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AUTUMN COURSE ON MATHEMATICAL ECOLOGY

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COMMUNITY DYNAMICS IN A SPATIALLY HOMOGENEOUS ENVIRONMENT

Part 3: Competition

Part 4: Cooperation

Part 5: Communities composed of populations with different or mixed functional roles

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3. Competition

3.1 Lotka - Volterra - Gause Models

Gause (1934) developed a theory of competition based upon experimental work and theoretical studies based on the Lotka - Volterra type model,

$$\frac{dx_1}{dt} = x_1(a_1 - b_1x_1 - b_{12}x_2)$$

(3.1)

$$\frac{dx_2}{dt} = x_2(a_2 - b_2x_2 - b_{21}x_1)$$

It can be demonstrated that there are four ecologically feasible outcomes to competition modelled by (3.1).

The two populations can coexist. In this case, the system has a unique positive equilibrium that is globally asymptotically stable. For later useage, it is convenient to denote this coexistence by the symbol $x_1 \leftrightarrow x_2$.

The positive equilibrium can also be a hyperbolic (saddle) point. The winner of the competition depends upon the initial population sizes. The function that governs the interaction is defined by the separatrices of the hyperbolic point. Notation for this outcome is $x_1 \overset{\uparrow}{\underset{\downarrow}{\rightarrow\!\leftarrow}} x_2$.

The remaining outcomes are when one population dominates the other so that independent of initial population size, this population always survives while the second goes to extinction. This is denoted by $x_1 >> x_2$ or $x_2 >> x_1$ according to whether x_1 or x_2 wins the competition respectively. There is another type of system that is excluded from the above classification. This is the case where the ecology of one population, x_1, is a constant multiple, k, of the other population, x_2. This leads to an infinite number of equilibria and the relationship $x_1 = (\text{constant})(x_2)^k$ must hold between the two populations. This situation is related to the concept of competitive exclusion discussed later in Section 3.5.

3.2 Competition Models of Kolmogorov Type

The Kolmogorov model

$$\frac{dx_1}{dt} = x_1f_1(x_1,x_2)$$

(3.2)

$$\frac{dx_2}{dt} = x_2f_2(x_1,x_2)$$

with competitive interactions has a relatively restricted asymptotic behavior in that no limit cycles can arise. The hypotheses required to achieve this result include

(C1) $\frac{\partial f_1}{\partial x_2}(x_1,x_2) < 0; \quad \frac{\partial f_2}{\partial x_1}(x_1,x_2) < 0.$

Hence, if either population in the competition increases, the growth rate of the other species decreases.

(C2) There exists a $K > 0$ such that for $x_i \geq K$, $i = 1$ or 2, then both $f_i(x_1,x_2)$ are nonpositive.

When either population is sufficiently large, neither of them can grow.

(C3) There exist carrying capacities x_1^c, x_2^c where $f_1(x_1,0) > 0$ for $x_1 < x_1^c$ and $f_1(x_1,0) < 0$ for $x_1 > x_1^c$; $f_2(0_1x_2) > 0$ for $x_2 < x_2^c$ and $f_2(0,x_2) < 0$ for $x_2 > x_2^c$.

Theorem 3.1 The limit of any solution of (3.2) exists and is an equilibrium; hence populations tend to one of a finite number of limiting populations.

Indication of Proof. The complete details of the proof may be found in Hirsch and Smale (1974). The basic analysis employs the decomposition of the population quadrant into regions determined by flows across isoclines. Then each type of region is analyzed to determine the characteristics of the feasible ω-limit sets. As indicated in the theorem statement, all ω-limit points are equilibria (and in particular, there are no cyclic behaviors associated with competitive systems of Kolmogovov type). The stability of these equilibria is relatively easy to determine and it is shown that there exists at least one asymptotically stable equilibrium.

3.3 Competition in Laboratory and Natural Communities

Gause (1932), stimulated by the theoretical work of Volterra, undertook some laboratory experiments that lead to outcomes much like the theoretical work predicted (Section 3.1). His work on two yeast populations were not definitive because of the production of ethyl alcohol (yeast are fine for making wine but not for interacting) which, in turn, shut down reproduction.

Apparently not discouraged, Gause continued his work in aquatic systems, this time using ciliates. Using *Glaucoma scintillans* and *Paramecium aurelia*, he found that the smaller organism, *Glaucoma*, was not inhibited by the *Paramecium* while the growth of the *Paramecium* population was hindered by the presence of *Glaucoma*.

Gause also employed three species of paramecium in some experiments; these were *P. aurelia*, *P. caudatum*, and *P. bursaria*. The outcomes of competition between these species are now indicated.

1. *P. caudatum* >> *P. aurelia* if metabolic products are completely removed.

2. *P. aurelia* >> *P. caudatum* in most other instances; hence the winner of the competition can be changed by a perturbation in environment.

3. *P. aurelia* ↔ *P. bursaria*. (This might not be direct competition for a resource since *P. bursaria* tends to feed on the sediments). The data indicates that multiple equilibria might result.

4. *P. caudatum* and *P. bursaria* mixtures led to inconclusive results. Stable equilibrium coexistence did occur in certain instances while *P. caudatum* << *P. bursaria* occurs if *P. bursaria* is initially present in sufficiently high densities.

Another classical competition experiment is that of Park (1954, 1962) using Metazoa. *Tribolium confusum* and *T. castaneum* were used in a homogeneous environment, with different temperature and humidity ranges.

T. confusum, grown by itself in a hot, wet environment, reached peak densities. However, when it was grown with *T. castaneum* (which did moderately well in a hot wet environment), *T. castaneum* won the competition. In a cool dry environment, neither species did well. In this setting, *T. confusum* dominated the competition. Hence, environmental conditions are important factors in competition. Also extraction of information from population to community levels is not, in general, a feasible objective.

Many factors can provide a basis for changing the outcome of competition. These include refuge, predation, and genetic effects. Crombie (1945, 1946) utilized flour beetles and by adding a refuge changed the outcome of competition from one of competitive dominance to stable coexistance. Pimentel et al. (1965), using houseflies and blowflies, were able to change the dominance in this system through selection for superior competitors.

As indicated in Figure 1.9, Connell (1961) studied the competition between two barnacle populations in an intertidal community. The barnacles, of the genera *Balanus* and *Chthamalus*, compete interspecifically for space on the rocks in the intertidal. The *Balanus* are vigorous and tend to dominate *Chthamalus* in the lower zones while the situation is reversed in the upper regions.

3.4 Competition for a Single Nutrient in Continuous Cultures of Microorganisms

Hsu, Hubble, and Waltman (1977) developed a theory of competition between microorganisms, such as phytoplankton, for a single limiting nutrient. Their modelling efforts were motivated by chemostat experiments in which the initial input, S^0, and dilution rate, D, of the nutrient are known constants and the environmental medium is homogeneous.

Let $x_i(t)$ denote the concentration of the ith population at time t; s(t) denote the concentration of substrate at time t; m_i is the maximum growth rate of the ith population; y_i is the all growth yield for the ith population and a_i is the Michaelis-Menten half saturation constant. The model is

$$\frac{dS(t)}{dt} = (S^0 - S(t))\, D - \sum_{t=1}^{n} \frac{m_i}{y_i} \frac{x_i(t)S(t)}{a_i + S(t)}$$

$$\frac{dx_i(t)}{dt} = \frac{m_i x_i(t)\, S(t)}{a_i + s(t)} - Dx_i(t)$$

$$S(0) = S^0$$

$$x_i(0) = x_{io} > 0$$

Theorem 3.2 (Extinction). Let $b_i = m_i/D$. If either $b_i \leq 1$ or $\frac{a_i}{b_i - 1} > S^0$ (when $b_i > 1$) then $\lim_{t \to \infty} x_i(t) = 0$.

Extinction results if the maximum growth rate m_i of the ith population is less than the dilution rate or if the metabolic needs of the population, $a_i/(b_i - 1)$ exceeds the initial amount of nutrient present in the system.

Theorem 3.3 (Persistence of one Population). Let i be an integer, $1 \leq i \leq n$, and suppose $0 < a_i/(b_i - 1) < a_j/(b_j - 1)$ for all $j \neq i$, $j = 1,2,111, n$. Let $S^0 > a_j/(b_j - 1)$ and $b_j > 1$. Then

$$\lim_{t \to \infty} S(t) = \frac{a_i}{b_i - 1},$$

$$\lim_{t \to \infty} x_i(t) = y_i \left(S^0 - \frac{a_i}{b_i - 1}\right),$$

$$\lim_{t \to \infty} x_j(t) = 0 \quad j \neq i.$$

The proof of this last theorem is long and involved, although not difficult to understand; the interested reader is referred to the original article for details.

This competition model has again led a globally asymptotically stable equilibrium. Survival of a population is determined by the smallest of the ratios: $a_i/(b_i - 1)$. This indicates that when a single resource is limiting for a community only one population can survive. The validity of this statement and the presence of cycles in competitive systems is explored in the next section.

3.5 The Proposition of Competitive Exclusion

Gause's experiments with Paramecium candatum and P.aurelia resulted in P.aurelia dominating in the competition for a single limiting resource. From these experiments and from the mathematical theory developed by Volterra arose the proposition that no ecological community in which there are n~~o~~ species can persist on less than n limiting resources. (A resource is limiting if it is necessary for maintenance and development of the community and its supply is exhaustable by sufficient utilization).

While Gause's research was in the laboratory, there also exist classical studies of competition with exclusion in natural ecosystems. R.MacArthur (1958) studied five species of warblers that appeared to be so similar in ecological preferences that competitive exclusion was violated. He found that they feed and occupy different levels in their forested environment and that competitive exclusion held for this community.

Theoretical aspects of competitive exclusion have been well developed in recent years. The work of Hsu, Hubble and Waltman (1977) mentioned previously in Section 3.4 supports the concept of competitive exclusion if the ratio of the Michealis-Minte~~r~~n parameters of each population is distinct from the others. They also demonstrate that whenever two species have equal Michaelis-Minte~~r~~n ratios that it is possible for both species to survive.

Related to competitive exclusion is the "paradox of the plankton" (Hu~~y~~tchinson, 1978). The coexistence of many species of phy to plankton in a well mixed body of water with only a few limiting nutrients (usually one) seems to violate competitive exclusion. The analysis of Hsu, Hubble, and Waltman suggests that, in order to survive, the Mi~~s~~chaelis-Minte~~r~~n parameter ratios should be very similar. Theoreticaly, this allows exclusion to proceed very slowly.

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Gause's experiments with *Paramecium caudatum* and *P. aurelia* resulted in *P. aurelia* dominating in the competition for a single limiting resource. From these experiments and from the mathematical theory developed by Volterra arose the proposition that no ecological community in which there are n species can persist on less than n limiting resources. [A resource is limiting if it is necessary for maintenance and development of the community and its supply is exhaustable by sufficient utilization]

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Levin (1970) also provides a theoretical basis for a higher dimensional competition exclusion. He considers the model

$$
(3.3)\qquad
\begin{aligned}
\frac{dx_1}{dt} &= x_1 f_1(x_1, \cdots, x_n; y_1, \cdots, y_m)\\
&\ \vdots \qquad\qquad \vdots\\
\frac{dx_n}{dt} &= x_n f_n(x_1, \cdots, x_n; y_1, \cdots, y_m)
\end{aligned}
$$

where x_i are state variables representing species in the community and y_j represent environmental parameters. Any quantity that influences f_i is called a limiting factor. He also allows combination of quantities; for example, if a species requires and utilizes two resources R_1, R_2 with utilization efficiencies α_1, α_2 then $\alpha_1 R_1 + \alpha_2 R_2$ is a single limiting factor. Assumptions made here are that i) there exist a minimal independent set of limiting factors $z_1(x_1, \cdots, x_n; y_1, \cdots, y_m), \cdots, z_p(x_1, \cdots, x_n; y_1, \cdots, y_m)$ where $p \le m+n$.

(i) $f_i = \alpha_{i1} z_1 + \alpha_{i2} z_2 + \cdots + \alpha_{ip} z_p + \gamma_i$

The growth rates are linear functions of the p linearly independent limiting factors.

Theorem 3.4 No asymptotically stable equilibrium can be attained in a community modelled by (3.3) in which some r components are limited by less than r limiting factors.

Indication of the Proof. If the first r components are limited by less than r factors, because of the linearity of the f_i, there exist β_i, δ not all zero such that

$$\beta_1 f_1 + \cdots + \beta_r f_r = \delta.$$

Employing the equations (3.3), the expression

$$\beta_1 \frac{\dot{x}_1}{x_1} + \beta_2 \frac{\dot{x}_2}{x_2} + \cdots + \beta_r \frac{\dot{x}_r}{x_r} = \delta$$

can be obtained. An integration leads to

$$x_1^{\beta_1}(t) \cdots x_r^{\beta_r}(t) = Ke^{\delta t}.$$

Using the equilibrium, it follows that δ must be zero and the equilibrium (and each solution) lies on the surface

$$x_1^{\beta_1} \cdots x_r^{\beta_r} = K,$$

for some K. Hence, the equilibrium cannot be asymptotically stable and the community cannot contain r populations.

While the above mentioned works support the proposition of competitive exclusion, not all theoretical research does.

McGehee and Armstrong (1976) show that for certain standard models where competitive exclusion occurs, that, topologically, the result is not robust. They take a model, modify it by several small nonlinear perturbations and end up a persistent system (in fact, one with a cyclic behavior)

Kaplan and Yorke (1977) demonstrate that Levin's work is not robust in that there exists an n-dimensional system

$$\frac{dx_i}{dt} = x_i f_i(r_1(x), \dots, r_k(x)), \quad k<n$$

which has an asymptotically stable periodic solution.

Related competitive exclusion ideas will be discussed in the next section.

The concepts of competitive exclusion and niche theory have been interrelated in the literature. The reader is referred to Hutchinson (1978) and Whittaker and Levin (1975) for discussions on the theory of niches

3.6 Stability in Higher Dimensional Competitive Communities

The analytical theory of higher dimensional communities of competitors is only beginning to evolve. To give an indication of the types of available results, first persistence in a three dimensional Lotka-Volterra model is presented. Next, stability in exploitative competitive models is explored.

Exploitative Competitive Communities at Equilibrium

Model Hypotheses and Preliminaries

The autonomous, Kolmogorov-type model

$$\dot{x}_i = x_i \, F_i(x) \qquad i = 1, 2, \ldots, n , \tag{3.8}$$

where $x = (x_1, x_2, \ldots, x_n)^T$, is assumed to have species growth rates F_i that are continuously differentiable in the n-dimensional nonnegative cone $\mathbf{R}_n^+ = \{x \in \mathbf{R}_n : x \geq 0\}$. In order that (3.8) model intraspecific competition, it is required that

$$\frac{\partial F_i(x)}{\partial x_i} < 0 \quad , \qquad i = 1, 2, \ldots, n . \tag{3.9}$$

Some density dependent hypothesis is necessary for the existence of an equilibrium community (Deakin, 1975). The requirement that all species exhibit a self limiting structure is imposed for our development.

The Implicit Function Theorem implies that, for each i , $i = 1, 2, \ldots, n$, there exists a continuously differentiable function $K_i = K_i(\overline{x}_i)$, where $\overline{x}_i = (x_1, x_2, \ldots, x_{i-1}, x_{i+1}, \ldots, x_n)^T$, with the property that

$$F_i(x_1, x_2, \ldots, x_{i-1}, K_i(\overline{x}_i), x_{i+1}, \ldots, x_n) = 0 .$$

The functions K_i represent the traditional isosurfaces for the system (3.8) One possible interpretation of these functions

interspecific interactions are given by $\frac{\partial F_i(x)}{\partial x_j} < 0$ for $x \in \mathbf{R}_n^+$. The competitive condition can sometimes be replaced with other hypotheses about the characteristics of the interacting species. We will indicate some of the settings in which such extensions are valid.

The primary purpose here is to provide insight into equilibrium competitive communities with special emphasis on exploitative competition. The novelty of the apprpach is based on the interpretation of the functions K_i and the implications which this interpretation has for explotative competition.

Stable Equilibrium Communities

The allocation and utilization of a community's resources can determine the existence and stability of an equilibrium for that community. When a community is at equilibrium, then its resources need only be allotted to the maintenance of its component populations. Here, it is also convenient to assume that in the absense of consumers all resources of the community are at equilibrium. This situation would be approximately valid even in the presence of consumers whenever resource growth is relatively fast as compared to consumer growth.

Let R denote the totality of resources available to a species and δ the average amount of those resources required for the sustenance of a single organism of that species. At least as an initial approximation, $R\delta^{-1}$ can be regarded as the carrying capacity of the environment for the species. This concept is utilized in (3.8) through the assumption that

$$K_i(\bar{x}_i) = R_i(\bar{x}_i)\delta_i^{-1} \quad , \quad i = 1, 2, \ldots, n \quad ,$$

where $R_i(\bar{x}_i)$ denotes the total resources available to species i when the populations of the remaining species are given by the $(n-1)$-vector $\bar{x}_i$ and δ_i is the (constant) average amount of resources required by a single species i organism. In this and the subsequent section, competition for resources is assumed to be <u>exploitative</u> in the sense that

(iii) At equilibrium, the total resources available to species i exceeds the totality of species i resources that are utilized by the remaining $n-1$ species:

$$\sum_{\substack{j=1 \\ j\neq i}}^{n} x_j^* \left|\frac{\partial R_i(\overline{x_i^*})}{\partial x_i}\right| < R_i(\overline{x_i^*}) \quad , \quad i = 1, 2, \ldots, n \, .$$

Condition (i) requires effects of an organism upon its resources to be more pronounced than the total effects of organisms of other species on its resources; that is, intraspecific effects dominate interspecific effects on resources. The satisfaction of this condition requires competing species to be nondominant in utilization of a common resource. To illustrate when (i) would not hold, consider two species that utilize the same (single) food source but one requires and consumes a much larger quantity for maintenance than the other. One of the inequalities in (i) would be violated for this setting.

Each of the conditions has implications for niche separation. They imply that each species, either individually or collectively, must in some sense, have sole access to some portion of the total resource spectrum. A strategy for formation of a stable equilibrium community that is suggested by these conditions is for each species to have a resource allocation which does not significantly overlap with the resources of the other components of the community. Such an no aggression or interference mechanism is utilized by any species and directed towards a different species. Such behavior is allowed between members of the same species. This implies that resources available to species i are diminished by a species j organism only by the amount of those resources actually utilized by the j-organism, and therefore $\partial R_i/\partial x_j$ represents the amount of resources available to species i which are utilized by a single species j organism.

Theorem 3.5. Each of the following is sufficient for x^* to represent a stable equilibrium community:

(i) The average resource requirement, δ_i, of a species i organism in an equilibrium community exceed the combined effects caused by a single organism of the other species on the resources, R_i, of species i:

$$\sum_{\substack{j=1 \\ j\neq i}}^{n} \left| \frac{\partial R_i(\overline{x}_i^*)}{\partial x_j} \right| < \delta_i , \quad i = 1, 2, \ldots, n \ ;$$

(ii) The average resource requirement, δ_i, of a species i individual in an equilibrium community exceeds the combined effects caused by a single organism of species i on the resources of the remaining $n-1$ species:

$$\sum_{\substack{j=1 \\ j\neq i}}^{n} \left| \frac{\partial R_j(\overline{x}_i^*)}{\partial x_i} \right| < \delta_i \quad i = 1, 2, \ldots, n \ ;$$

allocation of resources necessarily results in decreased competition and has been suggested as an evolutionary goal of competitive interactions (Pianka, 1978).

Conditions (i) and (ii) are not explicitly dependent upon the total population size although the size of the components of the equilibrium state are implicitly contained in each. As demonstrated below each of the conditions in Theorem 3.5 is obtained from the linear algebra concept of diagonal dominance. As such, the species interactions need not be restricted to be competitive; indeed, the type of interaction does not have to be specified to lead to a stable community. However, the interpretations of the mathematical expressions as presented above may no longer be appropriate. The proof is related to a subsequent theorem and will be given later.

EXPLOITATIVE COMPETITIVE COMMUNITIES

In this section, competition for resources is assumed to be exploitative in the sense that no aggression or interference mechanism is utilized by any species and directed toward a different species. On the other hand, such behavior is allowed between members of the same species. This implies that the resources available to species i are diminished by a species j organism only by the amount of those resources actually utilized by the j-organism, and, therefore, $\partial R_i/\partial x_j$ represents the amount R_i of resources available to species i which are utilized by a single species j organism.

The concepts in this section are explored by the introduction of mathematical formulations to represent species and resource interactions. We assume that the total resources available to an equilibrium community are partitioned into k distinct resources. For each species i, $i = 1, 2, \dots, n$, associate a *species utilization vector* $\overset{\downarrow}{\beta_i} = \overset{\text{Beta}\ \downarrow}{\beta_i}(x) = (\beta_{i1}, \beta_{i2}, \dots, \beta_{ik})$, where

$$\sum_{l=1}^{k} \overset{\text{beta}}{\overset{\downarrow}{\beta_{il}}} = \overset{\text{"delta"}}{\overset{\downarrow}{\delta_i}},$$

and $\beta_{il} = \beta_{il}(x)$ represents the amount of the individual requirement δ_i that is taken from resource l at community density x. The *species exploitation vector* $\epsilon_i = (\epsilon_{i1}, \epsilon_{i2}, \dots, \epsilon_{ik})$ has components defined by

$$\epsilon_{il}(x) = \begin{cases} 1 & \text{if } \beta_{il}(x) \neq 0 \qquad i = 1, 2, \dots, n \\ 0 & \text{if } \beta_{il}(x) = 0, \qquad l = 1, 2, \dots, k. \end{cases}$$

Analogous concepts are defined for a given resource l, $l = 1, 2, \dots, k$. A *resource utilization vector* is $b_l = (\beta_{1l}, \beta_{2l}, \dots, \beta_{nl})$ and a resource exploitation vector is

$e_\ell = (\epsilon_{1\ell}, \epsilon_{2\ell}, \dots, \epsilon_{n\ell})$ where $\beta_{i\ell}$ and $\epsilon_{i\ell}$ are defined above.

These formulations lead to a conceptually and mathematically simple interpretation of the competition coefficients, i.e., the elements a_{ij} of the community matrix $I-K'(x)$. Employing the above notation, and assuming exploitative competition, we find, for $i \neq j$, $\partial P_i/\partial x_j = -\epsilon_i \cdot \beta_j$, "partial derivative" and

$$a_{ij} = \partial K_i/\partial x_j = -\underset{\text{delta}}{\delta_i^{-1}}\,\epsilon_i \cdot \beta_j ,$$

where $\cdot$ denotes the inner product in R^n. This formulation depends strongly on the assumption that the competition is purely exploitative. Most other formulations of the competition ~~coefficients~~ coefficients $\partial K_i/\partial x_j$ utilize encounter probabilities (e.g., see ~~[illegible]~~ Levins (1968)). Here, the only way that a species j^{th} competitor can deprive species i of a portion of a resource is to utilize that portion as a part of its own requirement δ_j.

the utilization of resources proceeds as though neither species were aware of the presence of the other.

The notation introduced above results in a decomposition of the community matrix associated with (1):

$$I-K'(x^*) = D^{-1}E(x^*)\,B(x^*),$$

where

$D = \text{diag}(\overset{\text{delta}}{\delta_i})_{n\times n}$, $E = (\epsilon_{ij})_{n\times k}$, $B = (\beta_{ij})_{k\times n}$,

and $K'(x^*)$ is the Jacobian of K evaluated at x^*.

This decomposition is employed here to take a new look at some old concepts in the theory of competitive communities. The first of these ~~the~~ states that in an equilibrium community, the number of species cannot exceed the number of distinct resources; and the second, usually referred to as the competitive exclusion principle is that no two species which compete for exactly the same set of resources can be components of a stable equilibrium community, (see, e.g., MacArthur and Levins, 1967; Levin, 1970). ~~What~~ The novel contribution ~~is new lies~~ in the particular mathematical formulation for exploitative competitive communities and the simplicity with which both concepts are obtained by a cursory examination of a single matrix, the matrix $E(x^*)$. It is interesting to note the lack of quantitative information necessary for the following results. The only information needed is which resources are being utilized by which species, not the specific amount of resources being consumed. ~~The short proof is in the [illegible]~~.

Theorem 3.6. The exploitative competitive equilibrium community x^* cannot be stable if any of the following are satisfied.

(i) The number of species exceeds the number of resources $(n > k)$.

[illegible] that no equilibrium [illegible] community cannot be stable if [illegible] of the community [illegible] of the same set of competitors [illegible]

(ii) $k \geq n$ and ~~no~~ some set of i, $(1 \leq i \leq n-1)$, species exploit the community resources in the exact way as another species, that is, the sum of a set of i species exploitation vectors is equal to the species exploitation vector of another species.

(iii) $k \geq n$ and some set of j resources where $j > k-n+1$ are utilized by exactly the same set of competitors, that is, there are j resources, $(j > k-n+1)$, all of which have the same resource exploitation vector.

Part (ii) of the theorem is somewhat more general than the usual statement of the competitive exclusion principle. It says, for example, that if two species have no resources in common but together utilize the same set of resources as a third competitor, then the community cannot have a stable equilibrium.

(Check III)

~~The decomposition of the matrix [illegible]~~

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Condition (iii) imposes restrictions on resource similarity. Roughly stated, it says that an exploitative competitive community cannot be stable if too many of the resources attract the same set of competitors.

The decomposition of the matrix

to p 15

in terms of the exploitation and utilization matrices also impose certain restrictions on the structure of the mathematical model. First note that if a species j organism has no effect on the resources of species i, then a species i organism has no effect on the resources of species j; that is,

$$\epsilon_i \cdot \beta_j = 0 \text{ if and only if } \epsilon_j \cdot \beta_i = 0,$$

or in terms of the resource utilization,

$$\partial R_i/\partial x_j = 0 \text{ if and only if } \partial R_j/\partial x_i = 0 .$$

Hence the community matrix must have a symmetry in the zeros about the main diagonal.

A second restriction is that the effect that a species j ~~individual~~ organism can have on the resources of another species i cannot exceed the average resource requirement δ_j of that organism j, or

$$\delta_j = \epsilon_j \cdot \beta_j \geq \epsilon_i \cdot \beta_j = |\partial R_i/\partial x_j| ,$$

for each i, j, $i \neq j$. The inequality will be strict if there is at least one resource utilized by species j and not by species. If for some pair of distinct indices i and j, $\epsilon_i = \epsilon_j$, then part (ii) of Theorem 3.6 holds and the system cannot have a stable equilibrium. We will say that an exploitative competitive community is <u>feasible</u> if $\epsilon_i \neq \epsilon_j$ for $i \neq j$. In this case, it follows that for any set of distinct indices $i_1, i_2, \ldots, i_m$, at least one of the inequalities

$$\epsilon_{i_2} \cdot \beta_{i_2} \geq \epsilon_{i_1} \cdot \beta_{i_2}, \quad \epsilon_{i_3} \cdot \beta_{i_3} \geq \epsilon_{i_2} \cdot \beta_{i_3}, \quad \ldots, \quad \epsilon_{i_1} \cdot \beta_{i_1} \geq \epsilon_{i_m} \cdot \beta_{i_1}$$

must be strict, for otherwise, $\epsilon_{i_1} = \epsilon_{i_2} = \cdots = \epsilon_{i_m}$. Hence, if the community is feasible, then for any set of distinct indices $i_1, i_2, \ldots, i_m$

$$\left| \frac{\partial K_{i_1}}{\partial x_{i_2}} \frac{\partial K_{i_2}}{\partial x_{i_3}} \cdots \frac{\partial K_{i_m}}{\partial x_{i_1}} \right| < 1,$$

where the derivatives are evaluated at x^*, i.e., all cyclic products of elements of the community matrix $I - K'(x^*)$ are less than one. ~~[illegible]~~ the following theorem.

Theorem 3.9. The community matrix of a feasible exploitative competitive community is quasi-weakly diagonally dominant.

All community matrices that represent exploitative competition as modelled here must have the properties given above: ~~a~~ a symmetry in the zero entries and quasi-weak diagonal dominance. There are several examples of three dimensional systems in which dynamical behavior appears to be anomalogical. Goh (1977) ~~has given an~~ [illegible] example of a Lotka-Volterra system (where the positive equilibrium is asymptotically stable but there is also a region of extinction). ~~However, Goh's system~~ does not satisfy these requirements and so cannot represent exploitative ~~comp~~ competition. The same is true of Strobeck's ~~&~~ examples (1973) of two systems that have the same isoplanes and the same positive equilibrium but one is stable and the other is unstable. These systems do not allow a resource decomposition of the above type.

among those three dimensional competitive systems which have unusual behavior is the intransitive arrangement (May and Leonard, 1975). However, it is interesting to note that a resource allocation which is consistent with exploitative competition is modelled here is feasible for this system.

We will point out two consequences of the property of quasi-weak diagonal dominance for competitive systems. The first concerns ~~of~~ communities with only three competitors. Strobeck (1973) has shown that, in general, the community matrix of a three species competitive system does not contain enough information to determine whether an equilibrium community is stable or unstable. However, for feasible exploitative ~~system~~ three species systems, stability of an equilibrium is equivalent to the positivity of $\det(I-K'(x^*))$. Furthermore, feasibility and a positive determinant of $I-K(x)$ assures uniqueness of K-equilibria.

Theorem 5.8. (i) Let x^* be a feasible ~~three~~ exploitative equilibrium community with three species. Then x^* is asymptotically stable if and only if $\det(I-K'(x^*)) > 0$.

(ii) Suppose that $e_i(x) \neq e_j(x)$, $(i,j=1,2,\dots,n,\ i \neq j)$, for all $x \in \Omega_0 = \{x \in R_n^+ : 0 \leq x_i \leq K_j(\bar{0}_i), i=1,2,\dots,n\}$ and that $\det(I-K'(x)) > 0$ for all $x \in \Omega_0$. Then there exists a unique asymptotically stable K-equilibrium in R_n^+.

~~The second consequence of quasi-weak diagonal dominance applies to arbitrarily large systems.~~

~~Theorem . Suppose x^* is an equilibrium community such that $I-K'(x^*)$ $= A=(a_{ij})_{n\times n}$ $(n\geq 3)$ is quasi-weakly diagonally dominant, (in particular, a feasible exploitative competitive community), and let~~

~~$s = (\max_{i\neq j} a_{ij})^2 / (\min_{i\neq j} a_{ii} - (\min_{i\neq j} a_{ij})^2)$.~~

~~Then x^* is asymptotically stable if $s' > n-2$.~~

which have unusual behavior is the intransitive arrangement (May and Leonard, 1975). However, it is interesting to note that a resource allocation which is consistent with exploitative competition as modelled here is feasible for this system.

All of the conditions in Theorem 2 depend upon an equilibrium structure. There are several recent examples of persistent systems with the species number exceeding the number of resources (McGeehee and Armstrong, 1977; Yorke and Kaplan, 1977; Freedman, 1980). Of course, these persistent systems do not represent stable equilibrium communities.

These results also relate to the ideas of qualitative stability (Quirk and Ruppert, 1965; Jeffries, 1974; Pielou, 1977) where only the signs of the interaction matrix are known.

MATHEMATICAL PRELIMINARIES AND RESULTS

ℓ. c

A real $n \times n$ matrix $A = (a_{ij})$ is a Z-matrix if $a_{ij} \leq 0$ for $i \neq j$. The matrix A is a P-matrix if the principal minors of A are positive. The matrix A is an M-matrix if A is both a Z-matrix and a P-matrix. The matrix A is diagonally dominant if

$$|a_{ii}| > \sum_{\substack{j=1 \\ j \neq i}}^{n} |a_{ij}| \quad , \quad i = 1, 2, \ldots, n$$

$$\tilde{\epsilon}_i \cdot \tilde{\beta}_i = \delta_i > |\tilde{\epsilon}_i \cdot \tilde{\beta}_j| = |\partial R_i/\partial x_j| \text{ , for each}$$

$$i, j, \ i \neq j \ .$$

It then follows that for any set of distinct indices i_1, i_2, ..., i_m,

$$(4) \qquad \left|\frac{\partial K_{i_1}}{\partial x_{i_2}} \frac{\partial K_{i_2}}{\partial x_{i_3}} \cdots \frac{\partial K_{i_m}}{\partial x_{i_1}}\right| < 1 \quad ,$$

where the derivatives are evaluated at x^*, i.e., all cyclic products of elements of the community matrix $I - K'(x^*)$ are less than one. All community matrices that represent exploitative competition as modelled here must have this property. There are several examples of three dimensional systems in which dynamic behavior appears to be anomalogical. Goh (1977) has given an example of a Lotka-Volterra system where the positive equilibrium is asymptotically stable but there is also a region of extinction. The above necessary conditions imply that Goh's system does not represent exploitative competition since the community matrix does not satisfy (4). The same is true of Strobeck's examples (1973) of two systems that have the same isoplanes and the same positive equilibrium but one is stable while the other is unstable. These systems do not allow a resource decomposition of the above type.

Among those three dimensional competitive systems or if A^T has this property. The matrix A is quasi-diagonally dominant if there is a diagonal matrix D with positive diagonal entries such that $D^{-1}AD$ is diagonally dominant. The matrix A is weakly diagonally dominant if for each i, $|a_{ii}| > |a_{ji}|$, $1 \leq j \leq n$, $i \neq j$. A is quasiweakly diagonally dominant if there is a diagonal matrix D with positive diagonal entries such that $D^{-1}AD$ is weakly diagonally dominant.

The following result does not require that competition be exploitative.

Theorem ~~7~~ 3.7. Each of the following conditions is sufficient for the equilibrium, x^*, to be asymptotically stable.

(a) $I - K'(x^*)$ is quasi diagonally dominant.

(b) $I + K'(x^*)$ is a P-matrix.

(c) $I + K'(x^*)$ is an M-matrix.

(d) $I + K'(x^*)$ is quasi diagonally dominant

(e) There exists an $x > 0$ such that

$$[I + K'(x^*)]x > 0$$

(f) $[I - K'(x^*)]^{-1}$ is a Z-matrix with positive diagonal elements.

(g) There exists a neighborhood U of x^* such that whenever $x \in U$ with $x < x^*$, then $K(K(x)) > x$.

(h) There exists a neighborhood U of x^* such that if $x \in U$ with $x > x^*$ then $K(K(x)) < x$.

(i) There exists a neighborhood U of x^* such that if $x \in U$ with $x < x^*$ then $K(x) - x < 2(x^* - x)$,

(j) $I - K'(x^*)$ is diagonally similar to a matrix $C = (c_{ij})$ where $c_{ii} = 1$ and $|c_{ij}| < 1$ if $i \neq j$, and $(\max_{i \neq j} c_{ij})^2 = s(\min_{i \neq j} c_{ij}) + (1-s)(\min_{i \neq j} c_{ij})^2$ where $s^{-1} > n-2$, $n \neq 3$.

Some of these conditions (a) - (e) may be found, explicitly or implicitly, in the literature (Strobeck, (1973; Siljak, 1976; Travis and Post, 1979). The fact that they may interpreted in an ecological setting is the content of Theorem ~~6~~ 3.6.

Condition (f) is, as far as we know, new and it is therefore useful to find conditions under which $[I - K'(x^*)]^{-1}$ is a Z-matrix. To this end, let

$$B = [b_{ij}] = -F'(x^*) = -\operatorname{diag}\left(\frac{\partial F_i}{\partial x_i}\right)(I - K'(x^*)) .$$

For any matrix $M = [m_{ij}]$, let $C_{ij}(M)$ denote the (ij)-th cofactor of M. Note that $C_{ij}(B)$ and $C_{ij}(I - K'(x^*))$ have the same sign. It is apparent by writing $[I - K'(x^*)]^{-1} = \dfrac{\operatorname{Adj}[I - K'(x^*)]}{\det[I - K'(x^*)]}$ that if $\det(I - K'(x^*)) > 0$ then $[I - K'(x^*)]^{-1}$ is a Z-matrix with positive diagonal entries if and only if $C_{ii}(I - K'(x^*)) > 0$ and $C_{ij}(I - K'(x^*)) < 0$ for $i \neq j$.

This trivial result has an interesting interpretation. First, note that an obvious necessary condition for the asymptotic stability of x^* is that $\det(I - K'(x^*)) > 0$ or $\det B > 0$. Thus, one might expect that any factor which has the effect of decreasing (increasing) det B should have a destablizing (stabilizing) effect on the system. Most of the standard stability conditions for competitive systems can be translated roughly as "intraspecific competition is stronger then interspecific competition." The last two statements suggest that an increase in the intraspecific interaction terms, b_{ii}, should increase det B while an increase in b_{ij} should decrease det B. By noting that $\frac{\partial(\det B)}{\partial b_{ij}} = C_{ij}(B)$, we find that the above sign conditions on $C_{ij}(B)$ yield the appropriate changes in det B for the intraspecific effects to govern stability.

Condition (j) of Theorem 3.7 appears rather technical and unwieldy. We will say more about this condition in section 8.

EXISTENCE, UNIQUENESS, AND FEASIBILITY OF EQUILIBRIA FOR COMPETITIVE SYSTEMS.

We shall now discuss some sufficient conditions for the existence, uniqueness, and positivity of a competitive community equilibrium.

The competitive community (1) always has a K-equilibrium in the set

$$\Omega_0 = \{x \in \mathbb{R}_n^+ : 0 \leq x_i \leq K_i(\overline{0}_i)\ ,\quad i = 1, 2, \ldots, n\}$$

provided (3) holds. The nonnegativity of K implies that

or, $[I + K'(x^*)]\, x^* > 0$. Theorem 3.7(e) implies x^* represents a stable equilibrium community.

Proof of Theorem 3.6. In each case it will be shown that $\det EB = 0$ and, consequently, $I - K'(x^*)$ is singular. However, for x^* to be asymptotically stable, it is necessary that $\det[I - K'(x^*)] \neq 0$.

(i) If $n > k$ then the rank of EB cannot exceed k.

(ii) If $k \geq n$ then

$$\det EB = \sum_p (\det E_p)\,(\det B_p)$$

where E_p is an $n \times n$ submatrix of E obtained by choosing any n columns of E and B_p is the submatrix of B obtained by choosing the corresponding rows of B (Noble, 1969). The summation is over all such choices. Whenever (ii) is satisfied each of the matrices E_p will have linearly dependent rows; hence $\det E_p = 0$ for each p.

(iii) In this case each E_p will have linearly dependent columns. Condition (iii) is also a Corollary of (i) since if g resources are all utilized in the same way by all species, these resources can be regarded from the modelling perspective as a single resource and then (i) holds.

Indication of the Proof of Theorem 3.7

The following conditions are equivalent for any Z-matrix A (Plemmons, 1977):

~~and positivity of equilibria are also presented. Many of the above mentioned results are illustrated in the special case that the model is of Lotka-Volterra type.~~

~~Quasi weakly diagonally dominant matrices are shown to play important roles in models of exploitative competition; in particular, for such systems the community matrix must be quasi weakly diagonally dominant.~~

~~APPENDIX: PROOFS OF THEOREMS~~

Indication of the Proof of Theorem 3.8
~~Proof of Theorem 1.~~

(i). The condition is equivalent to condition (a) of Theorem ~~1~~ 3.7; hence, by Theorem ~~2~~ 3.7, which will be proved below x^* is a stable equilibrium community.

(ii). Let $D = [\text{diag } \delta_i]$. The inequality of (ii) holds if and only if $D(I - K'(x^*))D^{-1}$ is diagonally dominant; that is, $I - K'(x^*)$ is quasidiagonally dominant. Theorem 3 (a) implies x^* is a stable equilibrium community.

(iii). Multiply the inequality by δ_i^{-1} . At equilibrium, $\delta_i^{-1} R_i(\bar{x}_i^*) = x_i^*$; hence, for each i , $i = 1, 2, \ldots, n$

$$x_i^* - \sum_{\substack{j=1 \\ j \neq i}}^{n} x_j^* \left| \delta_i^{-1} \frac{\partial R_i}{\partial x_j} \right| > 0 .$$

This inequality can be written as

$$x_i^* + \sum_{\substack{j=1 \\ j \neq i}}^{n} x_j^* \frac{\partial K_i}{\partial x_j} (\bar{x}_i^*) > 0$$

over please

(i) A is an M-matrix

(ii) A has positive diagonal entries and is quasidiagonally dominant

(iii) There exists an $x > 0$ such that $Ax > 0$

(iv) All of the eigenvalues of A have positive real part.

Since $I + K'(x^*)$ is a Z-matrix, this result implies that (b), (c), (d), and (e) are all equivalent. It is clear that $I - K'(x^*)$ is quasidiagonally dominant is equivalent to $I + K'(x^*)$ is quasidiagonally dominant. A quasidiagonally dominant matrix with negative diagonal entries has eigenvalues with negative real parts (Gershgorin Theorem); hence, for each of (a) through (e), x^* is asymptotically stable.

(f). Since the matrix $[I - K'(x^*)]^{-1}$ is a Z-matrix, it is also an M-matrix. This is a consequence of the fact that when $x^* > 0$ then $[I - K'(x^*)]x^* \equiv w > 0$; hence, $[I - K'(x^*)]^{-1} w = x^* > 0$. The equilibrium, x^* , is asymptotically stable when the eigenvalues of $G'(x^*) = D(I - K'(x^*))$ have negative real part. However, since $[I - K'(x^*)]^{-1}$ is an M-matrix, so is $[I - K'(x^*)]^{-1}(-D)^{-1}$. Thus, the eigenvalues of $[I - K'(x^*)]^{-1}(-D)^{-1}$ and, consequently those of $-D(I - K'(x^*))$, have positive real parts.

(g). Let $H(x) = x - K(K(x))$; then, $H'(x^*) = I - [K'(x^*)]^2$. Employing Taylor's Theorem, $K(K(x)) - x = [I - (K'(x^*))^2][x^* - x] - \epsilon(|x - x^*|)$ where $\epsilon(|x - x^*|) =$

over please

$\underline{o}(|x - x^*|)$ as $|x - x^*| \to 0$. Whenever, $x \in U$, $x < x^*$ and x sufficiently close to x^* ,

$$[I + K'(x^*)]\,[I - K'(x^*)]\,(x - x^*) =$$

$$[I - (K'(x^*)^2]\,(x^* - x) > 0 \ .$$

Since all of the entries of $I - K'(x^*)$ are positive, then $[I - K'(x^*)](x^* - x) > 0$. Condition (e) implies that x^* is asymptotically stable.

(h). The proof of (h) is similar to the one above.

(i). For any $x \in U$, Taylor's Theorem applied to K in the inequality of (i) and some simplification lead to

$$[I + K'(x^*)](x^* - x) - \epsilon(|x - x^*|) > 0 \ .$$

Condition (e) is applicable again.

(j). In this case the hypotheses imply that C^{-1} is an M-matrix (Willoughby, 1977). As such, C^{-1} and, consequently, $[I - K'(x^*)]^{-1}$ and $I - K'(x^*)$ have eigenvalue with positive real part.

<u>Proof of Theorem</u> 4. That $K(\Omega_x) \subset \Omega_x$ is apparent, so again the Brouwer fixed point theorem gives a K-equilibrium in Ω_x . The 2n bounding faces of Ω_x are of the form

$$B_i = \{y \in \Omega_x \mid y_i = x_i\} \ , \quad i \le i \le n \ ; \text{ and}$$

4. <u>Models of Cooperation</u>

Perhaps the most interesting and beneficial association between two species is the act of cooperation. This interaction has been suggested as an evolutionary objective of selection by Odum (1974) and others. The interaction can be <u>facultative</u> in that the association is not obligatory or it can be <u>obligatory</u> in the sense that survival of each population depends upon the presence of the other.

Classical example of cooperation (which in various degrees has also been referred to as mutualism, symbiosis, commensalism, amensalism, in Odum, 1974) include the algal and fungal components of lichens, the clown fish <u>(Amphirion percula)</u> and sea anemones, the ant-<u>Acacia</u> system (Janzen, 1966), plant-pollinator systems.

4.1 <u>Lotka-Volterra Models with Facultative Associations</u>

In the absence of an interacting population, the individual populations are assumed governed by a logistic equation; hence the model with mass action interaction terms is

$$\frac{dx_1}{dt} = x_1 (a_1 - b_1 x_1 + C_{12} x_2)$$

$$\frac{dx_2}{dt} = x_2 (a_2 - b_2 x_2 + C_{21} x_1)$$

where

a_i, b_i, C_{ij} are positive constants.

This model has two possible types of asymptotic behaviour. There can exist a positive equilibrium that is globally asymptotically stable (in the case when $b_1 b_2 - C_{12} C_{21} > 0$). The second type of behavior occurs if $b_1 b_2 - C_{12} C_{21} \leq 0$ and the result is, as aptly described by May "an orgy of mutual benefaction", unbounded growth for each component.

4.2 Obligatory Interactions as Modelled by Lotka-Volterra Kinetics

For obligatory interactions it is assumed that each population, in the absence of the interacting species, will decay exponentially and that interactions are represented by mass action formulations. Hence, the resulting model is

$$\frac{dx_1}{dt} = x_1\,(-a_1 + b_1\,x_2)$$

$$\frac{dx_2}{dt} = x_2\,(-a_2 + b_2\,x_1) \qquad (4.1)$$

Models such as (4.1) can exhibit a stupendus orgy of mutuality since it can be demonstrated that they have solutions with a finite escape time (that is, there exists a $T < \infty$ such that $\lim_{t\to T} x_1(t) = \infty$ or $\lim_{t\to T} x_2(t) = \infty$). For example, with $a_1 = a_2 = b_1 = b_2 = 1$ the substitution $V = x_1 - x_2$ leads to the temporal representation $V(t) = V(0)e^{-t}$. To demonstrate a finite escape time the transformation $w = x_2^{-1}$ can be used to show that

$$dw/dt + (\,-1 + V(0)\,e^{-t})\;w = -1$$

The classification of those solutions w that vanish at a finite time can be obtained and these solutions correspond to those solutions of (4.1) with a finite escape time. There is also a threshold where small initial populations of each component populations result in extinction.

A graphical solution of (4.1) is presented in Figure 4.1. The equilibrium is a saddle point with regions of growth and extinction determined by the separatrices of the saddle point.

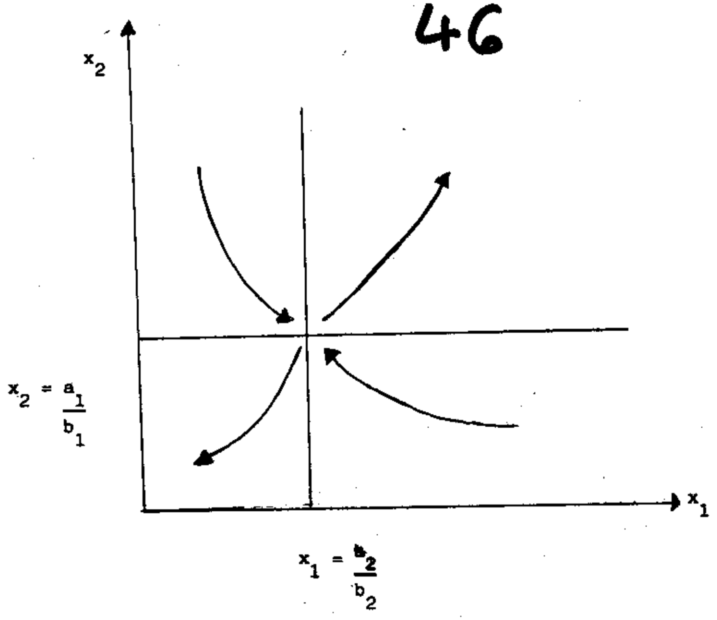

Figure 4.1. Phase plane diagram of a Lotka-Volterra model of obligatory cooperation

4.3 Other Models of Cooperation

While the preceeding model contains some desirable properties such as an extinction threshold, the unbounded growth of solutions is certainly undesirable from a modeling perspective. Vander Meer and Boucher (1978) address the question "How should the isoclines be constructed for cooperative systems?". If interspecific interactions become weaker as population densities become large, then this might have the effect of curving the isoclines towards each other so that they again intersect. At this second intersection will be stable equilibrium and the unpleasant unboundedness of solutions present in the original model (4.1) does not occur here (Fig. 4.2).

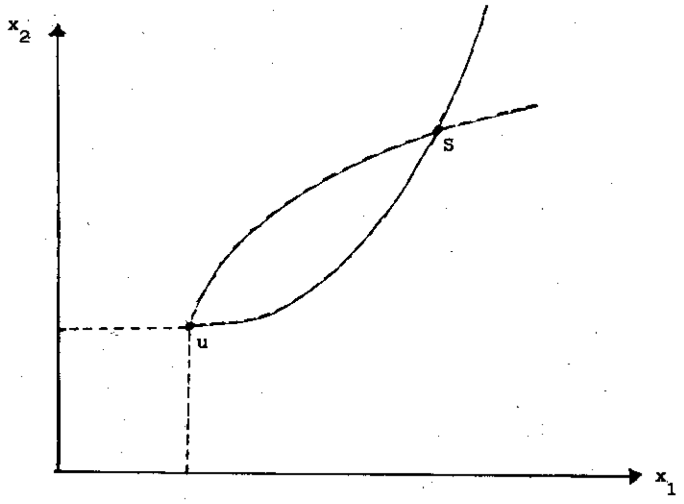

Fig. 4.2. Feasible isoclines for a cooperative system. u and S indicate an unstable and a stable equilibrium respectively

The model might now have the form

$$\dot{x}_1 = x_1\,(-\,a_1 + b_1\,(x_1x_2)x_2)$$
$$\dot{x}_2 = x_2\,(-\,a_2 + b_2\,(x_1x_2)x_1)$$

where b_1, b_2 are decreasing as both of x_1, x_2 increases.

An example of a community where this situation might exist is the legume and bacteria (Rhizobium) system. Properties of this interaction include

i) There is a minimal population of bacteria necessary for successful plant establishment. The few bacteria generally present as seed containments are insufficient for crop growth and innoculation is often required to achieve an establishable community.

ii) Additional bacteria inoculum have little effect on nodulation (and thus, presumably on plant growth and reproduction). This occurs above a certain threshold level; for example, on red clover seedlings grown in culture, additions above 10^4 $(ml)^{-1}$ of rhizosphere produces no discernable changes in growth

iii) The number of bacteria present in the soil when symbiotic with legumes are usually substantially greater than the number needed for nodulation.

In another attempt to formulate a realistic model, May proposes modifying the carrying capacity of the logistic equation to reflect dependence upon the density of the complementary population. The system is written here in a slightly different form to be consistent with earlier discussions:

$$\frac{dx_1}{dt} = x_1\left[r_1 - \frac{C_1x_1}{B_1 + \alpha_1x_2}\right]$$

$$\frac{dx_2}{dt} = x_2\left[r_2 - \frac{C_2x_2}{B_2 + \alpha_2x_1}\right]$$

This formulation has the effect of increasing the equilibrium values of each of the components (over the population carrying capacities).

Kolmogorov-Type Models

The general model of a cooperative two dimensional community of Kolmogorov-type is

$$\frac{dx_1}{dt} = x_1\,f_1\,(x_1,\,x_2)$$

$$\frac{dx_2}{dt} = x_2\,f_2\,(x_1,\,x_2)$$

where for $x_1 \geq 0$, $x_2 \geq 0$

1) $\frac{\partial f_1}{\partial x_2} > o$, $\frac{\partial f_2}{\partial x_1} > o$ (the interaction is cooperative)

2) $x_1 \frac{\partial f_i}{\partial x_1} + x_2 \frac{\partial f_i}{\partial x_2} \le -\alpha < o$, $i = 1,2$ (changes in f_i along outward vector from origin is negative)

3) $f_i(o,o) > o$, $i=1,2$ (small populations grow)

4) $f_i(K_1,o) = f_2(o,K_2) = o$ (there is a carrying capacity for each population)

Albrecht et al. (1974) demonstrate that there is a feasible equilibrium that is globally asymptotically stable.

4.4 Stability in Higher Dimensional Cooperative Communities

An equilibrium, x^*, of the Kolmogorov system

(4.2) $$\frac{dx_i}{dt} = x_i g_i(x), \quad i=1,2,\ldots,n. \quad x=(x_1,x_2,\ldots,x_n)^T$$

is asymptotically stable if and only if the eigenvalues of the community matrix $S=(S_{ij})$,

$$S_{ij} = \frac{\partial}{\partial x_j}(x_i g_i(x))/_{x=x^*}$$

have negative real parts. Since $S_{ij} = x_i^* \frac{\partial gi}{\partial xj}(x^*)$, x^* is asymptotically stable if any only if all of the eigen values of DA have negative real parts where D=diag $(x_1^*, x_2^*, \ldots, x_n^*)$ and A is the interaction matrix, $A = (\frac{\partial gi}{\partial xj}(x^*))$.

For competitive and predator-prey systems, stability is independent of the stability of the interaction matrix. That is, there exists competitive and predator-prey communities for which the community matrix DA is unstable even though the interaction matrix A has eigen values with negative real parts and, conversely, there exist communities for which the community matrix DA is asymptotically stable even though the interaction matrix is unstable.

A pleasant property of cooperative systems is that this is not true in that stability of an equilibrium is determined solely by the interaction matrix. Assuming that (4.2) is completely cooperative, that is,

$$\frac{\partial g_i}{\partial x_j}(x) \ge o, \quad x \in R_n^+, \quad i \ne j,$$

the following classification of stability can be obtained.

Theorem 4.1. A cooperative community modelled by (4.1) is (asymptotically) stable at the equilibrium x^* $(x^* > o)$ if and only if the interaction matrix A is asymptotically stable.

Indication of the Proof. The concept of an M-matrix is useful in the subsequent arguments. The following criteria are equivalent (Plemmons and Berman,)

1. A is an M-matrix
2. All eigen values of A have positive real parts
3. A is nonsingular and $A^{-1} \geq o$
4. There exists a $Z > o$ such that $AZ > o$
5. There exists a $y > o$ such that $A^T y > o$
6. The principal minors of A are positive

The off diagonal elements of the matrix DA are nonnegative. The matrix DA is asymptotically stable if and only if -DA is an M-matrix. Property 5 of M-matrix yields that -DA is an M-matrix is equivalent to the existence of a vector x, $x > o$, such that $-(DA)^T x = -A^T Dx > o$. Hence, this is equivalent to the existence of a $y > o$ such that $-A^T y > o$. Since $a_{ij} \geq o$ for $i \neq j$, this is equivalent to -A is an M-matrix. This results in the conclusion of the Theorem.

There are several interesting consequences of Theorem 4.1. Since -A is an M-matrix, the stability of an equilibrium, x^*, is equivalent to the existence of a vector $d > o$ such that $Ad < o$. Writing this statement in terms of the components we obtain the inequality

$$d_i \mid a_{ii} \mid > \sum_{\substack{j=1 \\ j\neq i}}^{n} d_j a_{ij} \quad , \quad i = 1,2,\ldots,n \tag{4.3}$$

When (4.3) holds, A is called quasi-diagonally dominant. An interpretation of (4.3) is that for stability of x^*, the intraspecific competition must dominate the inter-specific interaction terms. In an analagous manner, a column diagonal dominance property can be found.

Employing property 6 of M-matrices, a simple algebraic relationship may be obtained for the stability of an equilibrium;

$$(-1)^K \begin{vmatrix} a_{11} & a_{12} & \cdots & a_{1K} \\ a_{21} & a_{22} & \cdots & a_{2K} \\ \vdots & & & \vdots \\ a_{K1} & a_{K2} & \cdots & a_{KK} \end{vmatrix} > o, \quad K=1,2,\ldots,n$$

(is equivalent to -A has positive principal minors).

The above consideration has focussed upon local stability properties. There are global stability results that can be obtained in a similar fashion.

Theorem 4.2. For the Lotka-Volterra system of cooperation.

$$\frac{dx_i}{dt} = x_i \ \left(r_{io} + \sum_{j=1}^{n} a_{ij} \ x_j \right), \qquad a_{ij} > o \tag{4.4}$$

A feasible equilibrium, x^*, is globally asymptotically stable if and only if all the principal minors of -A are positive.

<u>Indication of the Proof.</u> It has been previously demonstrated that x^* is locally stable with this set of hypotheses. To establish global stability, a Liapunov function of Volterra type is useful. The function

$$V(x) = \sum_{i=1}^{n} C_i \ \left(x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*}\right)$$

has derivatives along trajectories of (4.4) expressed in terms of a quadratic form with matrix $CA+A^TC$ where $C = \text{diag}\ (C_1,C_2,\ldots C_n)$ (see Goh, 1977). If $CA+A^TC$ is negative definite, global asymptotic stability results. Johnson (1974) shows that when the negative of an M-matrix is stable there exists a matrix $C = \text{diag}\ (C_1,C_2,\ldots,C_n)$, $C_i > o$ such that $CA+A^TC$ is negative definite. Thus, global stability of x^* follows.

This material is related to that found in Siljak (1975), Goh (1979), and Travis and Post (1979).

5. Communities Composed of Populations with Different or Mixed Functional Roles

Models of interacting populations of two and three dimension are explored in this section. First, the stability of a community in which the functional role of a population changes with the density is considered. Next, we turn to some three dimensional communities of Lotka-Volterra type with determinate roles for populations but the coupling in the food web will be different than discussed previously. The community matrix role in three dimensional systems is investigated.

5.1 A Two Species Model with Density Dependent Functional Roles

Hastings (1978) has proved a general stability theorem for Kolmogorov type models.

Theorem 5.1. Sufficient conditions for the global stability of an equilibrium (x_1^*, x_2^*) of

$$(5.1) \qquad \frac{dx_1}{dt} = x_1 f_1 (x_1, x_2) \qquad \frac{dx_2}{dt} = x_2 f_2 (x_1, x_2)$$

are

i) (x_1^*, x_2^*) exist and are unique

ii) (x_1^*, x_2^*) is locally asymptotically stable

iii) Both species sustain density dependent mortalities at all densitites:

$$\frac{\partial f_1}{\partial x_1} < 0, \quad \frac{\partial f_2}{\partial x_2} < 0$$

iv) There exist constants $A > 0$, $B > 0$ such that

  a) for any $x_2 > B$, there is a $C > 0$ such that $f_1(C_1 x_2) < 0$

  b) for any $x_1 > A$, there is a $D > 0$ such that $f_2(x_1, D) < 0$

Indication of the Proof. Let (x_1°, x_2°) be any initial position. The rectangle bounded by the x_1, x_2 axes and the lines $x_1 = \tilde{x}_1 = \max(x_1^*, A, C, x_1^\circ)$, $x_2 = \tilde{x}_2 = \max(x_2^*, B, D, x_2^\circ)$ is invariant under the flow definied by (5.1). Transform

the system by using the Volterra transformation $u_1 = \ln x_1$, $u_2 = \ln x_2$. This leads to

$$\frac{du_1}{dt} = f_1(e^{u_1}, e^{u_2})$$

$$\frac{du_2}{dt} = f_2 (e^{u_1}, e^{u_2})$$

Since $\frac{\partial f_1}{\partial u_1} + \frac{\partial f_2}{\partial u_2} = \frac{\partial f_1}{\partial x_1} e^{u_1} + \frac{\partial f_2}{\partial x_2} e^{u_2} < 0$,

the Bendixson nonexistence criterion implies that (5.1) does not have a limit cycle Hence, global asymptotic stability results for (5.1).

A Functional Role Determined by Density Dependence

It is not a trivial task to determine the functional role of a population in a community; indeed, it is often the case that a species will assume many different roles depending upon average age of the population, the density of the population, and other factors. The snail (Thais) is both a competitor and a prey for the starfish (Pisaster), Paine (1966). Bluegill-bass interactions are also indeterminant in their interaction relationships as both predation and competition occur between both species.

A system that models two populations where predation is the dominant interaction at high densities of the population (the prey) and competition dominates at low population levels is

$$\frac{dx_1}{dt} = x_1 (1 - d_1x_1 - d_2x_2 - d_3x_1x_2)$$

$$\frac{dy_1}{dt} = x_2 (1 - d_4x_2 - d_5x_1 + d_6x_1^2)$$

Hastings (1978) has found sufficient conditions for a globally asymptotically stable equilibrium to be $4d_6 > d_5^2$, $d_4 > d_2$, and $d_2d_6 > d_3d_5$.

5.2 The Community Matrix in Three Population Communities

The community matrix has an important history in discussions of stability. Since the principal model with an essence of lower order nonlinearity is the classical Lotka-Volterra model

$$\frac{dx_i}{dt} = x_i \left(r_i - \sum_{j=i}^{n} b_{ij} x_j\right), \quad i=1,2,\ldots,n$$

These equations may be written in matrix form as

$$(5.2) \qquad \frac{dx}{dt} = (\mathrm{diag}(x_i))\,(r-Bx)$$

where $x = (x_1,x_2,\ldots,x_n)^T$, $r=(r_1,r_2,\ldots,r_n)^T$ and $B=(b_{ij})$. A nontrivial equilibrium x^* of (5.2) is (locally) asymptotically stable if and only if the eigenvalue of the matrix $-(\mathrm{diag}\ (x^*))B$ all have negative real parts. This matrix is more commonly written as $-(\mathrm{diag}\ (x_i^* b_{ij}))(I+A)$ where $A=(a_{ij})$, $a_{ij}=b_{ij}/b_{ii}$ if $i \neq j$ and $a_{ii}=o$. This matrix will be called the community matrix of (5.2). There have been numerous attempts to derive methods of estimating a_{ij} from field and laboratory data, especially in the case of competitive communities (e.g. Gause (1934), MacArthur and Levins (1967), Vandermeer (1969), Schoener (1974), Hallett and Pimm (1979)). Because of the infinite appeal of the community matrix and the fact that the parameters a_{ij} seem to have offered the best possibility for estimation in the past, it would be desirable to extract as much information as possible from the system (5.2) using only the matrix I+A. This approach can be developed without quantitative knowledge of r_i and b_{ii}.

As indicated in Section 4.4, the properties of I+A are sufficient to determine the stability of n dimensional cooperative communities and also some communities of mixed mutualism and competition (Travis and Post, 1979). However, the examples of Strobeck (1973) in Section 3.6 show that the properties of I+A are not sufficient to determine stability since both systems have the same community matrix.

The following result is valid only for dimension 3. Extensions to dimension 4 and higher are, at best, difficult (Clark and Hallam, 1983). Assumptions include r is a 3-vector with positive entries and B is a 3x3 matrix with positive diagonal elements. To indicate parameter dependence, the system (2) will be denoted by LV(r,B), the diagonal matrix $\mathrm{diag}(x_i^* b_{ii})$, (when $B^{-1}r = x^* > o$), by D(r,B), and the community matrix $I+A = \mathrm{diag}(b_{ii}^{-1})B$ by CM(B). The second order principal minors of I+A will be denoted by

$$M_1 = 1 - a_{23}a_{32},\ M_2 = 1 - a_{13}a_{31},\ M_3 = 1 - a_{12}a_{21}$$

The next theorem gives conditions which are sufficient to ensure that the stability of a positive equilibrium of LV(r,B) depends only on the community matrix. The conditions are also necessary in the sense that if they are not satisfied then either no positive equilibrium can exist for any choice of r and B or it is always possible to find examples, such as those of Strobeck, of distinct systems with the same community matrix but with different stability properties.

Theorem 5.2. Let A denote a 3x3 matrix whose diagonal elements are zero.

A. If I+A satisfies either

(i) $\det (I+A) \leq o$, or

(ii) $\det (I+A) > o$ and $M_i \leq o$, i = 1, 2, 3; then for any choice of r and B where CM(B) = I+A, LV(r, B) cannot have a positive stable equilibrium.

B. If I+A satisfies

(iii) $\det (I+A) > o$, $M_i \geq o$, i = 1, 2, 3, $\sum_{i=1}^{3} M_i > o$, and

$$\sqrt{\det\ (I+A)} \leq \sqrt{M_1} + \sqrt{M_2} + \sqrt{M_3}$$

where equality can hold only if $M_1M_2M_3 = 0$, then for any choice of r and B where CM(B) = I+A, a positive equilibrium of LV(r, B) is stable.

C. Suppose that I+A satisfies none of the conditions, (i), (ii), or (iii). If (iv) there is no positive vector x such that $(I+A)x > 0$, then for any choice of r and B where CM(B) = I+A, LV(r,B) can have no positive equilibrium. If (v) there exists $x > 0$ such that $(I+A)x > 0$, then there exist matrices r, B, $\tilde{r}$, $\tilde{B}$ with the properties $CM(B) = CM(\tilde{B}) = I+A$, $B^{-1}r = x^* > 0$, $\tilde{B}^{-1}\tilde{r} = \tilde{x}^* > 0$, x^* is a stable equilibrium of LV(r, B), and $\tilde{x}^*$ is an unstable equilibrium of LV(r, B).

Two observations are relevant to part C of Theorem 5.2. If C(v) holds, it is always possible to choose $x^* = \tilde{x}^*$. If $a_{ij} > 0$ so that the system represents competition, then c(iv) cannot hold and x^* and $\tilde{x}^*$ in C(v) may be chosen arbitrarily.

Quasi Weak Diagonal Dominance

A matrix $C = (c_{ij})_{nxn}$ is <u>weakly diagonally dominant</u> if $|c_{ii}| > |c_{ij}|$ for $i = 1, \dots, n$, and $j \neq i$. The matrix C is <u>quasi weakly diagonally dominant</u> if there exists a diagonal matrix D with positive diagonal elements such that $D^{-1}CD$ is weakly diagonally dominant. Quasi weak diagonal dominance might hold for many ecological systems as it relates interspecific and intraspecific interactions. The following theorem due to Fiedler and Ptak (1967) illustrates this and leads to some interesting observations.

Theorem 5.3. If $n \geq 2$ and C is any matrix, then C is quasi weakly diagonally dominant if and only if, for any set of distinct indices, $1 \leq i_1, i_2, \dots, i_k \leq n$,

$$|c_{i_1 i_2} c_{i_2 i_3} \cdots c_{i_{k-1} i_k} c_{i_k i_1}| \leq |c_{i_1 i_1} c_{i_2 i_2} \cdots c_{i_k i_k}| . \tag{5.3}$$

Applied to the matrix B of the system LV(r, B), the condition (5.3) is a direct generalization of the well known condition which is necessary and sufficient for the stability of a positive equilibrium of a competitive system when n = 2: $|b_{12}b_{21}| \leq |b_{11}b_{22}|$. This condition is usually translated as "intraspecific interactions are stronger than interspecific interactions", and this interpretation also seems appropriate when $n > 2$. Note that (5.3) holds for B if and only if it holds for CM(B) = I + A, and, in this case, takes the form:

$$|a_{i_1 i_2} a_{i_2 i_3} \cdots a_{i_k i_1}| \leq 1 \tag{5.4}$$

It is well known that det $(I+A) > 0$ is a necesssary condition for stability and also that it is not, in general, sufficient if $n > 2$. However, in the three species case, condition (5.4) simplifies matters considerably and leads to a simple classification of stable equilibria.

Theorem 5.4. Let n = 3; $r > 0$; and B be a matrix with positive diagonal elements such that B (or I+A) is quasi weakly diagonally dominant. Then, a positive equilibrium of LV(r, B) is stable if and only if det $(I+A) > 0$.

As remarked previously, quasi weak diagonal dominance might be valid for many community models. For a competitive community, it is a consequence of some of the formulations of the competition coefficients a_{ij}. As an illustration is it noted that one of the more familiar formulations first suggested by Gause for n = 2 and generalized by Levins (1968) and MacArthur (1968), can be generalized to include the case of a continuous resource spectrum as follows:

$$a_{ij} = \frac{\int_S p_i(x)p_j(x)dx}{\int_S p_i^2(x)dx} \tag{5.5}$$

where $p_i(x)dx$ denotes the probability that species i will utilize the portion $(x, x + dx)$ of the resource spectrum in a unit of time, and S denotes the resource continuum. If "/ //" denotes the inner product and norm in the appropriate inner product space, it follows, for distinct indices $i_1, i_2, \dots, i_k$

$$a_{i_1 i_2} a_{i_2 i_3} \ldots a_{i_k i_1} = \frac{(p_{i_1} \cdot p_{i_2})(p_{i_2} \cdot p_{i_3}) \ldots (p_{i_k} \cdot p_{i_1})}{\| p_{i_1} \|^2 \, \| p_{i_2} \|^2 \ldots \ldots \| p_{i_k} \|^2}$$

$$\leq \frac{(\| p_{i_1} \| \, \| p_{i_2} \|)(\| p_{i_2} \| \, \| p_{i_3} \|) \ldots (\| p_{i_k} \| \, \| p_{i_1} \|)}{\| p_{i_1} \|^2 \, \| p_{i_2} \|^2 \ldots \ldots \| p_{i_k} \|^2} = 1.$$

Therefore I + A is quasi weakly diagonally dominant.

There are extensions to these results to the Kolmogorov-type system

$$\frac{dx_i}{dt} = x_1 f_i(x), \quad i = 1,2,\ldots,n$$

where $\partial f_i / \partial x_i < 0$.

The proof of Theorems 5.2 and 5.3 are not given here; they may be found in Clark and Hallam, 1983.

5.3 A Two Dimensional Competitive Sub Community and Another Population

Assuming that a community contains a two dimensional competitive sub-community then various types of populations can be added to obtain a new community. We have studied the case where the added population was a competitor with each of the other two populations. In this section some consequences of introducing a cooperative population or a predator population are described. The mathematical details are similar to those for the Lotka-Volterra competitive model.

The Third Population is a Cooperator (Hallam 1981).

For a Lotka-Volterra model of a competitive subcommunity and an added cooperator, certain hypotheses about the coefficients are required to eliminate the "orgy" effect. With these imposed, extinction of the populations can be classified. Employing two populations interactions, there are some interesting outcomes. The introduction of cooperator can destroy the stable competitive subcommunity by driving one of the competitors to extinction. This can be accomplished by the symbiotic population helping one of the competitors too much.

The Third Population is a Predator

Models for a predator and two competing prey are numerous in the literature (e.g. Cramer and May, 1972; Vance, 1978; Gilpin, 1978). Most analyses have focussed upon "predator mediated coexistence" where the presences of a predator allows regulation of a dominant competitor in a competitive subcommunity.

An analysis of persistence and extinction shows that there can be two forms of predator mediated coexistence; these are given by the arrangements

$$V_1 \gg V_2 \; ; \quad V_1 \longleftrightarrow p \; ; \quad V_2 \longleftrightarrow p \; ;$$

and

$$V_1 \gg V_2 \; ; \quad V_1 \longleftrightarrow p \; ; \quad p \downarrow V_2 \; ;$$

In these arrangements, the competition notation is as in Section 3.6 for the prey populations V_1, V_2. The interactions between predator and prey indicated by $V_i \longleftrightarrow p$ and $p \downarrow V_i$ represent an asymptotic stability coexistence for both predator and prey and the survival of the prey population only respectively. Both arrangements require invasion capability of complementary species for equilibrium communities.

The persistence analysis also leads to another possible mechanism of coexistence, namely, "competition induced coexistence". An analysis of the Lotka-Volterra model shows that this can occur in two ways:

$$v_1 \longleftrightarrow v_2 \;;\quad v_1 \longleftrightarrow p \;;\quad p \downarrow v_2 \;;$$

and

$$v_1 \longleftrightarrow v_2 \;;\quad p \downarrow v_1 ;\quad p \downarrow v_2 \;;$$

Instances of predator mediated coexistence are well documented in the ecological literature (e.g. Paine, 1966; Connell 1975; Caswell, 1978).

The Third Population is a Predator

Models for a community containing a predator and two prey populations exist in the literature (e.g. Cramer and May, 1972; Vance, 1978; Gilpin, 1978). Most analyses have focussed upon the processes of predation and competition as mechanisms that can generate diversity in communities. Two of these mechanisms that can be identified by model analysis are predator mediated coexistence and competition induced coexistence.

Predator mediated coexistence is concerned with regulation of a dominant competitor by predation in order that a complete community might persist. According to the model, this type of coexistence, which tacitly assumes that the competitive subcommunity interacts in a competitively dominant manner, can occur in two ways: either both predator-prey subcommunities coexist stably or one coexists stably and the other exhibits predator extinction. The criteria for persistence and, hence for predator mediated coexistence, are that species complementary to stable predator-prey subcommunities are able to successfully invade at subsystem equilibrium densities. Instances of predator mediated coexistence are well documented in the ecological literature (e.g. Paine (1966), Connell (1975); Caswell (1978) references several experiments where predator mediated coexistence does and does not hold.

Other references, related at least peripherally to the model studied here, in which a predator is introduced into a competitive subcommunity include Maly (1975), Neill (1975), Addicott (1974). Yodzis (1976) has discussed effects of constant rate predation on competitive systems.

Gilpin (1978), using a model employed by Vance (1978), has numerically demonstrated that chaotic behaviour can arise in a three dimensional system composed of two prey and a predator. While the parameter set they utilize to find chaotic behaviour is a limiting case of an arrangement whose persistence development is indicated in Hallam (1981), it can be shown there are parameter sets in this arrangement that lead to chaotic motion. Not only is the phenomena of predator mediated coexistence of ecological interest, the mathematical description of the dynamics can be very complicated as well.

Another model generated mechanism that might exist in communities and which could lead to increased diversity is competition induced coexistence. Two arrangements of subcommunities were classified in this category. The largest increase in diversity occurs in an arrangement where a predator cannot survive on either of the prey species but it can persist if it is able to invade the stable competitive subcommunity at its equilibrium density. Certain herbivore-plants systems could theoreticall fit into this category.

A mechanism that guarantees (according to the model) diversity will not increase in three species systems is for the competitive subcommunity to exhibit competitive instability. That is, according to Lotka-Volterra kinetics, competition that is unstable cannot be regulated to a state of persistence by predation.

The terms predator mediated coexistence and competion induced coexistence refer to persistence in a community attained by effects of species upon subcommunities. Analysis indicates that determination of coexistence can be function of all subcommunities as well as species interactive capabilities. In the case of predator mediated coexistence, a persistent community can be theoretically achieved by introduction of a prey competitor into a predator-prey subsystem, in which the predator need not even survive. The phenomenon of predator mediated coexistence might be masked in such a situation. Persistence since it is dependent upon subsystems composition and interrelationships, is a community property and phrases as simple as predator mediated coexistence are probably not totally adequate descriptions