeying difference equations:
Stable points, stable cycles, and chaos.
Journal of Theoretical Biology 49:511-524.

May, R.M. 1976.
Simple mathematical models with very complicated dynamics.
Nature 261:459-467.

May, R.M. 1979.
Fluctuations in abundance of tropical insects.
Nature 278:505-507.

May, R.M. 1981.
Models for single populations.
Pages 5-29 in May, R.M., editor.
Theoretical Ecology (second edition).
Blackwell Scientific Publications, Oxford.

May, R.M. 1982.
Mutualistic interactions among species.
Nature 296:803-806.

May, R.M., Beddington, J.R., Clark, C.W., Holt, S.J. and Laws, R.M. 1979.
Management of multispecies fisheries.
Science 205:267-277.

May R.M., Conway G.R., Hassell, M.P. and Southwood, T.R.E. 1974.
Time delays, density-dependence and single-species oscillations.
Journal of Animal Ecology 43:747-770.

May, R.M. and MacArthur, R. 1972.
Niche overlap as a function of environmental variability.
Proc. Nat. Acad. Sci. USA 69:1109-1113.

May, R.M. and Oster, G.F. 1976.
Bifurcations and dynamic complexity in simple ecological models.
The American Naturalist 110:573-599.

Maynard Smith, J. 1971.
Mathematical Ideas in Biology.
Cambridge University Press.

McIntosh, R.P. 1980.
The background and some current problems of theoretical ecology.
Synthese 43:195-255.

McIntosh, R.P. 1985.
The Background of Ecology.
Cambridge University Press.

McMurtrie, R.E. 1975.
Determinants of stability of large randomly connected systems.
Journal of Theoretical Biology 50:1-11.

McMurtrie, R. 1976.
On the limit to niche overlap for nonuniform niches.
Theoretical Population Biology 10:96-107.

Miller, R.S. 1967.
Pattern and process in competition.
Pages 1-74 in Advances in Ecological Research.
Academic Press, New York.

Moulton, M.P. and Pimm, S.L. 1983.
The introduced Hawaiian avifauna: Biogeographic evidence for competition.
The American Naturalist 121:669-690.

Moulton, M.P. and Pimm, S.L. 1986.
The extent of competition in shaping an introduced avifauna.
Pages 80-97 in Diamond, J. and Case, T.J., editors.
Community Ecology.
Harper & Row Publishers, New York.

Moyle, P.B. 1986.
Fish introductions into North America:
Patterns and ecological impact.
Pages 27-43 in Mooney, H. and Drake, J., editors.
Ecology of biological invasions in North America and Hawaii.
Springer-Verlag, New York.

Mueller, L.D. and Ayala, F.J. 1981.
Dynamics of single-species population growth: Stability or chaos?
Ecology 62:1148-1154.

Murdoch, W.M. 1970.
Population regulation and population inertia.
Ecology 51:497-502.

Nassios, G. 1984.
Predator Mediated Coexistence.
(Manuscript of Ph.D. thesis.)

Nicholson, A.J. 1933.
The balance of animal populations.
Journal of Animal Ecology 2:132-178.

Paine R.T. 1966.
Food web complexity and species diversity
The American Naturalist 100:65-75.

Paine, R.T. 1974.
Intertidal community structure.
Oecologia 15:92-120.

Pianka, E.R. 1974.
Niche overlap and diffuse competition.
Proc. Nat. Acad. Sci. USA 71:2141-2145.

Pianka, E.R. 1978.
Evolutionary Ecology (second edition).
Harper and Row, New York.

Pianka, E.R. 1981.
Competition and niche theory.
Pages 167-196 in May, R.M., editor.
Theoretical Ecology (second edition).
Blackwell Scientific Publications, Oxford.

Pielou, E.C. 1977.
Mathematical Ecology.
John Wiley & Sons, New York.

Pielou, E.C. 1981.
The usefulness of ecological models: A stock-taking.
Quarterly Review of Biology 56:17-31.

Pimm, S.L. 1984.
Food chains and return times. Pages 397-412 in
Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., editors.
Ecological Communities: Conceptual Issues and the Evidence.
Princeton University Press.

Pomerantz, M.J. and Gilpin, M.E. 1979.
Community covariance and coexistence.
Journal of Theoretical Biology 79:67-81.

Popper, K. 1962.
Conjectures and refutations:
The growth of scientific knowledge.
Basic Books, New York.

Puccia, C.J. and Levins, R. 1985.
Qualitative modeling of complex systems-
An introduction to loop analysis and time averaging.
Harvard University Press, Cambridge, Massachusetts.

Plato.
The Dialogues of Plato: Volume 3, Timaeus & Other Dialogues.
Translated Jowett, B.
Hazell Watson & Viney Ltd., Great Britain, 1970.

Quinn, J.F. and Dunham, A.E. 1983.
On hypothesis testing in ecology and evolution.
The American Naturalist 122:603-617.

Richardson, J.L. 1980.
The organismic community: Resilience of an embattled ecological concept.
BioScience 30:465-471.

Roberts, A. 1974.
The stability of a feasible random ecosystem.
Nature 251:607-608.

Roberts, A. 1984.
When will a large complex system be viable?
Unpublished manuscript.

Rosenzweig, M.L. 1971.
Paradox of enrichment:
Destabilization of exploitation ecosystems in ecological time.
Science 171:385-387.

Roth, V.L. 1981.
Constancy in the size ratios of sympatric species.
The American Naturalist 118:394-404.

Roughgarden, J. 1983.
Competition and theory in community ecology.
The American Naturalist 122:583-601.

Ryser, H.J. 1957.
Combinatorial properties of matrices of zeros and ones.
Canadian Journal of Mathematics 9:371-377.

Ryti, R.T. and Gilpin, M.E. 1987.
The comparative analysis of species occurrence patterns on archipelagos.
Oecologia 73:282-287.

Schoener, T.W. 1974.
Resource partitioning in ecological communities.
Science 185:27-39.

Schoener, T.W. 1982.
The controversy over interspecific competition.
American Scientist 70:586-595.

Schoener, T.W. 1983.
Field experiments on interspecific competition.
The American Naturalist 122:240-285.

Schoener, T.W. 1984.
Size differences among sympatric, bird-eating hawks:
A worldwide survey. Pages 254-281 in
Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., editors.
Ecological Communities: Conceptual Issues and the Evidence.
Princeton University Press.

Simberloff, D. 1980.
A succession of paradigms in ecology:
Essentialism to materialism and probabilism.
Synthese 43:3-39.

Simberloff, D. 1981.
Community effects of introduced species.
Pages 53-81 in Nitecki, T.H., editor.
Biotic Crises in Ecological and Evolutionary Time.
Academic Press, New York.

Simberloff, D. 1982.
The status of competition theory in ecology.
Ann. Zool. Fennici 19:241-253.

Simberloff, D. 1983a.
Competition theory, hypothesis testing, and
other community ecological buzzwords.
The American Naturalist 122:626-635.

Simberloff, D. 1983b.
Sizes of coexisting species
Pages 404-430 in Futuyma D.J. and Slatkin M., editors.
Coevolution.

Simberloff, D. 1984.
The great god of competition.
The Sciences 24:16-22.

Simberloff, D. and Boecklen, W. 1981.
Santa Rosalia reconsidered: size ratios and competition.
Evolution 35:1206-1228.

Simberloff, D. and Connor, E.F. 1979.
Q-mode and R-mode analyses of biogeographic distributions:
Null hypotheses based on random colonization.
Pages 123-138 in Patil, G.P. and Rosenzweig, M.L., editors.
Contemporary Quantitative Ecology and Related Econometrics.
International Cooperative Publishing House, Fairland, Md.

Simberloff, D. and Connor, E.F. 1984.
Inferring competition from biogeographic data: A reply to Wright and Biehl.
The American Naturalist 124:429-436.

Simpson, G.G. 1964.
Species density of North American recent mammals.
Systematic Zoology 13:57-73.

Sousa, W.P. 1984.
The role of disturbance in natural communities.
Ann. Rev. Ecol. Syst. 15:353-391.

Southwood, T.R.E. 1977.
Habitat, the templet for ecological strategies?
Journal of Animal Ecology 46:337-365.

Southwood, T.R.E. 1981.
Pages 30-52 in May, R.M., editor.
Theoretical Ecology (second edition).
Blackwell Scientific Publications, Oxford.

Southwood T.R.E., May R.M., Hassell M.P. and Conway G.R. 1974.
Ecological strategies and population parameters.
The American Naturalist 108:791-804.

Strobeck, C. 1973.
N species competition.
Ecology 54:650-654.

Strong, D.R. 1980.
Null hypotheses in ecology.
Synthese 43:271-285.

Strong, D.R. 1983.
Natural variability and the manifold mechanisms of ecological communities.
The American Naturalist 122:636-660.

Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., editors, 1984.
Ecological Communities: Conceptual Issues and the Evidence.
Princeton University Press.

Strong, D.R. 1986.
Density vagueness: Abiding the variance in the demography of real populations.
Pages 257-268 in Diamond, J. and Case, T.J., editors.
Community Ecology.
Harper & Row Publishers, New York.

Strong, D.R. and Simberloff, D.S. 1981.
Straining at gnats and swallowing ratios: Character displacement.
Evolution 35:810-812.

Sutherland, J.P. 1981.
The fouling community at Beaufort, North Carolina:
A study in stability.
The American Naturalist 118:499-519.

Takeuchi, Y. and Adachi, N. 1980.
The existence of globally stable equilibria of ecosystems
of the generalised Volterra type.
Journal of Mathematical Biology 10:401-415.

Taylor, P.J. (Ph.D. thesis) 1985.
Construction and turnover of multi-species communities:
A critique of approaches to ecological complexity.
Harvard University, Cambridge, Massachusetts.

Terborgh, J.W. and Faarborg, J. 1980.
Saturation of bird communities in the West Indies.
The American Naturalist 116:178-195.

Tilman, D. 1982.
Resource competition and community structure.
Princeton University Press, Princeton, N.J.

Tilman, D. 1986.
A consumer-resource approach to community structure.
American Zoologist 26:5-22.

Toft, C.A. and Shea, P.J. 1983.
Detecting community-wide patterns:
Estimating power strengthens statistical inference.
The American Naturalist 122:618-625.

Tregonning, K. and Roberts, A. 1979.
Complex systems which evolve towards homeostasis.
Nature 281:563-564.

Tuljapurkar, S.D. 1976.
Stability of Lotka-Volterra systems.
Nature 264:381.

Tuljapurkar, S.D. and Semura, J.S. 1975.
Stability of Lotka-Volterra systems.
Nature 257:388.

Turelli, M. 1978.
Does environmental variability limit niche overlap?
Proc. Nat. Acad. Sci. USA 75:5085-5089.

Van Valen, L. and Pitelka, F.A. 1974.
Commentary- Intellectual censorship in ecology.
Ecology 55:925-926.

Van Valen, L.M. 1985.
Null hypotheses and prediction.
Nature 314:230

Vandermeer, J. 1980.
Indirect mutualism: variations on a theme by Stephen Levine.
The American Naturalist 116:441-448.

Vandermeer J., Hazlett, B. and Rathcke, B. 1985.
Indirect facilitation and mutualism.
Pages 326-343 in Boucher, D.H., editor.
The Biology of Mutualism.
Croom Helm, London & Sydney.

Verhulst, P.F. 1838.
Notice sur la loi que la population suit dans son accroissement.
Corresp. Math. et Phys. 10:113-121.

Volterra, V. 1926.
Variazioni e fluttua zioni del numero d'individui
in specie animali conviventi.
Mem. Acad. Lincei 2:31-113.

Volterra, V. 1928.
Variations and fluctuations of the number of individuals
in animal species living together.
J. Conserv. Intern. Explor. 3:3-51.

Wiens, J.A. 1977.
On competition and variable environments.
American Scientist 65:590-597.

Wiens, J.A. 1982.
On size ratios and sequences in ecological communities: Are there no rules?
Ann. Zool. Fennici 19:297-308.

Wiens, J.A. 1984.
On understanding a non-equilibrium world:
Myth and reality in community patterns and processes. Pages 439-457 in
Strong, D.R., Simberloff, D., Abele, L.G. and Thistle, A.B., editors.
Ecological Communities: Conceptual Issues and the Evidence.
Princeton University Press.

Wiens, J.A. and Rotenberry, J.T. 1981.
Habitat associations and community structure
of birds in shrubsteppe environments.
Ecological Monographs 5:21-41.

Wigner, E.P. 1967.
Random matrices in physics.
SIAM Review 9:1-23.

Wigner, E.P. 1955.
Characteristic vectors of bordered matrices with infinite dimensions.
Annals of Mathematics 62:548-564.

Wigner, E.P. 1958.
On the distribution of the roots of certain symmetric matrices.
Annals of Mathematics 67:325-327.

Williams, C.B. 1947.
The generic relations of species in small ecological communities.
Journal of Animal Ecology 16:11-18.

Williams, C.B. 1951.
Intra-generic competition as illustrated by Moreau's records
of east african bird communities.
Journal of Animal Ecology 20:246-253.

Wilson, J.B. 1987.
Methods for detecting non-randomness in species co-occurrences: A contribution
Oecologia 73:579-582.

Wilson, S.D. and Keddy, P.A. 1986.
Species competitive ability and position along
a natural stress/disturbance gradient.
Ecology 67:1236-1242.

Wolda, H. 1978.
Fluctuations in abundance of tropical insects.
The American Naturalist 112:1017-1045.

Wright, S.J. and Biehl, C.C. 1982.
Island biogeographic distributions:
Testing for random, regular and aggregated patterns of species occurrence.
The American Naturalist 11:,345-357.

Yodzis, P. 1981.
The stability of real ecosystems.
Nature 289:674-676.