THEORETICAL STUDIES OF THE LIMITING SIMILARITY

OF COMPETITORS

by

by

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ABSTRACT

This study consists of several theoretical investigations which bear on the question, "How similar may competing species be and still coexist?" It evaluates two previously suggested generalities, and suggests several factors which are important in determining the limiting similarity of competitors in a particular type of community.

The first part is a study of the limits to overlap in resource utilization for competitors which are linearly arranged. The question of whether there is a limit to the similarity of species competing on a one-dimensional resource axis has previously been investigated by a number of authors. These studies have all used the Lotka-Volterra model of competition, and have assumed that the competition coefficient α_{ij} may be calculated using MacArthur and Levins' (1967) expression,

$$\alpha_{ij} = \frac{\int U_i(R)U_j(R)dR}{\int (U_i(R))^2 dR} \quad ,$$

where $U_i(R)$ is the resource utilization curve of species i. The generality of this formula is questioned, and two

alternative expressions for α_{ij} are proposed. When these expressions are used in an analysis of limiting similarity, qualitatively different conclusions emerge regarding the existence and nature of this limit. The two alternative formulae considered suggest that under some circumstances very high overlap is possible in a linear array of competing species. The available experimental evidence does not strongly support the validity of MacArthur and Levins' formula for α_{ij}. Since a given method of calculating α_{ij} must be derived from a higher level model, it is suggested that the Lotka-Volterra model is not sufficient in an investigation of limiting similarity. Different assumptions about the nature of the resource utilization curves result in major differences in the limiting similarity. If the resources at a given position on the resource axis consist of a number of resource types, it seems likely that very close species packing should be possible.

The second part investigates the question of whether several forms of environmental variability will limit niche overlap in a group of competing organisms. A simulation methodology was used to answer this question for the Lotka-Volterra model of competition. The basic result of this analysis is that systems where competition coefficients are relatively high can tolerate nearly as high a level of environmental variability as systems where niche overlap is low if,

(i) environmental variability means variation in the supply
of the resource for which the animals are competing, or
(ii) there is a high level of correlation in the fluctuations
in the rates of increase of different species (which, in turn,
will be the case if the competitors share the same predators
or have similar tolerances to physical stresses in the
environment). High levels of variability may preclude the
persistence of systems with a high level of competition when
variations in the per capita rates of increase are uncorrelated
or negatively correlated, or when increased variability is
correlated with a lower average per capita rate of increase.

The third chapter develops and analyzes a simple
model of exploitative competition in which the resource
consumers do not influence the rate at which resources
become available to them. The goal of this analysis is to
determine what factors allow relatively high (or low) resource
overlap among competitors. The basic results are that:

(1) The maximum overlap which will allow coexis-
tence of two species, one of which has a slight competitive
advantage, is usually greater when exploitation is efficient
(i.e. when a large fraction of the resources entering the
system are consumed when the consumer populations are at
equilibrium).

(2) The effect of density independent predation
on this type of system is always to increase the niche

separation necessary for coexistence, and thus to decrease
species diversity. Predation increases the intensity of
competition and decreases the maximum overlap consistent
with coexistence for a pair of species. Environmental
fluctuations which result in a reduction of population levels
will have a similar effect.

These results appear to be fairly general, so it would be
desirable to try to determine whether the basic assumption
of the model is actually met in those natural systems where
it seems plausible.

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GENERAL INTRODUCTION

Ecologists have long recognized that competition is an important factor structuring natural communities. Specifically, competition sets limits to the similarity of competitors, since it is unlikely that two species with very similar resource utilization patterns will be able to co-exist. This investigation attempts to examine this phenomenon in a more quantitative manner using simple mathematical models. More specifically, it is concerned with the following questions:

(1) What is the nature of the limiting similarity of species which partition resources in a one-dimensional manner?

(2) Does environmental variability set a limit to the overlap in resource utilization of competing species?

(3) Under what biological circumstances (e.g. intensity of predation, level of environmental variability, environmental productivity) will relatively large overlap in resource utilization of competitors be likely?

Each of these questions is investigated using simple mathematical models of competition. A complete answer to any of the questions would require a study of a larger array of models than is practical for a single individual. In

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fact, the range of biologically possible communities is such that it is doubtful that it will ever be possible to give an answer to these questions that is valid for all cases. The present findings are necessarily somewhat limited by the range of models examined. Thus, conclusions are suggestive rather than definitive.

The emphasis throughout is on simple models. This stems from the conviction that, despite the complexity of most ecological systems, an understanding of real communities must be based on an understanding of simple models. A complex simulation model of a specific system may reveal, for example, that the maximum overlap in resource utilization of competitors is not altered by an increasing variance in the food supply. The same phenomenon might be suggested by measurement of niche overlap in a series of communities which differ in the variance of the food supply. However, such a study would contribute little to the understanding of similar systems. Would the same conclusions hold if some resource other than food was varying? Would the conclusions be valid for organisms with significantly different age structure? Without a study of models on a simpler level, even tentative answers to these sorts of questions cannot be supported. Thus, it would not be possible to say very much about the generality of the finding.

The present study is concerned both with the existence of general patterns and with the explanation for

differences between communities. Previous theoretical studies
(e.g. May, 1973a) have suggested two general results:

> (1) Species which partition resources in a
> one-dimensional manner must have utili-
> zation curves which are separated by a
> distance equal to the standard devia-
> tion of the curves.
>
> (2) Overlap in resource utilization by
> competitors can be greater in less
> variable environments.

The first two parts of this study are concerned with inves-
tigating the validity and range of applicability of these
generalizations. The third part then analyzes a simple model
of exploitative competition to suggest possible reasons for
the differences in the degree of resource overlap that has
been observed in groups of competitors (Schoener, 1974b).

Chapter 1

LIMITING SIMILARITY AND THE FORM OF THE
COMPETITION COEFFICIENT

INTRODUCTION

Beginning with Lotka, Volterra, and Gause, most
ecologists have held the view that extremely similar organisms
cannot coexist for long periods of time. It has not, however,
been until fairly recently that there has been a more quan-
titative attempt to determine how similar competing organisms
may be and still coexist in an equilibrium community. The
motivation for this line of study stems largely from Hutchinson's
(1959) observation that in several genera, sympatric species
form sequences in which each species is about twice as
massive as the next. This led to the conjecture that com-
petition may have resulted in this pattern. Several recent
studies have suggested that there is, in fact, a limiting
similarity of competing organisms, or that very high overlap
in resource utilization among competitors is unlikely if
not impossible (MacArthur and Levins, 1967; May and MacArthur,
1972; May, 1973a, 1974a). Although these studies have used

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different lines of analysis, they all reached approximately
the same conclusion; that for species competing on a one-
dimensional resource axis, there is a limit to similarity
corresponding to a pattern where the means of adjacent species'
resource utilization curves are separated by a distance
approximately equal to one standard deviation of the curves.
The terminology of this statement will be explained later,
but qualitatively, it prohibits high overlap in resources
used by competitors which segregate along some linear dimension
(by taking foods with different mean sizes or foraging at
different average heights, etc.).

May (1973a) has summarized much of the experimental
evidence which bears upon this contention. This evidence
will be discussed in more detail later, but there are at
least several cases where groups of competitors seem to be
close to the limiting similarity suggested by these authors.
On a more qualitative level, studies of the resource utiliza-
tion of closely related sympatric species have generally
revealed a high degree of resource partitioning (Schoener,
1974b).

Granting that resource partitioning is the result
of interspecific competition, there are still at least two
possible mechanisms which may account for it. The observed
segregation may be close to the minimum consistent with
persistence of all of the populations. Alternatively, par-
titioning may be much greater than the minimum possible,

and may be due to selection for the avoidance of competition. Before the cause of existing patterns of ecological segregation may be determined, it is necessary (among other things) to know the precise nature of the limits to similarity set by competition.

Since all of the previous studies regarding limiting similarity (MacArthur and Levins, 1967; May and MacArthur, 1972; May, 1973a, 1974a; Roughgarden, 1974) have at least two common assumptions, it seemed worthwhile to examine the effects of relaxing those assumptions. All of these studies have been based upon the Lotka-Volterra model of competitive interactions, although there have been several studies suggesting that this model may not be a good description of the population dynamics of at least some groups of competitors (Wilbur, 1972; Neill, 1974). Whether a limiting similarity may be derived from other models of competition will be the subject of a later study. The current paper is concerned with the second assumption; that the competition coefficient α_{ij} in the Lotka-Volterra model may be estimated by

$$\alpha_{ij} = \frac{\int U_i(R)U_j(R)dR}{\int (U_i(R))^2 dR} \tag{1}$$

where $U_i(R)$ is a curve plotting the probability density that a unit of species i's resources has come from position R on the resource axis. By examining the effect of relaxing this assumption, the current study should suggest something

about the generality of the previous result that utilization
curves must be separated by a distance equal to their standard
deviation. If the result is not completely general, this
analysis should suggest what circumstances might permit
greater overlap.

The first section of this paper re-examines the
rationale for using MacArthur and Levins' measure. The second
section presents and justifies two alternative formulae for
the competition coefficient, and the third section looks at
the effect that these alternative formulae have upon the
existence and nature of a limiting similarity. The paper
concludes with a review of some field evidence and a discussion
of the type of models which are likely to be valuable in
studying limiting similarity.

MacArthur and Levins' Method of Calculating α_{ij}

Formula (1) was originally proposed by MacArthur
and Levins in 1967. Before discussing the validity of their
estimate of the competition coefficient, it is first neces-
sary to explain the underlying model upon which it is based.
Most theoretical work dealing with limiting similarity has
concerned organisms which are characterized by the shape of
their resource utilization curve and by the position of that
curve on a one-dimensional resource axis. A resource axis
is a linear ordering of resource types for which the species

are competing. As noted above, the utilization curve of

species i is defined at each position R on the resource axis

as the probability density that a unit of the resources con-

sumed by species i came from position R on the resource axis.

Although it is common in the literature to speak of

the utilization curve as being a characteristic of a species,

such curves actually reflect the relative abundances of dif-

ferent resources as well as the species' ability to consume

a given resource. Since competitors alter the relative

abundances of resources, a given species' utilization curve

will generally change in the presence of competitors. It

is therefore convenient to specify that utilization curves

be measured in the absence of competitors. In addition,

since the utilization curves are a function of the resource

availabilities in a given environment, it only makes sense

to analyze competition in a specified environment. If

resource availabilities vary spatially or temporally within

that environment, utilization curves may be taken to be

averages over time or space. A given shape of the utilization

curve may arise in a number of ways. Take the case of an

assembly of insectivorous competitors and a resource axis

of food size. There are generally a large number of dif-

ferent types of insects of any given size. A low value of

U(R) may be the result of the insectivore eating only those

few species of insects of size R which are easiest to catch

and consume, and ignoring all other insects of that size (this will later be referred to as a type one utilization curve). Alternatively, the consumer may accept all of the insect species of size R, but be relatively ineffective at catching insects of this size relative to other sizes (a type two utilization curve). Many intermediate cases are, of course, possible.

In speaking of a resource utilization curve as a characteristic of a species, it is also implicit that the population is relatively uniform in terms of resource utilization patterns. If, for example, resource utilization were a function of age in two populations, a given amount of overlap could have greatly different meanings depending upon the age specific pattern of utilization in the two species.

In general, utilization curves are only very crude descriptions of a species' resource utilization pattern. Such a crude description may be inadequate in some cases. This paper is mainly relevant to species which have reasonably well defined resource utilization curves, are similar in their general ecology, which compete only by using common resources, and whose resources do not interact strongly with each other.

MacArthur and Levins' original justification of expression (1) was as follows: "

Basically, to compete for space, individuals
of species 1 and 2 must confront one another

> *and hence be present simultaneously.*
> *Similarly, when resources are rapidly*
> *renewed, individuals only compete if they*
> *are present within a short time of each*
> *other. In either case (expression (1))*
> *measures the relative probability of the*
> *simultaneous presence of species 1 and*
> *species 2 compared to species 1 and*
> *species 1. Hence it measures* α.

If resources are renewed immediately, resource supplies will play no role in population regulation. Hence there will be no exploitative competition. If resources are not renewed immediately after being consumed (and this seems to be generally true) it is possible for one species to reduce the resources available to a second species while never meeting an individual of the second species. A food item eaten by species one is no longer available to be eaten later by species two. There is no necessity for the two species to be present in the same place within a short time of each other in order for competition to occur. This is especially clear if the resources are mobile.

If space is being competed for, MacArthur and Levins' argument may be more reasonable, but there are still difficulties. Organisms which compete for space do not continuously search for space; generally they settle into an adequate habitat and remain and grow there, so that the amount of time an organism spends in a habitat and its growth rate and the dispersal of its progeny are important in determining the competition coefficient.

MacArthur (1972) and Schoener (1974a) have later
suggested that formula (1) may be justifiable since it can
be derived from a more explicit model of competition sug-
gested by MacArthur (1968). This model consists of differ-
ential equations specifying the rate of change of the competitor
and resource populations. Using Schoener's notation (1974b),
these may be written,

$$\frac{dN_i}{dt} = R_i N_i \left(\sum_k^m a_{ik} b_{ik} F_k - C_i \right), \qquad i = 1, \cdots, n$$

$$\frac{dF_k}{dt} = r_k F_k - \frac{r_k F_k^2}{K_k} - F_k \sum_i^n a_{ik} N_i \qquad k = 1, \cdots, m \qquad (2)$$

where b_{ik} represents the net energy per item of resource k
extractable by an individual of competitor i; a_{ik} is a con-
sumption rate of resource k by species i; r_k and K_k are the
intrinsic rate of increase and the carrying capacity of
resource k in the absence of the competitor populations;
C_i is the per-individual cost of maintenance and replacement
of competitor i; and R_i is the number of individuals of
competitor i that can be produced per unit of assimilated
energy. N is the competitor population density, and F is
the resource density. An expression for α may be derived
by assuming that all populations have non-zero equilibrium
values (unfortunately, they do not always), solving for the

equilibrium resource abundance, and substituting this expression in the equation for the rate of change of the competitor populations. If all of the resources have the same K, r, and b, and utilization curves are measured when the species are allopatric, then the expression for α reduces to expression (1). Unfortunately, no natural system described in the literature consists of predators which eat a variety of prey, all of which renew logistically. In fact, Schoener's 1973 study indicates that logistic growth may be less common than is usually supposed. When this basic requirement for logistic resource growth is coupled with the conditions of equal K, r, and b, and the further assumption that none of the resources go extinct with the addition of a competitor, it begins to appear that expression (1) may not be of very broad applicability. In addition, MacArthur's derivation assumes what was referred to earlier as a type two utilization curve, which means that all of the resource types at any position on the resource axis are consumed at equal rates.

In spite of these arguments, it is possible that MacArthur and Levins' formula is approximately correct for some cases. The point being made here is simply that it is unlikely to be adequate to describe all or even most instances of competition.

Other Measures of α_{ij}

In this section we will derive two alternative expressions for the competition coefficient α_{ij}. The first will be derived by assuming a model similar to the MacArthur-Schoener model presented above, but assuming type one utilization curves. The second expression will be derived by approximating a different model of interspecific competition by a set of Lotka-Volterra equations at the equilibrium point. These two examples certainly do not exhaust the range of models for which it is possible to derive a competition coefficient. They do, however, serve to show the range of expressions which may arise from different assumptions.

The assumption that all of the prey populations grow logistically, and the other assumptions of the MacArthur-Schoener model may not be very general. Nevertheless, this is the only model of exploitative competition which, to my knowledge, results in Lotka-Volterra behavior (the per capita growth rate of one species is a linearly decreasing function of the population density of the other species and of its own density). For this reason, it is worthwhile to analyze it further. The version of this model discussed in the previous section assumed that utilization curves were the result of different consumption rates of resources at different poisitions on the resource axis. In most natural systems, however, there will also be differences in the number of resource types taken at each position on the resource axis.

Take, as an example, two species which partition food resources
by size. Each food size consists of a number of different
types which differ in palatability or ease of capture. Since
partitioning is assumed to be on the basis of size alone,
the ranking of food items of a given size in terms of ease
of capture is the same for both competitors. The species
with smaller mean food size will take only those large food
items which are easiest to capture, but it may take them at
the same rate as the larger species (which takes a greater
number of large food types). Similarly, the larger competitor
takes only those small food types which are easiest to capture.

In this situation, the food taken by one competitor
may be divided into two classes; those which are shared with
the other species, and those which are not. If it is assumed
that the two competitors take approximately the same total
amounts of food, the fraction of the total resources used
by one of the species which are shared with the other species
will be proportional to the area in common under the two
utilization curves.

The competition coefficient then can be calculated
in basically the same manner as described before (or see
MacArthur, 1972). The result is that (if all resource types
have the same K, r, and b), the competition coefficient is
equal to the area in common under the two utilization curves.
Denoting this area by A_0, the first alternative expression
for α is

$$\alpha = A_0 \tag{3}$$

Roughgarden (1972) has previously proposed that the competition coefficient could be estimated by the area in common under two utilization curves, although he did not fully explore the consequences of that assumption regarding limiting similarity. It is probable that most utilization curves are intermediate between type one and type two. Not only will competitors take fewer food types far from the optimum size, but they will probably consume those food items at a lower rate than those near the optimum of their utilization curves.

It should be noted that expression (3) is not fundamentally different from expression (1). If $U(R)$ is defined in terms of resource type, rather than resource at a given position on the resource axis, then formula (3) has a similar form to formula (1). Here $U(R)$ is assumed to take on a certain positive value (for those types which are consumed) or zero (for those types which are not), with no intermediate values. This is analogous to the case of rectangular utilization curves, discussed later.

If the MacArthur-Schoener model were the only second level model of exploitative competition to which conclusions derived from Lotka-Volterra equations were relevant, then these equations would be of very limited value in analyzing exploitative competition. However, several

authors (e.g. MacArthur, 1972; May, 1973a) have argued that
conclusions derived from analyses of the Lotka-Volterra
equations may apply to a much wider class of models. The
Lotka-Volterra model then represents the first term in a
Taylor Series expansion of the alternative model about its
equilibrium point. Our second formula for the competition
coefficient is derived assuming a model of exploitative
competition which does not result in Lotka-Volterra behavior,
and then approximating this model by a Lotka-Volterra
model at the equilibrium point. Of course, if one were
interested in the limits to similarity in the original
model, that model should be analyzed directly, rather than
determining the limiting similarity for an approximation.
At present, however, we are concerned with Lotka-Volterra
systems.

This second alternative formula for α_{ij} also
assumes that utilization curves are of type one. Therefore,
resources may be divided into exclusive and overlapped
classes. The fraction of the total resources taken by a
species which are in the overlapped classes is equal to the
area in common under the utilization curves of the two
species. Resources do not, however, renew logistically.
Instead, it is assumed that resources are supplied at a
rate which is independent of the level of exploitation. For

this sort of situation Schoener (1973) has proposed the
following model:

$$\frac{dN_1}{dt} = R_1 N_1 \left(\frac{I_{E_1}}{N_1} + \frac{I_0}{N_1 + N_2} - C_1 \right)$$

$$\frac{dN_2}{dt} = R_2 N_2 \left(\frac{I_{E_2}}{N_2} + \frac{I_0}{N_1 + N_2} - C_2 \right) \qquad (4)$$

where R is the number of individuals produced from a unit of
energy. C is the energy cost of maintenance and replacement
of an individual. I_E is the energy extractable from a con-
sumer's exclusive resource per unit time, and I_0 is the
energy that individuals of a competitor species can extract
from resources used by both species (per unit time). It
is assumed here that individuals of the two species exploit
the overlapped resources with equal efficiency. Also, for
mathematical convenience we assume that $I_{E_2} = I_{E_1}$, $R_1 = R_2$,
and $C_1 = C_2$; i.e. that competition is symmetrical.

If the population densities of either species
become very low, this model becomes unrealistic, since a
very small population would be unable to exploit the same
amount of resources as a large population, as implied by
(4). However, the model may be an accurate description of
many systems in a large neighborhood around the equilibrium
point.

To approximate this system by a set of Lotka-Volterra equations, α is calculated according to the following formula:

$$\alpha_{12} = \left.\frac{\left\{\frac{d(\text{per capita growth rate of species 1})}{d\,N_2}\right\}}{\left\{\frac{d(\text{per capita growth rate of species 1})}{d\,N_1}\right\}}\right|_{\hat{N}_1\hat{N}_2} \tag{5}$$

where $\hat{N}_1$ and $\hat{N}_2$ are the equilibrium levels of the two populations. The competition coefficient α_{12} thus measures the effect of species 2 on species 1 relative to the effect of species 1 on itself. The details of this calculation are given in Appendix I. The result is that $\alpha_{12} = I_0/(4I_E + I_0)$. Equivalently, $\alpha = A_0/(4A_E + A_0)$ where A_0 is the area in common under the utilization curves of the two species and A_E is the area under one curve but not the other. Since the curves are normalized, $A_E = 1 - A_0$, and the above formula becomes

$$\alpha_{ij} = A_0/(4 - 3A_0) \tag{6}$$

The remainder of this study examines the different consequences that expressions (1), (3), and (6) have regarding the existence and nature of a limiting similarity. Before proceeding it should be noted that formulae (1), (3), and (6) all assume approximately equal harvesting efficiencies of the competitors. This results in an upper bound of one for the competition coefficient and a symmetrical competition matrix ($\alpha_{ij} = \alpha_{ji}$).

Limiting Similarity and the Competition Coefficient

There are two basic lines of analysis which argue
for the existence of a limiting similarity. The first sug-
gests that there should be a limit to the overlap of com-
petitors even when there is no environmental variability,
while the second argues that it is environmental fluctuations
which limit overlap. Limiting similarity in constant environ-
ments will be discussed first.

Limiting Similarity in Constant Environments -
MacArthur and Levins' Theory

In 1967 MacArthur and Levins suggested that the
similarity of competitors was limited because of both of the
following factors:

> (1) Invasion by a third species between
> two resident species on some resource
> axis becomes impossible if the overlap
> between the residents is great enough,
> and the carrying capacity of the invader
> is not greater than that of the residents.

> (2) If the species in a three species com-
> petitive guild have high enough overlap,
> there will be selective pressures for
> the inner species in the array to con-
> verge toward and eliminate one of the
> outer ones.

As was mentioned earlier, these arguments were
made on the basis of a study of a Lotka-Volterra system and

the assumed formula (1) for the competition coefficient.
We begin by re-examining their first argument.

The condition required for the successful invasion
of a third species midway between the two resident species
on a resource axis is that

$$\alpha(2d) - (2/(K_2/K))\alpha(d) + 1 > 0, \qquad (7)$$

where 2d is the distance on the resource axis between the
two resident species, K_2 is the carrying capacity of invader,
and K is the average carrying capacity of the residents.
We will begin by considering the case where the carrying
capacity of the invader is equal to that of the residents.
In this case the above requirement translates into

$$L(d) \equiv 2\alpha(d)/(1 + \alpha(2d)) < 1. \qquad (8)$$

MacArthur showed that if expression (1) is assumed for α
and the utilization curves are normal in shape with a
standard deviation of w, the function L(d) is greater than
one if the distance between the resident species is greater
than 1.56w. More recently Roughgarden (1974) has calculated
this limiting value for a wider family of utilization curves,
and has found that closer packing is possible for more
leptokurtic curves (curves with thick tails and thick peaks
relative to the normal curve), but that there is still a

limiting value for the case of equal carrying capacities. Thus, the assertion that there is a limiting similarity under this assumption of equal carrying capacities does not appear to be sensitive to changes in the shape of the utilization curves. It is, however, sensitive to the assumption that α is given by (1).

In Appendix II it is shown that any function $\alpha(d)$ which is concave upwards will not result in a limit to the similarity of competitors with equal carrying capacities, and that expression (3) and (6) both result in $\alpha(d)$ being concave upward. However, the validity of MacArthur and Levins' theory depends on both halves of their argument, and the second half appears to be invalid regardless of which of the three formulae is assumed for α.

MacArthur and Levins argued that a species which had a high enough carrying capacity to invade between two residents would converge towards and eliminate one of the residents. In fact, as is shown in the next section, if the resident species are separated by significantly less than d/w = 1, an invader with a large enough carrying capacity to invade successfully is likely to eliminate both resident species without any convergence. Even if there were some selective pressure for convergence, a very small shift would generally be sufficient to result in exclusion of one of the residents. In addition, the argument is suspect on other grounds. It assumes that position, but not shape of

a utilization curve is evolutionarily flexible. It assumes that the positions of the residents' utilization curves are fixed, but not that of the invader. It also assumes that the carrying capacity is independent of the position on the resource axis, and that competition is the only selective force acting upon the position of the invader's utilization curve.

Finally, it is possible to examine the effect of the competition function on MacArthur and Levins' argument, granting the questionable assumptions. Although they did not present their analysis very explicitly, it appears that they assumed that the evolution of the invader occurred when its population was small relative to that of the residents. Then, if the invader occupies a position a distance x from one of the residents, and a distance 2d-x from the other, its per capita growth rate may be written as

$$F(x) = K_2 - \frac{\alpha(x)K + \alpha(2d-x)K}{1 + \alpha(2d)} \qquad (9)$$

If this expression is unimodal and has a maximum at x = d, then there will be no selective pressure for convergence of the invader toward one of the resident phenotypes. Differentiating (9) one obtains

$$F'(x) = \frac{K}{1 + \alpha(2d)}\left[-\alpha'(x) + \alpha'(2d - x)\right], \qquad (10)$$

which clearly vanishes at x = d. Since $\alpha(x)$ is unimodal, there are no other zeros. The second derivative is,

$$F''(x) = \frac{K}{1 + \alpha(2d)}\left[-\alpha''(x) - \alpha''(2d - x)\right]. \qquad (11)$$

The second derivative of F(x) will be negative, and x = d will be a maximum if the second derivative of $\alpha(x)$ is positive. Thus, MacArthur and Levins' second argument, which has more recently been reiterated by Cody (1974), also depends upon the formula assumed for α. Expressions (3) and (6), which generate $\alpha(x)$ curves which are concave upwards, would not support the argument for evolutionary convergence.

Invasion of a third species into a two species guild will always be possible if its carrying capacity is high enough regardless of the formula used for α_{ij}. Therefore, MacArthur and Levins' analysis does not justify the existence of a limiting similarity.

Limiting Similarity in Constant Environments - May's Theory

Although most of Robert May's work deals with limits to similarity in fluctuating environments, he has also advanced a line of argument to suggest that overlap may be limited in deterministic systems as well (May, 1973a, 1974a).

Briefly, his argument is that if overlap is high, the shape of the resource spectrum (which reflects the relative abundances of resources at different positions on the resource axis) must lie within very narrow limits for the species in a competitive guild to coexist. This implies that high overlap is very unlikely, although not impossible.

The argument can best be illustrated by studying a three species system, since some of the arguments made earlier will apply here as well. Assume that $K_1 = K_3$ (the resource spectrum is symmetrical), and that the second species (with carrying capacity K_2) is located midway between the first and third. Then the equilibrium populations are given by

$$\hat{N}_1 = \hat{N}_3 = \frac{K_1 - K_2\alpha(d)}{1 + \alpha(2d) - 2(\alpha(d))^2}$$

$$\hat{N}_2 = \frac{K_2 + K_2\alpha(2d) - 2K_1\alpha(d)}{1 + \alpha(2d) - 2(\alpha(d))^2} \tag{12}$$

The requirement that these populations be positive leads to the following criterion for a stable three species equilibrium:

$$\left[1 + \alpha(2d)\right]/2\alpha(d) > K_1/K_2 > \alpha(d) \tag{13}$$

Figure 1 (after May, 1973a) illustrates this criterion for normal utilization curves, assuming expression (1) for α.

Figure 1. The ratios of K_1/K_2 which allow a stable
three species community, calculated using
MacArthur and Levins' expression for α,
and plotted as a function of the separation
of neighboring resource utilization curves.
The permissible ratios lie between the two
curves. Utilization curves are normal in
shape.

For d/w less than 1, it is clear that the ratio of K_1/K_2 must fall within very narrow bounds for there to be a stable community.

Similar results can be obtained for systems with more species. For the case of a four species guild where $K_1 = K_4$ and $K_2 = K_3$, the criterion for a stable community works out to be

$$\frac{1 + \alpha(3d)}{\alpha(d) + \alpha(2d)} > \frac{K_1}{K_2} > \frac{\alpha(d) + \alpha(2d)}{1 + \alpha(d)} , \qquad (14)$$

This is illustrated in Figure 2, again assuming normal utilization curves and formula (1) for α. The results here are quite similar; the ratio of K_1/K_2 must lie within narrow bounds for a stable community if d/w is much less than one. These results have already been illustrated by May (1974a).

If one regards differences in the carrying capacity to be due to differences in the resources available to the competitors (as does May), then Figures 1 and 2 are rather misleading. This is true because, as overlap between adjacent species becomes greater, the chance that one species will have a larger amount of resources available to it decreases. In the case of 100% overlap, the two carrying capacities must be equal if carrying capacities are determined solely by resource availabilities. Thus, although the range of permissible carrying capacity ratios becomes smaller as overlap becomes greater, the range of possible ratios becomes smaller as well.

Figure 2.   The ratios of K_1/K_2 which allow a stable,
            symmetrical four species community, calculated
            using MacArthur and Levins' expression for α,
            and plotted as a function of the separation
            of neighboring resource utilization curves.
            The permissible ratios lie between the two
            curves. Utilization curves are normal in
            shape.

K1/K2

D/W

27b

The carrying capacities may also differ due to a difference in the efficiency of the two species in converting resources into individuals (the parameter C_i in the two models noted earlier (equations (2) and (4)). Two species may differ significantly in efficiency even though they exploit the same resources. Therefore overlap of significantly less than $d/w \doteq 1$ is indeed unlikely if utilization curves are normal and expression (1) is used for α. To give a more quantitative meaning to the limiting similarity it is possible to define this entity as the value of d/w for which the range of permissible carrying capacity ratios first attains a given (small) value.

Before the limit of $d/w \doteq 1$ is accepted as being generally applicable, however, it is necessary to determine whether the result is altered either by the shape of the utilization curves or the formula assumed for α. Therefore the criteria for stability for three and four species systems (expressions (13) and (14)) were reexamined for utilization curves which were rectangular and curves which had the shape of back-to-back exponential decay curves (Laplace distribution curves) using formula (1) for α. In addition, all three utilization curve shapes were studied using expressions (3) and (6) for α. The results are shown in figures 3 through 6.

Figures 3 and 4 show that if expression (1) is valid, tighter species packing is possible either for curves which are leptokurtic (sharp peak and thick tails), or for

Figure 3. The ratios K_1/K_2 which allow a stable three
           species community with Laplace distribution
           utilization curves, assuming MacArthur and
           Levins' formula for α.

Figure 4. The ratios K_1/K_2 which allow a stable three
species community with rectangular utilization
curves assuming MacArthur and Levins' formula
for α.

curves which are platykurtic (broad peak and thin tails) relative
to the normal curve (the former result has previously been noted
by Roughgarden (1974)). In this and subsequent figures only
the three species case is illustrated, since results for the four
species community are very similar.

For the case of rectangular utilization curves there is
no value of d/w below which the range of permissible carrying
ratios rapidly becomes very small. However, it is still possible
to define the limiting similarity as that value of d/w for which
the difference between the largest and smallest permissible ratios
of carrying capacities is an arbitrary (small) value. The limit-
ing similarity for the case of rectangular curves will be much
smaller than that for either normal or Laplace curves, assuming
expression (1).

Expression (3) yields the same formula for α as does
expression (1) in the case of rectangular utilization curves.
Figures 5A and 5B show that normal or leptokurtic utilization
curves result in an even lower value for the limiting similarity
than for rectangular utilization curves if formula (3) is
applicable. The difference between systems with rectangular
and normal utilization curves is relatively slight. However,
significantly closer species packing is possible if the utiliza-
tion curves have the shape of Laplace distribution curves.
In this case, for d/w = .03, the range of K_1/K_2 values which
will result in a stable three species system is approximately
.6 to 1.5. This range is large enough so that it would not be
at all surprising to find a system with d/w = .03 or less if
utilization curves are type one.

Figure 5.   The ratios of carrying capacities which allow
a stable three species community assuming
$\alpha = A_0$. (A) assumes Laplace distribution
utilization curves, and (B) assumes normal
curves. The graph for rectangular curves
is the same as Figure 4.

K1/K2

0.0   0.357   0.714   1.071   1.429   1.786   2.143   2.5

5 B

Expression (6) yields lower values of α than (3), and consequently results in an even lower value for the limiting similarity. Figures 6A, 6B, and 6C illustrate the region of stable coexistence for a three species community for normal, Laplace, and rectangular curves respectively. For any of these utilization curve shapes there is a wide range of K_2/K_1 ratios which will allow coexistence when $d/w = .1$ or less.

Thus, of the three utilization curve shapes and three possible expressions for α considered here, only one combination leads to a deterministic limit to similarity near $d/w = 1$ (Expression (1) for α and normal utilization curves).

None of the three expressions for α considered here lead to an absolute limit to the similarity of competitors in a constant environment. If there were an absolute limit, it would be impossible for any stable community to exist if utilization curve separation were less than a certain amount. Such a limit would exist in the three species case if

$$\frac{1 + \alpha(2d)}{2\alpha(d)} = \alpha(d) \ . \tag{15}$$

Were satisfied for some value of d greater than zero. For the four species system, the requirement is that

$$\frac{1 + \alpha(3d)}{\alpha(d) + \alpha(2d)} = \frac{\alpha(d) + \alpha(2d)}{1 + \alpha(d)} \ . \tag{19}$$

Figure 6. The ratios of carrying capacities which
allow a stable three species community
assuming $\alpha = A_0/(4-3A_0)$. (A) assumes
Laplace distribution utilization curves,
(B) assumes normal curves, and (C) assumes
rectangular curves. The upper curve in
(A) did not fit on the graph.

K1/K2

0.0　　0.357　　0.714　　1.071　　1.429　　1.786　　2.143　　2.5

0.0

0.4

0.8

1.2

1.6

2.0

2.4

2.8

3.2

3.6

6 A

K1/K2

K1/K2

6 C

In general, there is an absolute limit to the similarity of competitors if the determinant of the following matrix is equal to zero for some value of d greater than zero:

$$
\begin{bmatrix}
1 & \alpha(d) & \alpha(2d) & \cdots & \alpha((n-1)d) \\
\alpha(d) & 1 & \alpha(d) & \cdots & \alpha((n-2)d) \\
\cdot & & & & \cdot \\
\cdot & & & & \cdot \\
\cdot & & & & \cdot \\
\alpha((n-1)d) & \cdot & \cdot & \cdot & 1
\end{bmatrix}
\tag{17}
$$

If this criterion is satisfied, there can be no n species community with a species spacing d/w less than that value at which the determinant vanishes. This is true regardless of the carrying capacities of the component species.

There cannot be an absolute limit to similarity for any of the three formulae for α considered here. May (1974) has shown that MacArthur and Levins' method of calculating α leads to matrices which are positive definite for unimodal resource utilization curves, so that the above matrix does not have a determinant equal to zero for d greater than zero. Expressions (3) and (6) result in $\alpha(d)$ curves which are concave up. For the three species case, this means that the left hand side of (15) is nondecreasing, so (15) can never be satisfied. A similar argument can be used to show that (16) or (17) cannot be satisfied either.

There is no reason to believe, however, that the three expressions for α considered here exhaust the range

of biologically realistic formulations. There are a number
of plausible $\alpha(d)$ curves which do result in an absolute
limit to similarity. For example, if $\alpha(d) = 1/(1+d^3)$,
no three species community is possible if d is less than
approximately .59. If $\alpha(d) = \exp(-d^3)$, the limiting simi-
larity will be d = .68 in the three species case. (In
both of these cases d represents the absolute value of the
distance between two utilization curves.) These results are
similar for larger communities. For example, if $\alpha(d) =
1/(1+d^3)$, an eight species community cannot be stable unless
d is greater than about .69. These two forms for $\alpha(d)$ are
reasonable in the sense of being decreasing functions with a
maximum of 1 at d = 0, and approaching 0 as d becomes very
large. Whether and when such functions with broad peaks
and narrow tails are reasonable estimates of the competition
coefficient is a question that can be answered only by inves-
tigating models of competition where the degree of overlap
in resource utilization enters the equations explicitly.

Similarity Barriers and Distributions of Niche Separation Distances

Roughgarden (1974) has recently published a re-
analysis of MacArthur and Levins' (1967) findings. He
examined the ease of invasibility (as measured by the per
capita rate of increase of an invader when its population

was small and the residents were at equilibrium densities)
of a two species guild as a function of the separation of
the resident species. The per capita rate of increase of
the invader is proportional to

$$G(d) = K_2 - \frac{2\alpha(d)K_1}{1 + \alpha(2d)} \tag{18}$$

where 2d is the distance between the means of the utiliza-
tion curves of the resident species. This expression is a
linear function of expression (7). Roughgarden assumed that
α could be estimated by formula (1). For the case of normal
utilization curves (and all of the other curves he investi-
gated with the exception of rectangular curves), this method
of computing the competition coefficient will result in
$\dot{G}(d)$ curves having a minimum at some positive value of d
(say d_m). Thus, invasion should be easier if the resident
species are separated by large distances or very small
distances than if they are separated by approximately d_m.
Roughgarden termed this phenomenon a "similarity barrier,"
and claimed that it could result in a bimodal distribution
of niche separation distances. In fact, as Robert May has
also noted (Cody, 1974, p. 114), an invasion below the
"similarity barrier" is likely to result in the exclusion
of both residents (as can be seen from Figure 1 for example).
Thus it does not seem likely that a bimodal distribution
of of niche separation distances should arise for this
reason.

In addition, the existence of a similarity barrier
depends on the form of $\alpha(d)$ in the same way that the existence
of a limiting similarity for the case of equal carrying
capacities did. This is clear since expression (18) is a
linear function of expression (7). Thus, there will be a
similarity barrier for cases where expression (1) for α
is appropriate, but not when expression (3) or (6) is valid.
Both Roughgarden (1974) and Cody (1974) have interpreted
field data using this theory. The dependence of Roughgarden's
results on the form of $\alpha(d)$ suggests, however, that before
natural patterns are interpreted in light of his theory,
it is necessary to justify the use of expression (1) for α
in the particular case being studied.

Limiting Similarity of Competitors in Fluctuating Environments

Although the suggestion that environmental variability
may limit the degree of overlap of competing species has
been made by several authors (Pianka, 1966; Miller, 1967;
Slobodkin and Sanders, 1969), Robert May has been responsible
for developing this theory in a quantitative fashion (May
and MacArthur, 1972; May, 1973a, 1973b, 1974a). We will
begin by summarizing those aspects of his work which are
relevant to the present study.

May studied a Lotka-Volterra system whose com-
ponent populations experience random fluctuations in their

per capita rates of increase. The rate of change of the
ith population is given by

$$dN_i/dt = N_i \left[K_i + \mu_i - \sum_j N_j \alpha_{ij} \right],$$ (19)

where μ_i is a random term (white noise) with a normal
distribution with mean of zero and a variance σ^2.

May argued that the persistence of this sytem
depends upon the minimum eigenvalue of the interaction
matrix whose ijth entry is $\hat{N}_i \alpha_{ij}$, where $\hat{N}_i$ is the equilibrium
population level of the ith species in the deterministic
system. In general, he assumes that the equilibrium popu-
lations of the various species are equal. This tends to give
the most stable community for a given degree of niche overlap,
and is therefore appropriate in investigating the limits
of similarity. Specifically, May argues that the minimum
eigenvalue must be larger than the variance in the per
capita rate of increase about its deterministic value if
the populations are to persist ($\lambda_{min} > \sigma^2$). This criterion
is very approximate, and it depends upon the assumption
that there are no cross correlations in the stochastic
terms of the competing species (see Chapter 2), an assumption
which may not often be met in natural situations. Never-
theless, if cross-correlations are small enough, a system
with a very small minimum eigenvalue is not likely to persist

for long. For a more detailed justification of this criterion
of stability see May (1973b).

May assumes that α can be calculated by formula (1),
and proceeds to show that in a many species community with
gaussian utilization curves, the minimum eigenvalue of the
interaction matrix rapidly becomes very small once the dis-
tance between the means of neighboring utilization curves
(d) becomes less than the standard deviation (w) of the
curves. This result implies that there is a limit to niche
overlap of approximately d/w = 1, and that this limit is
relatively insensitive to the degree of environmental varia-
tion unless the fluctuations are quite severe. The basic
result does not depend strongly on the shape of the utili-
zation curves, although one exception to this will be noted
later.

The purpose of the present study is to show that
very different results may be obtained if alternative formulae
are assumed for the competition function. Specifically, we
will examine the interaction matrices which arise from
formulae (3) and (6) for α. Figure 7 shows the values of
the three forms of the competition coefficient as a function
of d/w for normal resource utilization curves. Table I gives
comparable results for triangular utilization curves.
Since the minimum eigenvalue of a two species competitive
system is $\hat{N}(1-\alpha)$, it is clear that either formula (3) or

Figure 7. Plots the three expressions for α as a
function of utilization curve separation for
normal utilization curves. Curve A plots
expression (1); curve B plots expression
(3); and curve C plots expression (6).

ALPHA

Table I. α as a function of utilization curve
         separation for triangular resource
         utilization curves.

Table I

D/W	Formula (1)	Formula (3)	Formula (6)
.050	.998	.960	.858
.098	.991	.922	.746
.147	.980	.884	.655
.196	.965	.846	.579
.245	.946	.810	.516
.294	.924	.774	.462
.392	.871	.706	.375
.490	.808	.640	.308
.612	.719	.563	.243
.710	.642	.504	.203
.808	.562	.449	.169
.906	.483	.397	.141
1.004	.405	.348	.118
1.225	.250	.250	.077
1.421	.148	.176	.051
1.617	.079	.116	.032
1.813	.035	.068	.018
2.001	.012	.032	.008
2.204	.002	.010	.003
2.449	.000	.000	.000

formula (6) allows higher overlap for a given degree of
environmental variability. The difference between the three
curves is especially striking for relatively small d/w, so
that the difference in the limiting degree of overlap is
greatest for small to moderate levels of environmental vari-
ability. The same trends are illustrated for normal and
triangular curves. As noted before, expressions (1) and (3)
converge as the utilization curves approach a rectangular shape.

For competitive systems with more than two species,
it is generally necessary to use numerical methods to solve
for the minimum eigenvalue. Eigenvalues were calculated
using Symal, a subroutine written for the U.B.C. IBM 370-168
computer. This routine reduces a symmetric matrix to a
symmetric tridiagonal matrix using Householder transformations,
and then uses QL transformations to find the eigenvalues
and eigenvectors of the matrix.

Results for four and eight species systems with
triangular and normal resource utilization curve shapes are
shown in Tables II, III, and IV. Although there are slight
differences depending upon whether the system has four or
eight species, and whether utilization curves are triangular
or normal in shape, the general features which emerge are
the same for the three tables. If d/w is significantly
greater than one, the minimum eigenvalue is comparable for
all three formulae for α. However, as d/w drops below

Table II.   The minimum eigenvalue of the interaction
            matrix of an eight species community with
            triangular resource utilization curves as
            a function of the separation of adjacent
            utilization curves.

Table II

D/W	λ_{min} (formula (1))	λ_{min} (3)	λ_{min} (6)
.000	0.	0.	0.
.012	$.52 \times 10^{-7}$	.005	.021
.049	$.15 \times 10^{-4}$	.021	.082
.110	$.16 \times 10^{-3}$	.047	.179
.196	$.92 \times 10^{-3}$	.083	.298
.306	.002	.130	.421
.441	.005	.187	.536
.600	.009	.256	.638
.784	.053	.332	.723
.992	.243	.392	.788
1.225	.530	.530	.855
1.429	.728	.674	.906
1.633	.861	.791	.943
1.838	.941	.883	.969
2.042	.983	.948	.987
2.246	.998	.987	.997

Table III.   The minimum eigenvalue of the interaction
             matrix of a four species community with
             normal resource utilization curves, as a
             function of the separation of adjacent
             utilization curves.

Table III

D/W	λ_{min}(formula (1))	λ_{min} (3)	λ_{min} (6)
.02	10^{-5}	4.62×10^{-3}	1.84×10^{-2}
.06	10^{-5}	1.40×10^{-2}	5.53×10^{-2}
.1	10^{-5}	2.33×10^{-2}	9.16×10^{-2}
.2	10^{-5}	4.67×10^{-2}	.178
.3	2.70×10^{-5}	7.61×10^{-2}	.256
.4	1.47×10^{-4}	9.36×10^{-2}	.326
.5	5.49×10^{-4}	.117	.389
.6	1.59×10^{-3}	.141	.445
.7	3.83×10^{-3}	.165	.495
.8	8.08×10^{-3}	.189	.544
.9	1.53×10^{-2}	.214	.580
1.0	2.66×10^{-2}	.239	.616
1.1	4.30×10^{-2}	.265	.648
1.2	6.53×10^{-2}	.292	.678
1.3	9.37×10^{-2}	.319	.706
1.4	.128	.347	.736
1.5	.169	.376	.753
1.6	.214	.406	.774
1.7	.263	.435	.793
1.8	.315	.465	.811
1.9	.368	.495	.827
2.0	.421	.526	.842

Table IV. The minimum eigenvalue of the interaction
matrix of an eight species community with
normal resource utilization curves, as a
function of the separation of adjacent
utilization curves.

Table IV

D/W	λ_{min}(formula (1))	λ_{min} (3)	λ_{min} (6)
.1	10^{-5}	2.06×10^{-2}	8.20×10^{-2}
.2	10^{-5}	4.14×10^{-2}	.161
.3	10^{-5}	6.23×10^{-2}	.234
.4	10^{-5}	8.32×10^{-2}	.301
.5	10^{-5}	.104	.362
.6	10^{-5}	.125	.417
.7	4.85×10^{-5}	.147	.466
.8	2.53×10^{-4}	.168	.511
.9	9.98×10^{-4}	.190	.551
1.0	3.10×10^{-3}	.212	.588
1.1	7.96×10^{-3}	.235	.621
1.2	1.74×10^{-2}	.258	.652
1.3	3.31×10^{-2}	.281	.680
1.4	5.64×10^{-2}	.306	.706
1.5	8.80×10^{-2}	.331	.729
1.6	.127	.358	.751
1.7	.174	.385	.770
1.8	.225	.413	.789
1.9	.280	.442	.806
2.0	.337	.472	.822

approximately one, MacArthur and Levins' formula results in minimum eigenvalues which decrease very rapidly, whereas formulae (3) and (6) result in eigenvalues which decrease in an approximately linear fashion from d/w = 1 to d/w = .1. For a system where α is calculated using expression (6), the minimum eigenvalue changes fastest as a function of d/w for values of d/w less than .1. As a consequence, it is impossible to isolate any particular value of d/w as a general limit to similarity. The limit depends senstively on the level of environmental variability and the precise definition chosen for the limiting similarity. In addition, for a given level of variability, formula (3) or (6) will allow considerably higher overlap among the competing species than does expression (1). For example, if the minimum permissible eigenvalue is .05, utilization curves are triangular and there are eight species in the competitive guild, formula (1) allows a minimum d/w of approximately .77; formula (3) allows d/w = .11; and formula (6) permits a d/w of about .03. It is worth noting that this last value is probably not far enough different from complete overlap to be distinguishable from it in field situations. Similar results could be drawn for the four species system or the eight species system with normal utilization curves.

In addition to being sensitive to the expression used to calculate the competition coefficient, May's result

is also not preserved if utilization curves are rectangular
in shape. Figure 8 is a plot of the minimum eigenvalue as
a function of niche separation for an eight species system
with rectangular utilization curves. The curve behaves in a
rather strange fashion, but there is no clear limit to
similarity. It is worth noting that May's result is restored
quite rapidly if the rectangular curves are altered slightly,
so that they are not quite so sharply cut off (for example,
if the utilization curve is given by $U(x) = 1/(1 + x^4)$),
so that the form of the minimum eigenvalue for rectangular
curves may not be of much biological significance.

It should be noted that if very close species pack-
ing is possible (as suggested by formulae (3) or (6)) the
implicit assumption in the previous analysis that the equili-
brium population sizes of the component species did not change
with the number of species or degree of overlap becomes
untenable. In the exact linearized analysis, the terms
α_{ij} of the interaction matrix are multiplied by the equili-
brium numbers of species i. If equilibrium populations of
the different species are equal, the minimum eigenvalue
decreases linearly with the equilibrium population size.
If packing is close, similarity may be limited by the size
of the equilibrium populations, rather than by an instability
inherent in any system with the given number of species
and competition coefficients. If this is the case, however,

Figure 8. The minimum eigenvalue of the interaction
matrix of an eight species community with
rectangular utilization curves assuming
formula (1) for α. The minimum eigenvalue
is plotted as a function of the separation
of neighboring curves.

MINIMUM EIGENVALUE

D/W

the minimum eigenvalue does not decrease abruptly at a certain value of the species packing parameters, d/w, so that again it is not possible to state a general value as the limit to species packing.

In general, the results of this analysis of stochastic systems parallels the earlier treatment of deterministic systems. The existence of a limiting similarity clearly depends upon the form assumed for the competition coefficient.

Evidence from Natural Populations

If natural communities exhibitng one-dimensional competition generally had niche separations corresponding to d/w of approximately one, this could lend some support to the generality of formula (1), so it is worthwhile to examine the field data on communities exhibiting approximately one-dimensional competition. Much of the evidence available regarding species packing in linear competitive systems has been summarized by May (1973a). It should be noted that most detailed studies have found that resource partitioning occurs along several dimensions (Schoener, 1974b), and that the competitors are not linearly arranged, so that in most cases May's theory does not appear to be applicable. In many of the cases cited by May, the presumed one-dimensional nature of the competition may simply be a result of inadequte

study of the organisms involved, and May himself has stressed that the limit $d/w \doteq 1$ will only apply to situations where competition is one-dimensional.

Although May interprets ten or so examples as supporting his general conclusions (i.e. exhibitng $d/w \doteq 1$), the evidence is, in fact, fairly weak. The examples are basically of three sorts: (1) size differences of congeneric competitors which, May contends, imply that d/w is approximately equal to one, (2) examples of groups which show constant average niche overlaps in very different environments, which May interprets as indicating that limiting similarity is not sensitive to the level of environmental variability, and (3) four examples where actual resource utilization data was available, showing d/w about equal to one.

This evidence may be criticized on a number of grounds. The first category is relatively indirect evidence. In addition, several authors who have accumulated data on prey size selection in flycatchers, seed size selection in finches, and seed selection by desert rodents, all obtained similar results; there was great overlap in the sizes and kinds of food particles used, in spite of large differences in body size or bill size (Brown and Lieberman, 1973). Therefore, overlap in resource utilization may be higher than that inferred from size, bill dimensions, or other measurements.

The fact that niche overlap is not correlated with environmental variability (the second category of evidence) may simply mean that environmental variability is not limiting niche overlap, that the animals in question are not competing, or that competition is not for some one-dimensional resource.

None of the four examples of resource utilization has been studied thoroughly enough to rule out segregation along niche dimensions other than the ones noted by May. In one case (two Plethodontid salamanders studied by Dumas (1956)) the author concluded that there was no competition for food, the resource dimension discussed by May (1973a).

Finally, it should be mentioned that there are a number of competitively based systems where very high overlap has been documented; flower and fruit eating birds (Terborgh and Diamond, 1970), hermit crabs (Nyblade, 1974), seed eating finches (Pulliam and Enders, 1971), and seed eating rodents (Brown and Lieberman, 1973), although species are not exactly linearly arranged in all of these systems. There are additional examples of high overlap in systems which have not been very thoroughly studied (Sycamore leaf-hopeers (Ross, 1957); hoverflies (Diver, 1940); cichlid fishes of Lake Malawi (Ricklefs, 1973); and gammarid amphipods of Lake Baikal (Ricklefs, 1973)). In any case, available

field evidence does not suggest that expression (1) is of general validity, even for one dimensional systems.

Recently, Roughgarden (1974) has attempted to explain some examples of high overlap in guilds of coral reef fish by noting that if the utilization curves are leptokurtic, d/w may be much less than one. However, this result does not explain the observed high overlap in diet, since leptokurtic curves do not overlap significantly until d/w is very small. In addition, there is no evidence that the fish that Roughgarden cites have leptokurtic utilization curves, or even that they compete on a linear resource axis. The present analysis suggests that this and other examples of high overlap could be expected if the competition coefficient α can be estimated by formula (3) or (6). Therefore, a possible explanation of high overlap could be that utilization curves for the species are type one rather than type two (i.e. each species has a set of exclusive resources). Many of the traditional examples of one-dimensional systems may consist of organisms with type one curves, since resources at a given position on the resource axis consist of a number of different types. This is true of competitors which segregate by food size or foraging height in the canopy, for example. In some other cases, however, it seems likely that utilization curves must be type two. This seems to be true of the wasps studied by

Heatwole and Davis (1965) which differ in ovipositor lengths, thus exploiting hosts at different depths in rotting logs. It should also be true of any system where the resources at a given position on the resource axis consist of only one resource type.

Given the sensitivity of results regarding limiting similarity to the form of the competition function, it would seem to be more useful to explain the differences in niche overlap in different communities rather than looking for universal patterns.

Use of the Lotka-Volterra Equations

The gist of this study has been that an analysis of limiting similarity using the Lotka-Volterra model depends upon the form of the competition function. Therefore, if one wants to explain differences in the degree of overlap in different communities, it is necessary to be able to decide how the competition coefficients are to be computed in the various cases. Although it is possible to make some intuitive arguments about the form of the competition function, it is generally necessary to support one form or another by deriving it from a higher level model which incorporates more specific information about the nature of the competition, as was done for formula (6). In this case, however, it makes more sense to analyze limiting similarity

using the higher level model, rather than the Lotka-Volterra approximation to that model.

As Levins (1966), May (1973a), and others have stressed, there is a wide range of models that may be applied to any particular problem. Some of these will be too simple to make realistic predictions, and others will be too detailed to allow generalizable results. The analysis of the Lotka-Volterra model developed here can only suggest that, if there are limits to similarity in natural systems, these limits will depend sensitively on the form of the competition function, which must be derived from another model. Thus, the Lotka-Volterra equations, although useful, are not sufficient to analyze the limits to the similarity of competing species. A later paper will examine several more detailed models of exploitative competition.

Chapter 2

NICHE OVERLAP AND ENVIRONMENTAL VARIABILITY

INTRODUCTION

The explanation for differences in species di-
versity in different communities has been a subject of con-
siderable interest to ecologists, and environmental vari-
ability has played a major role in speculations regarding
the cause of gradients in species diversity (e.g. Pianka,
1966; Slobodkin and Sanders, 1969). The general trend is
for species diversity to be higher in environments which are
presumed to be less variable. The tropics are often assumed
to be less variable than temperate regions, and species
diversity is usually higher in the tropics (MacArthur, 1972).
Species diversity in several groups of benthic organisms
generally increases with depth (Sanders, 1968; Buzas and
Gibson, 1969), and this corresponds to the fact that a number
of physical factors become less variable with depth.

One hypothesis to explain such patterns is that a
lower degree of niche overlap can be tolerated in variable

environments. This hypothesis is difficult to test in the field, since a difference in the observed degree of overlap need not reflect a difference in the limiting degree of overlap. However, an indication of the validity of this hypothesis may be obtained from a study of mathematical models of competitors in variable environments, and this is the approach used here.

It has been common in the ecological liaterature to speak of environmental variability as a single factor, and previous theoretical work (May, 1973a) has modelled environmental variability in a single way. However, there are many independent elements that constitute an organism's environment, and it is not clear whether variability in different elements should have similar effects on the limits to niche overlap. This paper attempts to determine the effect of different types of environmental variability on the maximum tolerable niche overlap in competitive communities. This question is examined for a stochastic version of the Lotka-Volterra competition equations using Monte Carlo simulation. The Lotka-Volterra model was chosen for illustrative purposes, since it was simple and widely used. Also, since previous work on this topic used the Lotka-Volterra model, it seemed desirable to compare those results with the current ones. However, the major qualitative results derived here are not restricted to cases where the Lotka-Volterra

model is accurate. This assertion will be justified in more detail later.

The first section of the study presents the basic model which will be investigated here. The second section describes the method used to determine the maximum level of variability a given system can tolerate. There follows a discussion of the different types of environmental variability which are modelled here. Part four is an extensive analysis of two species competition. Section five presents an extension of these results to competitive guilds with more than two species. The final portion of the article discusses the generality of the findings, and the implications which these simple models have regarding species diversity in real communities.

The Model

The model which will be investigated here is a modification of the familiar Lotka-Volterra equations to include the effects of environmental variability. The rate of change of the population density of competitor i is given by

$$\frac{dN_i(t)}{dt} = N_i(t)\left[K_i - N_i(t) - \sum_{j \neq 1} \alpha_{ij} N_j(t) + \mu_i(t)\right] \quad (1)$$

Here $\mu_i(t)$ is a random variable which gives the increase (or decrease) in the per capita rate of increase of species i over (under) the value it would have in a constant environment. Different types of environmental variability will be modelled by making different assumptions about the cross correlations between $\mu_i(t)$ and $\mu_j(t)$, and by making different assumptions about how the mean of the distribution of $\mu(t)$ changes with a change in its variance. The species are assumed to have similar intrinsic rates of increase, so that factor has been scaled into the time variable. α_{ij} is assumed to be an increasing function of the overlap in resources used by species i and species j.

In effect, equation (1) models the effect of the environmental variability (i.e. altered population growth rate), rather than the actual fluctuations in temperature, food supply, or whatever. Since the variance in $\mu_i(t)$ should be an increasing function of the variance in the relevant environmental parameter, σ^2 is a measure (albeit indirect) of the level of environmental variability. Unless environmental fluctuations have some effect on mortality and/or fecundity, they are of no interest from the standpoint of population dynamics.

Robert May (1973a, 1973b) has recently analyzed the model presented above under one set of assumptions about the $\mu_i(t)$ (that $\mu(t)$ was Gaussian white noise, and that $\mu_i(t)$ and $\mu_j(t)$ were uncorrelated). However, May used a

different method to analyze the system than that used here.
His basic conclusion was that such a system would persist
for a long time if the smallest eigenvalue of the interaction
matrix was larger than the variance of the white noise terms.
The elements of the interaction matrix are $a_{ij} = \alpha_{ij} N_i^*$,
where N_i^* is the deterministic equilibrium population size.
Conversely, one or more populations would quickly become
extinct if the variance were larger than the minimum eigen-
value. If (1) is approximated by a set of difference equa-
tions with a time interval Δt, May's criterion for persistence
becomes $\sigma^2 \Delta t < \Lambda_{min}$ where σ^2 is the variance of $\mu(t)$ and
Λ_{min} is the minimum eigenvalue. In his analysis, May scales
the minimum eigenvalue by dividing by the average carrying
capacity, so the criterion becomes $\frac{\sigma^2 \Delta t}{K} < \lambda_{min}$, where λ_{min}
is the rescaled minimum eigenvalue.

Simulation was chosen as a method for investigating
the model used here because it involved less labor and was
more flexible than available analytical techniques. Two
different analytical methods have been applied in studying
the two species Lotka-Volterra system. These are described
by May (1973b) and Ludwig (1974). May's method involves
linearizing the Lotka-Volterra equations about their equili-
brium point, so that the system he studies (for the two
species case) is actually:

$$dN_1/dt = K(K + \mu_1(t) - N_1 - \alpha N_2)/(1 + \alpha)$$

$$dN_2/dt = K(K + \mu_2(t) - N_2 - \alpha N_1)/(1 + \alpha). \qquad (2)$$

This is a fairly good approximation to the Lotka-Volterra system near the equilibrium point (where N_1 and N_2 are approximately $K/(1 + \alpha)$), but variations which are large enough to cause extinction or near-extinction will obviously carry the system far from the equilibrium point, so that May's method is questionable on these grounds. May also assumed that a system would persist if the expected value of ϵ were less than one, where ϵ is defined as $(N(t) - N^*)/N^*$, N^* being the deterministic equilibrium population level. In reality, if the expectation of ϵ were equal to one, this would imply virtually immediate extinction, and it must be significantly less than one for long term persistence. However, when "significantly less" is translated into quantative terms, it may mean quite different values for different systems. For these reasons, May's method did not seem suitable, and the present study was motivated in part to test the accuracy of May's method for the one type of environmental variability which he studied.

Ludwig (1974) has used more accurate methods to solve for the expected time to extinction for a two species Lotka-Volterra system with a single value of α. However, the difficulty of solving this single case (or any single

case) was sufficient to make this method impractical for the present investigation, where a large number of systems were studied, using several definitions of persistence. Thus, Monte Carlo simulation seemed to be the best means for analyzing the problem at hand.

The Simulation Methodology

For each of the models investigated in this study, we were interested in determining the maximum variance in the per capita rates of increase of the component species about their deterministic values (equivalently $\mu_i(t)$) which was consistent with long term persistence of all of the populations in that system. The object was not to determine the absolute level that each system could tolerate, since this clearly depends upon the shape of the distribution of $\mu_i(t)$. Rather, the aim was to determine the relative values of the maximum levels of variation for two systems which differed in the level of competition. For example, the fourth section is concerned with determining the maximum levels of variability as a function of α in a two species (Lotka-Volterra) system. Before proceeding, it is necessary to discuss the meaning of persistence and maximum tolerable variance, and to explain how the latter was determined.

Persistence

If the models which we investigated incorporated the population levels as discrete variables, it is clear that a population will persist as long as the population number N is greater than zero. For models like the ones considered here, where the population density is a continuous variable, technically extinction will not occur until N equals zero, although small values of N may actually represent fractional individuals. This is clearly unrealistic. In general, as population sizes become small, "demographic stochasticity" becomes important (May, 1973a), and models where the population size is a continuous variable are no longer accurate. In addition, the underlying model governing population dynamics is likely to change when densities become small. Many populations have lowered fitness at low densities because of difficulties in potential mates locating each other or for other reasons (the Allee effect). In such a case, extinction is virtually assured if the population goes below some positive value. Whether or not there is an Allee effect, if the population size becomes too small too often, extinction due to demographic stochasticity seems assured. Thus, for the models we will be studying, extinction is better defined as the reduction of the population to some small but positive value, rather than the vanishing of the population. This same point has been stressed by Capocelli and Riciardi (1974)

and Ludwig (1974). The exact value of this threshold popula-
tion level will vary from one system to another, so several
possible values were examined in the simulations described
below.

No population persists forever; this is true of
natural situations and of mathematical models in which the
population is a discrete variable. It is also true of the
continuous models used here if extinction is defined as the
reduction of the population size to a threshold value. There-
fore, in speaking of the maximum variability which will allow
persistence of a population, we are concerned with persistence
for a relatively long time. This is discussed in more detail
below.

Maximum Tolerable Variability

There is, of course, no single value of the variance
of the stochastic terms $\mu_i(t)$ such that any larger variance
will result in quick extinction, and any smaller variance
will allow the system to persist indefinitely. However, for
most of the models discussed here, there is a relatively narrow
range of values of the variance such that the expected time
to extinction is relatively short for values above this range
regardless of the initial values of the populations. If the
variance is below this range, the expected time to extinction
is many orders of magnitude larger (the expected persistence

time is so long that extinction is unlikely to be observed
in a simulation run of a duration that is economically feasible).
Here the expected time to extinction is again very large
regardless of the initial values of the populations, as long as
none are initially very close to extinction. It would be
possible to define a single value of the variance to be the
maximum tolerable variance if that value resulted in a certain
moderately small expected time to extinction. However, this
level of precision was unnecessary in the current investigation,
and it is not likely to be very useful in general, since the
maximum tolerable variance would change with the shape of the
distribution of the $\mu_i(t)$, and the exact value would have to be
chosen arbitrarily. Thus, it does make sense to speak of a
maximum tolerable variance in the per capita rates of increase,
although it can only be specified approximately with reference
to any given distribution of the stochastic term $\mu_i(t)$.

The situation is slightly different if the original
deterministic system is neutrally stable or has only a very weak
tendency to return to its equilibrium point. In this case, the
initial population levels may make a large difference in the
expected time to extinction if the variance is small. For the
case of the Lotka-Volterra system analyzed in the fourth section
if $\alpha = 1$, there is no tendency for the ratio of $N_1 : N_2$ to
return to its initial value if it is displaced from that
value. Thus, in a random environment, the system will always
drift to extinction. If the variance of the stochastic term

is small, it will take a long time for extinction to occur
if the initial populations of the two species are equal to K/2.
In fact, the expected time to extinction will be arbitrarily
large if the variance is made small enough. This does not
imply, however, that a two species system with $\alpha = 1$ is likely
to be found in environments which exhibit very small fluc-
tuations, since there does not seem to be any way that such a
system would begin with both populations equal to K/2. It
seems probable that the second species would invade after the
first had achieved a high population density, and for this
case, the expected time to extinction (of one of the species)
is much shorter. This type of effect is important in determ-
ining the length of (or the initial values used in) a simu-
lation run to determine the maximum tolerable variability.
Since we consider the maximum tolerable variability of a
neutrally stable system to be zero, the simulation runs should
be long enough so that a neutrally stable system will usually
drift to extinction within that time, given the initial
population levels used in the simulation run.

The models analyzed here are systems of stochastic
differential equations describing the population dynamics
of a number (usually two) of competitors. These differential
equations were approximated by a set of difference equations,
whose behavior was investigated by iteration on a computer.
The values of the stochastic terms were produced by a random
number generator which drew from a normal distribution.

It is important to choose the time interval to be small enough so that the system of difference equations actually does approximate the differential equation system. If the time interval is very large, the equilibrium point disappears, and complex limit cycles can result, as May (1974b) has pointed out. At smaller values of the time interval, this behavior disappears, but it is still possible for the population to become negative if $\mu_i(t)$ has a large enough negative value. The time interval in the simulations described below was chosen so that negative population values would not occur (in effect, so that negative population values were extremely improbable to result). In addition, results were checked by performing the same simulations with a time interval which was an order of magnitude smaller than the original.

The explicit methodology used here was as follows. For a system with a given set of parameters (e.g. for a given α in system (1)), a series of simulation runs was made, each with a different value of the variance of the stochastic term, $\mu(t)$. In general, the initial values of the populations were their equilibrium values, and the length of the simulation was chosen so that a neutrally stable system would usually become extinct at the lowest level of the variance which was simulated. When comparing a series of systems (for example, a series of two species systems with different α's and with $\mu_1(t)$ and $\mu_2(t)$ uncorrelated), each simulation run utilized

the same random number sequence in generating values for the stochastic terms. To insure that the results were not dependent upon an unusual feature of the given random number sequence, the entire series was run again, with two different random number sequences. In general, different random number sequences were used for the different cases considered (i.e. different schemes of cross correlation). Similar results were obtained for some of the systems by using shorter simulation runs, but specifying initial population levels in which one population was much smaller than the others.

For each value of the variance it was noted whether the population persisted for the duration of the simulation run. This was done for several values of the threshold population level (i.e. several different definitions of persistence). The maximum level of the variance for which the system did not go extinct was then chosen as the maximum tolerable variance. Since only a finite number of variances were tested, this number could only be specified to within one variance-interval. For example, if the system were run for variances of 10,20,30,···,100 (a variance interval of 10) and extinction was first observed at a variance of 60, the maximum tolerable variance would be defined as 50. In general the variance interval used was fairly large, but a higher level of precision did not seem necessary, since the exact value depended upon the random number sequence. Even with the variance

interval chosen, the maximum tolerable variance determined
using two different random number sequences might differ.

Types of Environmental Variability

In this section three major types of environmental
variability are discussed. The goal is to determine how
increasing variability in each of these environmental factors
is likely to alter the per capita rate of increase of the popu-
lations in a competitive guild. Specifically, it is noted
whether $\mu(t)$ should have a mean of zero, and whether the mean
will change as the environmental fluctuations become larger.
Secondly the type of cross-correlation between $\mu_i(t)$ and $\mu_j(t)$
is discussed.

Variation in the supply of the resource for which
the animals are competing is discussed first. If the
resource supply (e.g. food supply) of an animal varies about
some mean value, the per capita rate of increase is likely
to vary as well. Within certin bounds, a higher level of food
results in a higher per capita rate of increase and a lower
level of food results in a lower rate of increase. Thus
$\mu(t)$ will usually have a mean of approximately zero, corre-
sponding to average resource levels.

If the supply of the resource fluctuates, then
the resulting fluctuations in the per capita rates of increase
of two competing species will, in general, be positively

correlated. In addition, the strength of the correlation
will usually increase as the degree of overlap in resource
utilization patterns increases. The only case when the
correlation would not increase with overlap is when the degree
of correlation is high even when overlap is low. This might
happen if the same factor which causes the resources used by
competitor i to decrease (or increase) affected the resources
used by competitor j in the same way. Thus $\mu_i(t)$ and $\mu_j(t)$
will be positively correlated, and the level of correlation
will be a nondecreasing function of α_{ij}. In the limiting
case of $\alpha = 1$, the two species have equivalent resource
utilization patterns, and $\mu_i(t)$ and $\mu_j(t)$ will be identical
(assuming that the variation in the supply of the resource
is the only reason for variation in the per capita rates of
increase). The only situation which could lead to a negative
correlation between $\mu_i(t)$ and $\mu_j(t)$ would be if α were low,
and if an increase in the resources available to species i
was correlated with a decrease in the resources available to
species j. This second condition will probably not often be met,
since the abundance of similar types of resources usually
seems to be positively correlated. If overlap is relatively
high, negative correlations are impossible.

The second type of environmental variability con-
sidered here is fluctuation in the level of predation on the
competing species. Here again, we discuss the form of the
distribution of $\mu_i(t)$ and the nature of cross correlations

in these terms. A deterministic model of population dynamics can be viewed as incorporating an average level of predation, even if the phenomenon of predation is not explicit in the model. For example, the carrying capacity K in the Lotka-Volterra equations can be regarded as being composed of two terms; $K = K' - aP$, where K' is the (hypothetical) carrying capacity in the absence of predators, P is the predator population density, and a is the rate of successful attacks by the predator on the prey. If the predator population levels or the rate of successful attacks varies, then the per capita rate of increase of the population will be modified by a random term which can take on positive or negative values, and can be defined so as to have a mean of zero.

To the extent that the different species in a competitive guild share the same predators, there will be positive cross-correlations in the $\mu_i(t)$. If they have different predators, the $\mu_i(t)$ will often be uncorrelated, although this is not necessarily true.

Variation in physical parameters (such as temperature, exposure, salinity, humidity, etc.) represents the third type of environmental variability considered here. For this category, the relation between the variance in the environmental parameter and the form of the distribuiton of the $\mu_i(t)$ can be somewhat different than in the previous two cases. Many populations are optimally adapted to the average physical conditions prevailing in their environment, so that for this

case variation in physical parameters is likely to result in a nonpositive value of $\mu_i(t)$. Values of physical parameters that are far from the average, whether high or low, are likely to be detrimental to population growth. Thus, a more variable environment will also be harsher, in the sense of permitting a lower average per capita rate of increase for any given population level. $\mu_i(t)$ will generally take on only negative values, and its mean will consequently decrease as environmental variation increases. Sympatric competitors are likely to often have similar physical tolerances, so that the magnitude of the $\mu_i(t)$ will often be positively cross correlated, although there are circumstances when this will not be so. If two competitors are sensitive to two independent environmental factors, the $\mu_i(t)$ will be uncorrelated. If they have opposite tolerances to a single factor, the magnitudes of the $\mu_i(t)$ will be negatively correlated.

Variation in physical factors can also result in $\mu_i(t)$ which take on both positive and negative values. For example, in many poikilotherms, foraging is an increasing function of temperature (up to a point), so that if temperature fluctuates with a greater variance, so will food intake, and presumably the rate of increase. High temperatures result in positive values of $\mu_i(t)$ and low temperatures result in negative values.

The relationship between environmental variability and variation in the per capita rates of increase of

competitors is quite complex, and is likely to vary quite a
bit in its details for different organisms. It is possible
for both the mean and the distribution function of $\mu_i(t)$ to
change with increasing variance, but it is difficult to make
any generalization about how they will change, so this compli-
cation is not considered in the models below.

Two Species Lotka-Volterra Competition

The basic model which will be investigated here is
the two species version of equation (1). In addition, it is
assumed that competition is symmetrical (that $K_1 = K_2$, and
$\alpha_{12} = \alpha_{21}$). The assumption of symmetry was made mainly to
simplify the analysis, but our general results are not re-
stricted to this type of situation. $\mu_1(t)$ and $\mu_2(t)$ are
normally distributed and there is no correlation between
successive values of $\mu_i(t)$.

$\mu_1(t)$ and $\mu_2(t)$ Uncorrelated with a Mean of Zero

This is the system analyzed by May (1973b). It
should be applicable to at least the following cases:

    (1)   Predation intensity is the factor
           which varies, and different com-
           petitors have different predators.

    (2)   The foraging activity of each of the
           two species is limited by a different
           independent physical factor which
           varies.

It seems, however, that there are probably relatively few situations that can reasonably be modelled by this sort of variability.

Simulations were performed for $\alpha = 0$, $\alpha = .25$, $\alpha = .5$, $\alpha = .75$, and $\alpha = .9$. The parameters used in the simulation were: K = 300 (this should be interpreted as a population density, rather than absolute numbers, so its value is arbitrary), t = .0001, $N_1(t = 0) = N_2(t = 0) = K/(1 + \alpha)$. For each value of α, simulation runs were made for variances of $\mu(t)$ of 240,000, 480,000, $\cdots$ 2,400,000. In general, unless otherwise noted, subsequent systems use the same parameters. The system was iterated 15,000 times for each value of α and each variance. This enabled a determination of the maximum tolerable variance for each value of α. Table V shows the results of one such series of runs for six definitions of persistence. Instead of giving the variance of $\mu(t)$, Table V (and subsequent tables) gives the variance multiplied by the time interval which is the quantity May compares to the minimum eigenvalue of the interaction matrix. The values of the minimum eigenvalue of each system are shown. The definitions of persistence which were used were: (1) the population density does not drop below 10, (2) the population density does not drop below 5, (3) the population density does not drop below 1, (4) the population density does not drop below .5, (5) there are fewer than one per cent of the time intervals when one population density is less than 10, and (6) there are fewer

Table V. The maximum tolerable variance as a function
of the competition coefficient in a two
species system with $\mu_1(t)$ and $\mu_2(t)$ uncor-
related and normally distributed. Parameters
of the simulations are given in the text.
Numbers given in the table are the maximum
tolerable variances multiplied by .0001 (Δt).
The subscripts on the variances on the left
hand side of the table indicate the defini-
tion of persistence which was used. For
example, σ_{10}^2 means that the maximum tolerable
variances were calculated assuming that the
system persisted if neither population dropped
below 10 during the course of the simulation.
The subscript A corresponds to definition
(5) in the text and the subscript B corresponds
to definition (6). K is 300. The minimum
eigenvalue is denoted by Λ_{min}.

Table V

ALPHA

	0	.25	.5	.75	.9	1.
σ_{10}^2	144	120	48	24	24	0
σ_5^2	168	144	72	48	24	0
σ_1^2	240	216	144	96	48	0
$\sigma_{.5}^2$	264	240	168	120	48	0
σ_A^2	192	144	96	48	24	0
σ_B^2	240	192	120	72	24	0
Λ_{min}	300	180	100	42.86	15.79	0

than one per cent of the time intervals when one species'
population density is less than five.

Figures 9, 10, and 11 show the population density
of two competitors as a function of time (for 100 time intervals)
for $\alpha = 0$, $\alpha = .5$, and $\alpha = .9$, with a variance of 10^6. The
systems with higher competition coefficients come closer
to extinction.

The general features which can be drawn from these
results are:

(1) Although the maximum tolerable variance
decreases with increasing α, the relationship is not that
predicted by using the relative value of the minimum eigenvalue
as a criterion of the relative stability of different systems.
Specifically, the maximum tolerable variance is greater than
that predicted on the basis of the relative values of the
minimum eigenvalue, especially for high values of α. For
example, using .5 as the critical population size, a system
with $\alpha = .9$ can tolerate a variance about one fifth as large
as a system with $\alpha = 0$, although the minimum eigenvalue is
one-nineteenth as large.

(2) Table V shows that May's criterion $\sigma^2 \Delta t < \Lambda_{min}$
does give some qualitative insight into the behavior of the
system. It tends to overestimate the maximum tolerable
variance for low α, and underestimate for high α. For α
less than .9, this criterion results in an estimated maximum

Figure 9. Population size as a function of time for
a two species system in a varying environ-
ment with $\alpha = 0$. Length of simulation run
is 100 time units, and the variance is 10^6.

POPULATION SIZE

TIME

Figure 10. Population size as a function of time for
            a two species system in a varying environment
            with α = .5. Length of the simulation run
            is 100 time units, and the variance is 10^6.

POPULATION SIZE

0.0   83.333   166.67   250.0   333.33   416.67   500.0

TIME

0.0   12.5   25.0   37.5   50.0   62.5   75.0   87.5   100.0

Figure 11. Population size as a function of time for
a two species system in a varying environment with α = .9. Length of simulation run
is 100 time units, and the variance is 10^6.

variance that is never off by as much as an order of magnitude
for any of the definitions of persistence.

(3) An examination of Table V indicates that the
definition of persistence does have an effect on the rela-
tionship between α and the maximum tolerable variance. The
smaller the critical population size, the more concave downward
the curve of the maximum variance vs. α. It seemed worthwhile
to examine some more extreme values for the critical popula-
tion size, so two additional series of simulations were per-
formed. In one, the variance interval was 100,000, and in
the second it was 400,000. From these runs, the maximum
tolerable variance was determined using the following values
of the critical population density: 30, .1, .01, .0001.
The results are shown in Table VI, and they confirm the general
features found in Table V. In addition, it should be noted
that a difference of an order of magnitude in the minimum
population makes little difference in the relationship between
the maximum tolerable variance and the minimum eigenvalue.
However, if the critical population size is relatively small,
environmental variability is less likely to limit niche overlap
than if the critical population is relatively large. When the
threshold population density is 10, a system with α = .9
can tolerate about 1/6 the variance that a system with α = 0
can. With a threshold density of .0001, the corresponding
value is 4/9. Thus a change in the critical population of

Table VI. Maximum tolerable variances for the two
species system with uncorrelated $\mu(t)$ for
four extreme definitions of persistence.
As in Table V, the subscript of the
variance indicates the critical value of the
population level defined as extinction.
Variances were multiplied by .0001.

Table VI

ALPHA

	0	.25	.5	.75	.9	1.
σ^2_{30}	90	50	30	10	10	0
$\sigma^2_{.1}$	280	200	160	120	40	0
$\sigma^2_{.01}$	320	280	240	160	80	0
$\sigma^2_{.0001}$	360	320	280	240	160	0
Λ_{min}	300	180	100	42.86	15.79	0

five orders of magnitude changes this ratio by less than a

factor of 3. If the threshold population size is identified

with a density at which demographic stochasticity becomes

significant, then it will be a larger fraction of the carry-

ing capacity for populations with relatively small carrying

capacities. A similar relationship between the critical

population size and the nature of the plot of α vs. the maximum

tolerable variance could be found for any of the systems

discussed below, although usually only one value of the

critical population is used in subsequent tables. In general

a value less than 1% and greater than .1% of the carrying

capacity was examined, since these values seemed intermediate

among the ranges of biologically plausible values.

The problem of determining an appropriate time

interval in approximating differential equations by difference

equations was mentioned earlier. As a check to determine

whether the length of the time interval chosen above was

likely to influence the results, the system was studied with

a time interval of .00001. The smaller time interval required

a larger variance in the $\mu(t)$ to produce extinction, so the

variances which were run were 4,000,000, 8,000,000, $\cdots$

40,000,000. Here, and for subsequent models, the results

of only a single random number sequences are shown, since

results were similar for different sequences. the results

are shown in Table VII. The relationship between α and the

Table VII. Maximum tolerable variances for the two
species system with uncorrelated $\ddot{\mu}(t)$
for a time interval one-tenth that used
in Table V. Variances are multiplied by
.00001.

Table VII

ALPHA

	0	.25	.5	.75	.9	1.
σ_5^2	240	160	120	40	0	0
$\sigma_{.5}^2$	320	280	200	120	40	0

maximum tolerable variance does not appear to be qualitatively different from that for the system with the longer time interval.

$\mu_1(t)$ and $\mu_2(t)$ Positively Correlated with a Mean of Zero

This category probably includes the majority of natural types of environmental variability. We will consider two separate models under this general heading: (1) $\mu_1(t)$ and $\mu_2(t)$ have a positive correlation which is an increasing function of α, and (2) $\mu_1(t)$ and $\mu_2(t)$ have a positive correlation which is independent of α.

The first model is applicable to the situation where the supply of the resource for which the organisms are competing varies. It is assumed that the proportion of commonly utilized resources is equal to α, which is not precisely true all of the time, but is probably close most of the time. The different resource types are assumed to vary independently, so that a reasonable method of modelling this situation is to assume , $\mu_1(t)$ and $\mu_2(t)$ have a positive correlation which is independent of α.

The first model is applicable to the situation where the supply of the resource for which the organisms are competing varies. It is assumed that the proportion of commonly utilized resources is equal to α, which is not precisely true all of the time, but is probably close most of

the time. The different resource types are assumed to vary independently, so that a reasonable method of modelling this situation is to calculate $\mu_1(t)$ and $\mu_2(t)$ by the following scheme:

$$\mu_1(t) = \alpha A(t) + (1-\alpha)B(t)$$
$$\mu_2(t) = \alpha A(t) + (1-\alpha)C(t) \qquad (3)$$

where $A(t)$, $B(t)$, and $C(t)$ are independent, identically distributed random variables here assumed to have a normal distribution with a mean of zero. The variances of A, B, and C are adjusted so that the variance of $\mu(t)$ does not change with α. To the extent that fluctuations in the supplies of different food items are positively correlated (which may often be the case in nature) then there may be a relatively high level of correlation in the $\mu(t)$ even for low values of α, and the model discussed below may be more appropriate.

The second type of positive correlation could also model a situation where predation pressure varies and the two species have some common predators. The greater the number of common predators, the higher the correlation. It could also be a model of at least some types of fluctuations in physical variables, if the two species have similar tolerances to the physical variables, and if fluctuations in the physical factors can result in positive as well as negative deviations in the per capita rate of increase. Correlation is modelled in essentially the same manner as for the above case:

$$\mu_1(t) = kA(t) + (1-k)B(t)$$

$$\mu_2(t) = kA(t) + (1-k)C(t) \qquad (4)$$

where k is a positive constant less than one, and A, B, and C are as above. A higher k indicates a higher level of correlation. The correlation coefficient is k^2.

Table VIII shows the results of simulation runs of the system described here for values of k of .25, .5, .75, and .9. For all cases, the relationship between α and the maximum tolerable variance is closer to horizontal over the range $\alpha = 0$ to $\alpha = .9$ than the same relationship for the case of no correlation (Table V). As the positive correlation becomes very high, the curve approaches a rectangular shape, so that if k = .9, there is very little difference between the maximum tolerable variability for a system with $\alpha = 0$ and one with $\alpha = .9$. Figure 12 shows the actual population dynamics of a system with k = .9. This should be compared with Figure 11 for the case of no correlations.

The same results can be used to illustrate situation (1) where k = α. This is shown in Table IX. Here there is no clear increasing or decreasing relationship between α and the maximum tolerable variance. If anything, systems with a high value of α can tolerate a higher level of resource fluctuations than those with a relatively low value of α. Table X shows an extension of this relationship to high values of α. If the only type of variation in the system is variation in the resource supply, then systems with high α

Table VIII. Maximum tolerable variances for five
values of α and four levels of cross
correlation in the $\mu(t)$. Definition
of persistence was that neither popu-
lation density dropped below .5.
Variances are multiplied by .0001.

Table VIII

ALPHA

k	0	.25	.5	.75	.9
.25	216	168	144	96	24
.5	192	192	192	144	48
.75	216	192	192	192	168
.9	216	216	216	216	192

Figure 12. Population size as a function of time for
a two species system in a varying environ-
ment with α = .9 and $\mu_1(t)$ and $\mu_2(t)$ cross
correlated with k = .9.

POPULATION SIZE

TIME

988

Table IX.   Maximum tolerable variances for a two
species system as a function of α for the
case of $\bar{\mu}_1(t)$ and $\mu_2(t)$ cross correlated
with a correlation which increases with α
as described in the text. Variances were
multiplied by .0001. The definition of
persistence was that neither population
density dropped below .5.

Table IX

ALPHA

	0	.25	.5	.75	.9
$\sigma^2_{.5}$	216	168	192	192	192

Table X.   Maximum tolerable variances for a two
species system for the case of $\mu_1(t)$ and
$\mu_2(t)$ cross correlated with a correlation
which increases with α as described in the
text.   High values of α are shown.   Variances
were multiplied by .0001.   The different
value of the maximum tolerable variance for
$\alpha = .9$ here and in Table IX is due to the
fact that different definitions of persistence
were used.

Table X

ALPHA

	.9	.91	.92	.93	.94	.95	.96	.97	.98	.99	.999	1.
σ_5^2	168	192	192	192	192	216	216	216	216	240	240	240

will actually be slightly more stable than systems with lower values of α over the range from $\alpha = .9$ to $\alpha = 1$.

Another method of looking at the relative stability of systems with different values of α was to plot the minimum population size of either population as a function of α for a series of runs at a given (high) level of variability, assuming that correlation varied with α as before. The results, for two different series of random numbers, are shown in Figures 13 and 14. The results of the two runs vary slightly, but there appears to be maximum stability for either very high or very low values of α.

$\mu_1(t)$ and $\mu_2(t)$ Negatively Correlated

As a third example, we will consider the case where $\mu_1(t)$ and $\mu_2(t)$ are negatively correlated. It is likely that this is not often the case in nature, but it could arise if the two competitors had different predators, and the density of the predators was for some reason negatively correlated. It might also arise if two species' foraging activity were limited by a physical variable to which they had opposite tolerances. Here the coorelation is modelled by the following scheme:

$$\mu_1(t) = kA(t) + (1-k)B(t)$$
$$\mu_2(t) = -kA(t) + (1-k)C(t) \tag{5}$$

where A, B, and C are as before, and the magnitude of the
negative correlation increases with k. The results of a series
of simulations with k = .9 is shown in Table XI. Comparing
this with corresponding results for the case of uncorrelated
$\mu(t)$ (Table V) suggests that negative correlations result in
a slight decrease in the relative maximum variability for a
given value of α. For this case, the relative value of the
minimum eigenvalue is a fairly accurate predictor of the
maximum tolerable variance.

Mean $\mu(t)$ Decreases with Increasing Variance

The previous analysis has assumed that the carrying
capacities of the two competitors were equal. If the mean of
the $\mu_i(t)$ does not decrease with increasing variance, relax-
ing this assumption does not qualitatively alter the basic
conclusions. If, however, variability results in lower average
per capita rates of increase (equivalently, lower carrying
capacities) it is necessary to consider cases where the carry-
ing capacities of the two species differ. The criterion for
coexistence of the two species in a constant environment is
that

$$\frac{1}{\alpha_{21}} > \frac{K_1}{K_2} > \alpha_{12} \quad . \tag{6}$$

If the carrying capacities are lowered by an amount x due
to environmental fluctuations, this criterion becomes

Table XI. Maximum tolerable variances for the two
            species system with $\mu_1(t)$ and $\mu_2(t)$
            normally distributed but negatively cor-
            related. Variances were multiplied by
            .0001.

Table XI

ALPHA

	0	.25	.5	.75	.9
σ_5^2	216	144	72	24	0
σ_2^2	264	192	96	48	0

$$\frac{1}{\alpha_{21}} > \frac{K_1 - x}{K_2 - x} > \alpha_{12} \ .$$

(7)

For any case where (6) is satisfied, there is some value of x such that (7) is not satisfied for any x larger than that value, unless $K_1 = K_2$. Since it is very improbable that two carrying capacities will be exactly equal, this implies that overlap may be greater when fluctuations are less severe, if fluctuations have the effect of reducing the average carrying capacity (which, in turn, is often true when a physical factor in the environment varies). This conclusion holds even when the species react to environmental factors in very similar ways.

Two Species Conclusions

This analysis of two species systems has resulted in these major conclusions about when environmental variability will set a limit to the level of competition in a group of species:

(1) If the only type of environmental variation is variation in the supply of the resources for which the animals are competing, then the presence of a high level of environmental fluctuations will not set a limit to the value of the competition coefficient of two competing species. A two species system with high overlap (actually α) can

Figure 13. Minimum population size (of either of the two species) for a two species system with $\mu_1(t)$ and $\mu_2(t)$ cross correlated with $k = \alpha$. Length of simulation was 10,000 time units. Variance was 1.44×10^6.

Figure 14. Minimum population size (of either of the
            two species) for a two species system with
            $\dot{\mu}_1(t)$ and $\mu_2(t)$ cross correlated with
            $k = \alpha$. Parameters are same as in Figure 13,
            except that a different random number
            sequence was used.

tolerate as high (or higher) levels of environmental vari-
ability as can a system with relatively low or moderate
overlap.

(2) If the fluctuations in the per capita rates
of increase of the two species are highly positively cor-
related (if they have common predators or are sensitive to the
same physical factor), a very variable environment will
only exclude systems with very high overlap. The maximum
tolerable variance does not decrease rapidly as a function of
α until α is quite large. Since competitors are often tax-
onomically closely related, it is likely that they will
react similarly to environmental fluctuations, resulting in
positive correlations.

(3) The level of environmental fluctuations may
determine the maximum overlap in two species systems where
fluctuations are not highly positvely correlated. For a
given degree of environmental variability, the limiting
similarity will be less (the maximum α consistent with per-
sistence will be smaller) when the critical population size
is a relatively large fraction of the carrying capacity.
This may be true for rare species (species with a low carrying
capacity), but it is difficult to generalize. Maximum overlap
will be still lower if fluctuations in the per capita growth
rates of the two species are negatively correlated.

(4) The ratio of the maximum tolerable variance of a system with relatively high α to one with $\alpha = 0$ is greater than the ratio of the corresponding minimum eigenvalues. This is true if fluctuations in the rates of increase are uncorrelated or if they are positively correlated.

(5) If more variable systems are harsher in the sense of having lower average carrying capacities, the maximum level of overlap will decrease with increasing levels of variability.

The increased stability for systems with high overlap when the $\mu(t)$ are positively correlated is due to an increased tendency for a population which is displaced from its equilibrium value to return to that value. For example: if species one decreases from its equilibrium value by an amount δ_1 at time t, then it is likely that species two will also decrease from its equilibrium value at time t (by an amount δ_2). The rate at which population one increases in the next time interval will be proportional to $\delta_1 + \alpha\delta_2$. This term is an increasing function of α, so that positive correlations (which result in δ_1 and δ_2 being of the same magnitude) will stabilize systems with high overlap (α). If the ratio of species one to species two is displaced from its equilibrium value, the rate of return will depend upon the minimum eigenvalue. If the $\mu_i(t)$ are highly correlated, however, the chance of the ratio being displaced from its

equilibrium value by a large amount is greatly reduced. In the limiting case of perfect correlation and $\alpha = 1$, the system is equivalent to a single species model where the individuals are arbitrarily divided into two equal groups. The same reasoning explains why, if the $\mu_i(t)$ are negatively correlated. systems with high overlap will be less stable than if the $\mu_i(t)$ were uncorrelated. Here, if at time t, N_1 decreases, N_2 is likely to increase. Then at time t + 1 the rate of increase of N_1 will be proportional to $\delta_1 - \alpha\delta_2$ (where δ_1 and δ_2 are greater than zero), a decreasing function of α. This leads to destabilization of systems with relatively high overlap.

The above argument is applicable to a much larger class of models than just the Lotka-Volterra. More generally, the rate of increase of species one (after the two populations have decreased by δ_1 and δ_2) will be an increasing function of $\delta_1 + \alpha\delta_2$ rather than being directly proportional to this quantity, but the rest of the argument is basically the same.

The argument that overlap must be lower in harsher environments is also likely to be fairly general. In a more accurate model, the competition coefficients will be functions of population density. If α_{ij} increases with a decrease in population density, or if it only decreases slightly, the inequalities (6) and (7) still indicate that overlap must be lower in harsher environments. If, on the other hand, the competition coefficients decrease significantly with a decrease in population

densities, (7) may be satisfied for all of the cases where (6) is satisfied. It is necessary to specify a model of the competitive process before deciding between these alternatives, but at least one other model (see Chapter 3) supports the argument that overlap must be lower in harsher environments.

The argument that greater overlap is possible when the critical population size is small is likely to be true of many models other than the Lotka-Volterra, but the quantitative features of the relationship would have to be determined for the specific model under consideration. Conclusions about the precise relationship between the minimum eigenvalue of the interaction matrix and the maximum tolerable variance are mainly relevant to the Lotka-Volterra model.

Systems with More than Two Species

There did not seem to be any reason to believe that the general features derived for the two species system would be altered if there were more than two species in the competitive guild. However, several series of simulations of three and four species guilds were run to verify this assertion.

Figure 15 shows the maximum tolerable variance for several three species systems. It was assumed that $\mu_1(t)$, $\mu_2(t)$, and $\mu_3(t)$ were uncorrelated and normally distributed. The three competitors were linearly arranged, the carrying

Figure 15. The maximum tolerable variance as a function
of α_{12} in a three species system where the
competitors are linearly arranged and the
$\dot{\mu}_i(t)$ are uncorrelated. $\alpha_{13} = \alpha_{12}^2$.

Asterisks represent results of simulations.
X's represent results predicted from the
minimum eigenvalue. Variances are divided
by 10^4. The criterion for extinction is
that a population drops below .5.

capacities of the first and third species were equal, and the carrying capacity of the second was changed with α so that the equilibrium population sizes of the three species were equal. In the figure, α is the value of $\alpha_{12}(=\alpha_{21})$ which is assumed equal to $\alpha_{23}(=\alpha_{32})$. $\alpha_{13}(=\alpha_{31})$ is assumed to be equal to α_{12}^2. This particular relationship is designed to model the case of three competitors linearly arranged on a resource axis, and it is realistic at least to the extent that α_{13} is less than α_{12}, and the difference between α_{13} and α_{12} has a maximum for intermediate values of α_{12}. However, it was chosen here merely for illustrative purposes. Figure 15 also shows the maximum tolerable variances predicted on the basis that the maximum tolerable variance for a system with α greater than zero was equal to the maximum variance for $\alpha = 0$ times the minimum eigenvalue for a system with the given α divided by the minimum eigenvalue for $\alpha = 0$. As in the two species case, the actual maximum tolerable variance is substantially higher than the predicted.

Figure 16 shows the results of a similar series of simulations assuming that $\mu_1(t)$, $\mu_2(t)$, and $\mu_3(t)$ were positively correlated. Specifically, $\mu_1(t) = .9A(t) + .1B(t)$; $\mu_2(t) = .9A(t) + .1C(t)$; $\mu_3(t) = .9A(t) + .1D(t)$, where A, B, C, and D are independent normally distributed random variables. As for the two species case, positive correlations resulted in systems with high overlap (α) being able to tolerate nearly the same level of environmental variability as systems with low overlap.

Figure 16.   The maximum tolerable variance as a function
of α_{12} in a three species system where the
competitors are linearly arranged and the
$\mu_i(t)$ are cross correlated as described in
the text with k = .9. $\alpha_{13} = \alpha_{12}^2$. Asterisks
represent results of simulations. X's repre-
sent results predicted from the minimum
eigenvalue. Variances are divided by 10^4.
The criterion for extinction is that a
population drops below .5.

Tables XII, XIII, and XIV present similar results for four species systems. The major differences between the two species case and the many species case is that, for a given average value of α_{ij}, the more species, the smaller the equilib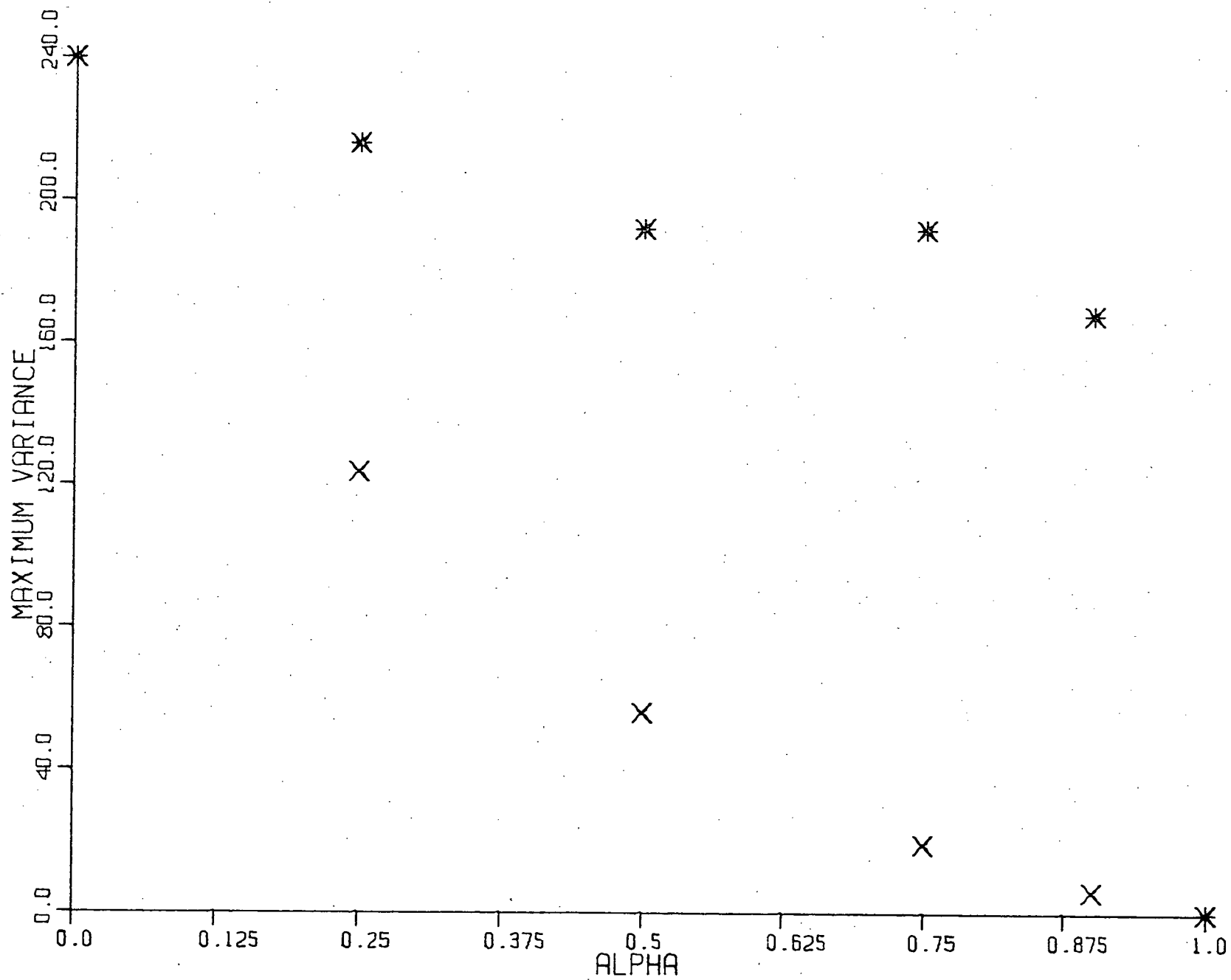rium values of the populations. As a result, environmental variation seems more likely to set a limit to the degree of overlap in many species systems. However, a high degree of positive correlation in the $\mu(t)$ will stabilize systems with high overlap, so that systems with high values of the competition coefficient are able to tolerate nearly as much environmental variability as a single species system.

Modelling systems with different degrees of correlation between different species pairs becomes difficult for the many species case, but when overlap is very high, results will be approximately the same as for the case of a constant high level of correlation (with the same level of correlation between the different species pairs).

Discussion

The preceding analysis has involved many simplifying assumptions, including the fact that attention was restricted to the Lotka-Volterra model. Although the results of this analysis are not universally applicable, they are no doubt true for many systems where the assumptions are not met. It is likely, for example, that the assumption that the $\mu_i(t)$ are normally distributed, and that the other parameters of the

Table XII.   Maximum tolerable variances for a four
              species system with the competitors
              linearly arranged. Alpha denotes the
              value of α_{12} (which is equal to α_{23} and
              α_{34}). $\alpha_{13} = \alpha_{12}{}^4$ • $\alpha_{14} = \alpha_{12}{}^9$ • $\alpha_{24} = \alpha_{13}$.
              The minimum eigenvalue is denoted by Λ_{min}.

              Other parameters were the same as in the
              two species system, except that the length
              of the simulation was 4000 time units.
              Variances are multiplied by .0001. The
              $\mu_i(t)$ are uncorrelated and normally

              distributed.

Table XII

ALPHA

	0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.
σ_2^2	240	216	192	168	120	96	72	48	24	0	0
$\sigma_{.5}^2$	264	240	216	192	144	120	96	72	48	24	0
Λ_{min}	300.	229.	169.	120.	79.	47.1	24.1	9.7	2.5	.25	0

Table XIII. Maximum tolerable variances for a four
species system with the competitors arranged
in a nonlinear fashion. $\alpha_{12} = \alpha_{13} = \alpha_{14} = \alpha$.
The $\mu_i(t)$ were uncorrelated and normally

distributed. Length of the simulation was
4000 time intervals. Variances are multi-
plied by .0001. The minimum eigenvalue
is given by Λ_{min}.

Table XIII

ALPHA

	0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.
$\sigma^2_{.5}$	264	240	192	168	144	120	96	72	48	24	0
Λ_{min}	300	208.	150.	100.	81.8	60.0	42.9	29.0	17.7	8.1	0

Table XIV. Maximum tolerable variances for a four
species system with the competitors arranged
in a nonlinear fashion. $\alpha_{12} = \alpha_{13} = \alpha_{14} = \alpha$.
The $\mu_i(t)$ were correlated with $k = .75$.

Other parameters of the simulation were the
same as for Table XIII.

Table XIV

ALPHA

	0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.
σ_1^2	264	240	240	240	216	216	192	168	144	96	0
Λ_{min}	300	208.	150.	100.	81.8	60.0	42.9	29.0	17.7	8.1	0

distribution function do not change with increasing variance, is not often satisifed. However, within limits, the major results of this analysis are probably applicable to many cases where this assumption is not met. This is due to the fact that we are concerned with the relative values of the maximum variance for two systems rather than the absolute value for any particular system. Take, for example, a two species Lotka-Volterra system with $\alpha = .5$. If, for a given degree of environmental variability, the variance of $\mu_1(t)$ and $\mu_2(t)$ decreased with decreasing population sizes, the system could tolerate a higher degree of variation than if this were not the case. However, the ratio of the maximum tolerable environmental variability for a two species system with $\alpha = 0$ to a similar system with $\alpha = .5$ will be altered to a much lesser extent by the assumption that the variance of the $\mu_i(t)$ is independent of population size.

The mathematical analysis presented here suggests that for many types of environmental variability, the level of fluctuations will not prohibit the persistence of systems with very high niche overlap (high values of the competition coefficients) in a Lotka-Volterra system. Therefore, if this analysis is fairly general, most examples of greater species diversity in stable environments probably cannot be explained by the argument that stable environments permit higher niche overlap unless more variable environments are also harsher.

There is relatively little information available
on the relationship between niche overlap and environmental
variability in natural communities. However, Cody (1974)
has found that overlap in horizontal habitat among birds is
higher in environments which have a higher degree of climatic
predictability. However, this pattern need not reflect a
difference in the limiting degree of overlap. It is possible
that lower overlap is due to lower population densities in
the less predictable areas. This would lead to lower intra-
specific competition, so that the birds may utilize only the
optimal habitats. This would lead to lower overlap, although
the limiting degree of overlap may not be different.

Robert May also predicted that the level of environ-
mental variation would not greatly alter the maximum level
of competition consistent with stability (May, 1973a). How-
ever, his results are not likely to be generally applicable,
since,

(1) As May himself stressed (1973a), his argu-
ment only applies to levels of environmental fluctuations at
least an order of magnitude less than the maximum tolerable
variance for a single species system.

(2) His conclusions were based on a model of
competitors which are linearly arranged along a resource
axis (or which may be rescaled to be linear), which does not
appear to be true of most real competitive guilds (Schoener,
1974b).

(3) May's results depend on a particular method of calculating the competition coefficients, which may not be generally valid (see Chapter I).

This study has been concerned with nonperiodic temporal variability, and thus deals mainly with unpredictable events in an organisms' environment. It is not clear whether the conclusions arrived at here are relevant to regular seasonal changes. In fact, Stewart and Levin (1973) have developed a model where coexistence of two species on a single resource is possible in a seasonal environment, but not in a constant one.

It should be stressed that the present analysis can only provide a small part of the theory necessary to explain higher species diversity in more stable environments. Other proposals which must be tested include the hypothesis that niche breadth is greater in more variable environments and that stable environments are usually closer to an evolutionary equilibrium (MacArthur, 1972). In addition, further analysis of the present question using other models would be instructive.

Chapter 3

LIMITING SIMILARITY IN A SIMPLE MODEL OF
EXPLOITATIVE COMPETITION

INTRODUCTION

There has been a great deal of theorizing in ecology concerned with explaining differences in species diversity under different conditions. With reference to groups of competitors, differences in species diversity have been explained in at least four ways (MacArthur, 1972):

(1) differences in the range of resources available;

(2) differences in the number of potential invaders or the amount of time for speciation,

(3) differences in the niche breadths of the competitors (more competitors may coexist if the species are specialists than if they are generalists), and

(4) differences in the limiting similarity of competitors.

Here the term "limiting similarity" is taken to mean the minimum difference in resource utilization patterns which will

allow coexistence of two competitors, one of which has a slight competitive advantage. This definition is discussed in more detail later.

The present paper is a theoretical investigation of the fourth point. Specifically, a simple model of exploitative competition is proposed, and is analyzed to see how the limiting similarity of competitors depends upon the parameters of the model. The next section of the article discusses the implications which this analysis has regarding the effect of predation and environmental fluctuations on species diversity in competitive communities. The final section discusses the generality of the results derived here. This type of model is designed to suggest possible explanations for patterns rather than to make precise predictions about any specific system.

The Model

This section is divided into two parts. The first describes those communities where the present model may be applicable. The second presents the details of the model.

The Assumption

This study deals with a specific type of consumer-resource model in which the consumers do not alter the rate at which resources enter the system (here system is taken

to mean the area in which consumers may encounter resources).
If resources are not consumed, they eventually leave the
system; the residence time may or may not be constant. Thus,
resources enter the system at a rate which is independent
of consumer density, and leave either by being consumed or
through some other process, such as decay. This type of
model was chosen both because it was simple, and because it
seemed to include a large fraction of the competitive guilds
which had been studied. If consumers can alter the rate at
which resources enter the system, then it is necessary to
specify the functional relationship between resource numbers
and resource reproduction before one can draw conclusions
about the limits to similarity.

A large number of organisms depend upon resources
which do not reproduce themselves, so they necessarily satisfy
the basic assumption of this model. Scavengers generally
cannot increase the rate at which their food becomes avail-
able. The ant communities studied by Culver (1974), for
example, fall into this basic category. Benthic sediment
feeders depend on a rain of nutrients from higher levels.
By consuming those nutrients, they can neither increase nor
decrease the rate at which nutrients become available.
Many nectivores and frugivores probably do not alter the
rate at which nectar or fruit is produced. In addition,
there are more specialized cases, such as hermit crabs, which
compete for empty gastropod shells (Vance, 1972a,b). Since

the crabs do not kill the gastropods themselves, they cannot alter the rate at which shells become available.

There are several sorts of systems in which the resources reproduce themselves, but only a very small fraction of the resource population ever becomes available to the consumer population. This is no doubt the case for fish that feed on insects that fall onto the surface of the water. Another example is oceanic birds which feed on small fish which are chased to the surface of the water by aquatic predators. Ashmole (1968) states that,

> *Since predation by all tropical oceanic*
> *birds is restricted to a surface layer*
> *only a few meters thick, it seems un-*
> *likely that birds exert major effects in*
> *determining the numbers of many of their*
> *prey items.*

The triclad flatworms studied by Reynoldson (e.g. 1966) only attack prey which are injured or behaving abnormally, so that they are unlikely to alter the rate at which their prey becomes available. A similar situation probably exists for many insectivorous birds and lizards, and should often be true when consumers are "prudent predators" in Slobodkin's (1961) sense.

The general assumption may also be satisfied for a large number of cases in which the resources do reproduce themselves and the consumers utilize a large fraction of the resources. Most insectivores consume only one stage of the life cycle of any insect species in their diet. The abundance

of this stage in the next (insect) generation is affected
by many factors other than mortality during the particular
stage. Therefore, the correlation between the abundance of
that stage in generation t + 1 and mortality in generation t
may be negligible. Many seed-eaters consume a large fraction
of the available seed crop, but seed production in the next
plant generation will not be reduced if the plant population
is limited by density dependent mortality among young plants.
Even if the level of seed predation affects the plant popula-
tion, there will often be a very long time lag involved.
This will be true if the seeds eaten are produced by slowly
growing long-lived perrenial species. If the lag is long
enough with respect to population processes of the consumer
species, it may be possible to treat the system as though the
level of consumption did not alter the resource production.

The majority of the eighty-one studies of resource
partitioning reviewed by Schoener (1974b) fall into the second
or third category. The resources reproduce themselves, but
it is certainly possible that the level of consumption does
not alter the rate at which resources become available to the
consumers. There are, of course, situations where the
assumption is not satisfied. In most classical predator-
prey models with no prey refuge, the level of consumption
does alter the rate at which resources enter the system.
For example, the assumption is not likely to be satisfied by
competing zooplankton which consume a large proportion of the
nannoplankton in a pond.

The Model

In general, the population dynamics of a group of m competitors may be modelled by a set of m differential equations of the following form,

$$\frac{dN_i}{dt} = N_i f_i \left[g_i(N_1, N_2, \cdots, N_m) \right] \qquad (1)$$

Here, g_i is a function which describes the per capita share of resources of species i as a function of population densities. f_i is a function describing the per capita growth rate of species i's population as a function of the per capita share of resources. For present purposes, we will only be concerned with the form of the function g_i and the value of g_i for which $f_i(g_i) = 0$. This value will be denoted T_i, so $f_i(T_i) = 0$. f_i is assumed to be monotone increasing (per capita growth rate is an increasing function of the per capita food supply). Thus $f_i(g_i) = 0$ has a unique solution, T_i. Otherwise, the precise form of f_i is left unspecified. The rationale for ignoring the form of f_i will be explained later. It is implicit that f_i is a function only of g_i, so that such phenomena as social facilitation and interference competition are not considered in the model.

First, it is necessary to derive a form for g_i. the assumption that the consumers do not influence the rate at which resources are supplied to the system constrains the form of g_i. Consider first the case in which there is one

resource type and one consumer. The simplest possible assumptions are that:

    (1) resources enter the system at a
         constant rate,

    (2) resources are consumed at a rate
         directly proportional to resource
         density and consumer density,

    (3) resources present in the system at
         a given time leave at a rate which
         is proportional to the density of
         resources in the system.

Let F denote the rate at which resources enter the system, C denote the per capita rate at which consumers encounter a unit density of resources, and S denote the rate at which resources leave the system. Then the rate of change of resource levels can be described by the following differential equation,

$$dR/dt = F - SR - CRN ,$$
(2)

where R is the resource density and N is the consumer density. It may often be reasonably assumed that population processes in the consumer population occur at a rate which is much slower than in the resource population, so that the resource density at any time may be found by setting the right hand side of (2) equal to zero, and solving for the equilibrium resource density, $\hat{R}$. The per capita share of resources is then $C\hat{R}$, or

$$g(N) = CF/(S + CN) .$$
(3)

It is straightforward to generalize this expression to a
case where there are many consumers and many resources. For
the general case of m resources and n consumers,

$$g_i = \sum_{j=1}^{m} \frac{c_{ij} F_j}{S_j + \sum_{i=1}^{n} c_{ij} N_i} \tag{4}$$

This general expression is rather difficult to work with,
so the following section analyzes a particular case con-
sisting of two competitors and three resource types.

The three assumptions made in writing equation
(2) are not in general satisfied. The rate at which resources
enter a system generally varies. However, this will not
change the basic form of equation (3). The functional
response of the consumers will often be nonlinear. This
possibility is discussed in more detail in the final section,
but it does not change the qualitative features derived
below. Resources do not necessarily leave the system at a
constant rate, and the result of relaxing this assumption is
also discussed in the final section. Again, however, the
basic features of the analysis do not depend upon this
assumption. Other implicit assumptions are also discussed
in the final section.

Limiting Similarity in a two species model

The case which will be examined here is given by
the following equations:

$$g_1 = \frac{F_1}{Q + N_1} + \frac{F_2}{Q + N_1 + N_2} \qquad F_1(T_1) = 0$$

$$g_2 = \frac{F_1}{Q + N_2} + \frac{F_2}{Q + N_1 + N_2} \qquad F_2(T_2) = 0$$

Species one and species two are each assumed to have an
exclusive class of resources which is not utilized by the
other species. In addition, there is a class of resources
which is utilized by both species. It is assumed that the
entry rate of species one's exclusive resources (F_1) is equal
to that of species two's exclusive resources, that the
resources leave the system at equal rates (in the absence of
consumers), and that the two species exploit resources with
equal efficiencies. The per capita share of resources at which
each individual of species i replaces itself is T_i. Q is
equivalent to the quotient S/C using the terminology intro-
duced earlier. All of these assumptions are made to simplify
the analysis, and it is argued later (in the final section)
that the basic conclusions are not restricted to cases where
these assumptions are met. In a more realistic model, each
species would exploit a number of resources, some of which
are utilized with similar efficiency by both species, and
other of which are much more heavily used by one species
than the other. Although the division of resources into
shared and exclusive classes was intended mainly to simplify
the mathematics, there is some biological justification for

this division. In several competitive guilds, each species possesses a "resource refuge" (Reynoldson and Davies, 1970) which it utilizes exclusively or to a much greater extent than its competitors (e.g. triclad flatworms (Reynoldson, 1966), water mites (Lanciani, 1970), foliage gleaning birds (Root, 1967)).

As stated in the introduction, the limiting similarity is that approximate level of similarity in resource utilization at which coexistence of two competitors, one of which has a slight competitive advantage, becomes impossible. Of course, the exact value of the limiting similarity depends upon how similarity in resource utilization patterns is measured and upon the nature of the "slight advantage" of the superior competitor. In the model above, similarity in resource utilization is easily measured by the ratio $F_1/(F_1 + F_2)$, the fraction of the resources entering the system that are of a type exclusively utilized by one of the species. A species has a competitive advantage if individuals of that species are able to maintain and replace themselves at a lower level of resources than individuals of the other species (i.e. the T value is lower). Coexistence is possible if each species can increase when the other is at equilibrium densities (its carrying capacity). A more detailed justificiation of this criterion for coexistence for a more general class of two species models may be found in Resigno and Richardson (1967). Since (for a given F_1, F_2, and Q), equilibrium densities are determined by the T values, it is sufficient to know the values of T_1 and T_2 to

determine whether the two species will coexist. It is un-
necessary to know the precise form of the function f_i which
determines the per capita growth rate of a species as a func-
tion of resource availabilities. It is necessary only that
f_i be an increasing function of g_i.

To determine the limiting similarity in the model
given by equations (5) for a certain set of parameter values
(Q, T_1, T_2) it is necessary to solve for the smallest value
of $F_1/(F_1 + F_2)$ which will allow either species to increase
when its density is close to zero, and the other species'
density is near its carrying capacity. If we assume that
species two has the competitive advantage (so that $T_2 = T_1 - \delta$,
where $\delta \ll T_1$), it is sufficient to determine that species
one can increase when species two is near its carrying
capacity in order to establish that coexistence is possible.

The carrying capacity of species two, N_2^*, may be
found by solving $(F_1 + F_2)/(Q + N_2^*) = T - \delta$ for N_2^*. This gives

$$N_2^* = \frac{F_1 + F_2 - QT_1 + Q\delta}{T_1 - \delta} \tag{6}$$

Species one will be able to increase when species two is
at equilibrium densities if,

$$\frac{F_1}{Q} + \frac{F_2}{Q + N_2^*} > T_1 \tag{7}$$

This requires that

$$\frac{F_1}{F_1 + F_2} > \frac{T_1Q^2 + T_1QN_2^* - QF_2}{(Q + N_2^*)(F_1 + F_2)} \tag{8}$$

Substituting for N_2^* from above, we obtain the criterion,

$$\frac{F_1}{F_1 + F_2} > \frac{T_1Q^2 + T_1Q\left(\frac{F_1 + F_2 - QT_1 + Q\delta}{T_1 - \delta}\right) - QF_2}{(F_1 + F_2)\left(Q + \frac{F_1 + F_2 - QT_1 + Q\delta}{T_1 - \delta}\right)} \tag{9}$$

Denoting $F_1/(F_1 + F_2)$ as p, and $F_1 + F_2$ as F_t, this expression may be simplified to give,

$$p > \frac{Q\delta}{F_t - T_1Q + Q\delta} \tag{10}$$

Therefore, the minimum value of p which will allow coexistence (p_{min}) is given by the right hand side of (10).

There are basically four parameters in this model. The following section examines how the limiting similarity of competitors varies with each of these parameters.

Q

From the derivation of equation (3), it may be seen that Q is directly proportional to the rate at which resources leave the system and inversely proportional to the consumption rate of an individual competitor. Thus Q will be relatively large if resources turn over quickly or

if the consumers are relatively inefficient at exploiting them. In order for species one to persist in the absence of species two, it is necessary that $Q < F_t/T_1$. Therefore, we examine the derivative $\partial p_{min}/\partial Q$ over the range $Q = 0$ to $Q = F_t/T_1$. The partial derivative is,

$$\frac{\partial p_{min}}{\partial Q} = \frac{F_t \delta}{(F_t - T_1 Q + Q \delta)^2} \tag{11}$$

Since this quantity is positive, the minimum separation required for coexistence increases as the turnover rate of resources increases or as the consumption rates of the consumers decrease (either of which will result in a large value of Q). In the limit as Q approaches F_t/T_1, p_{min} approaches one, so that no overlap is tolerated. In the limit as Q approaches zero, p_{min} approaches zero, so that nearly complete overlap in resource utilization is tolerated.

$\underline{\delta}$

δ is the difference between T_1 and T_2, and thus represents the competitive advantage of species two. One would expect that, other things being equal, the larger the competitive advantage, the larger the resource separation necessary to allow coexistence. As expected, the derivative of p_{min} with respect to δ is positive.

$$\frac{\partial p_{min}}{\partial \delta} = \frac{F_t - T_1 Q}{(F_t - T_1 Q + Q\delta)^2} \qquad (F_t > T_1 Q) \qquad (12)$$

F_t

F_t is the rate at which resources used by a species enter the system, and it is thus a measure of environmental productivity. The derivative of p_{min} with respect to F_t is negative.

$$\frac{\partial p_{min}}{\partial F_t} = \frac{-Q\delta}{(F_t - T_1 Q + Q\delta)^2} \qquad (13)$$

Therefore, in a more productive environment, the maximum tolerable overlap will be greater. As F_t approaches QT_1, p_{min} approaches one. As F_t becomes very large, p_{min} approaches zero.

T_1

T_1 is the share of resources necessary to maintain and replace an individual of species one. The magnitude of T_1 depends upon several factors. If the organism is inefficient at converting resources into new individuals, T_1 will be high. If the species is subjected to heavy mortality from harvesting or adverse physical condition, T_1 will be high. The partial derivative of p_{min} with respect to T_1 is positive.

$$\frac{\partial p_{min}}{\partial T_1} = \frac{Q^2 \delta}{(F_t - T_1 Q + Q\delta)^2} \tag{14}$$

Therefore, if the per capita resource requirements of a species are relatively high, a large niche separation will be required to allow coexistence compared to a case where T_1 is lower. If T_1 is very low, most of the resources which enter the system are consumed when the species are at their equilibrium densities. If T_1 is relatively large, a relatively large fraction of the resources which enter the system leave without being consumed.

The Efficiency of Exploitation

An increase in F_t, a decrease in T, or a decrease in Q will all result in an increase in the efficiency of exploitation, defined as the fraction of resources which enter the system which are consumed. Therefore, there should be a trend for the maximum tolerable overlap to increase as the efficiency of exploitation increases. However, the limiting similarity is not equally sensitive to all of the parameters, so it is possible for the efficiency of exploitation to decrease while the maximum tolerable overlap increases. For a single species, the fraction of all resources which may be consumed which actually are consumed is equal to $\hat{N}/(Q + \hat{N})$. Since $\hat{N} = F/T - Q$, the fraction of resources which are consumed is $(F - TQ)/F$. Thus, the efficiency of

exploitation will remain the same if T increases and Q decreases but TQ remains constant. However, p_{min} decreases under the same conditions. Although it is probable that relatively large niche separations are required for coexistence when the efficiency of exploitation is low, a small enough value of Q will allow high resource overlap with inefficient exploitation.

Discussion of the Two Species Model

Limiting Similarity with no Competitive Advantage

The term "limiting similarity" in the preceding analysis has been used in a somewhat different manner than its usage by previous authors (e.g. May (1973a), MacArthur and Levins (1967)). These authors have examined the question of whether two competitively equal species have a minimum niche separation consistent with coexistence. May (1973a) notes that for a deterministic Lotka-Volterra type model with the assumption that α_{ij} may be calculated by MacArthur and Levins' (1967) formula, there is no such limiting similarity. For the model given by equations (5), such a limit does not exist either. It may be seen from expression (11) that if $\delta = 0$, the minimum value of p is zero; i.e. there is no limiting similarity in May's sense.

Will Niche Overlap be Higher Where Exploitation is
More Efficient?

Having analyzed the limiting similarity of competitors based on the model given by (5), it is worth asking whether niche overlap will be higher in those communities in which exploitation is more efficient. If the model discussed above is applicable and if competitive exclusion is the only factor which determines niche overlap, this should be the case. However, selection for the avoidance of competition also influences observed patterns of niche overlap. This section is a semi-quantitative analysis of the circumstances under which there will be a selective advantage to niche shift in the presence of a competitor. "Niche shift" is being used in a broad sense to describe any change in the consumption rates of different resources as a consequence of interspecific competition (i.e. a change in C in equation (2)). The shift could be strictly behavioral, or it could involve genetic change.

We begin with a single species exploiting a set of resources with a common turnover rate. The per capita share of resources will be $F/(Q + N_1)$ where F is the total rate of entry into the system of all the resources which the species exploits. In the presence of a second species which uses a subset of those resources used by species one, the per capita share of resources of species one will be

$F_1/(Q + N_1) + F_2/(Q + N_1 + N_2)$. The question is then, when will
it be advantageous for species one to shift its utilization
so that F_1 increases (by ΔF_1) and F_2 decreases (by ΔF_2)?
Since the original utilization pattern of speices one is the
product of natural selection, one can assume that ΔF_1 is
smaller than ΔF_2. If it were larger, the indicated niche
shift would have occurred in the absence of the competitor.

Niche shift will be advantageous when,

$$\frac{F_1 + \Delta F_1}{Q + N_1} + \frac{F_2 - \Delta F_2}{Q + N_1 + N_2} > \frac{F_1}{Q + N_1} + \frac{F_2}{Q + N_1 + N_2} \qquad (15)$$

If Q is very large relative to N_1 and N_2, the inequality
becomes approximately, $\Delta F_1 - \Delta F_2 > 0$. This cannot be satisfied
since ΔF_1 is less than ΔF_2. As Q becomes smaller (or as N_1
and N_2 become larger, due to a larger F_t or smaller T), there
is a larger range of values of ΔF_1 and ΔF_2 which will satisfy
the inequality. A larger niche shift will result in a larger value
of $\Delta F_2 - \Delta F_1$, so that when exploitation is more efficient,
a larger range of niche shifts will be advantageous. This
result is basically intuitive. The greater the reduction in
the supply of a resource by a competitor, the larger the
range of niche displacements where the advantage of lowering
competition outweighs the disadvantage of exploiting non-
optimal resources. When exploitation (by both species) is
relatively efficient, competitors will effect a greater
reduction in each other's food supply for a given amount of
resource overlap.

It should be noted that this same sort of reasoning
suggests that interference competition will evolve only when
exploitation by both species is relatively efficient. Here
interference may be thought of as reducing or eliminating
the competitors feeding on the shared resource, at the expense
of a higher value. of T. Roughly, interference will be
advantageous when

$$\frac{F_1}{Q + N_1} + \frac{F_2}{Q + N_1} - (T + \Delta T) > \frac{F_1}{Q + N_1} + \frac{F_2}{Q + N_1 + N_2} - T \qquad (16)$$

Again, this inequality is unlikely to be satisfied if Q is
large relative to N.

   If there are a large number of potential invading
species and the competitive community is near equilibrium with
respect to species number, then competitive exclusion will
be the most important factor in determining niche overlap.
In this case, niche overlap should be greater where p_{min} is
smaller. If, on the other hand, the community is not close
to being saturated with species, niche shift may play an
important role in determining observed overlap when exploi-
tation is efficient, and it is no longer clear whether higher
niche overlap will be correlated with efficient exploitation
or with p_{min}. A comparison of niche overlaps in communities
which differ in the efficiency of exploitation may suggest
whether niche shift or competitive exclusion is more important
in determining observed patterns of resource partitioning.

Evidence from Natural Communities

If communities are relatively saturated, the present model suggests that niche overlap will usually be higher in those cases where exploitation is more efficient. Although there is some data available on niche overlap in bird and lizard communities (e.g. Pianka (1973), Cody (1974)), there generally is not sufficient information to judge whether the present model is applicable, let alone to determine relative parameter values in different communities. However, some patterns seem to be consistent with the predictions made here, and should be examined in more detail. For example, frugivorous birds typically show less resource partitioning than insectivorous species (Schoener, 1974b). It seems at least possible that the parameter Q is usually larger for fruit than for insects, since many of the latter are available during only a brief part of their life history, or while engaged in a certain type of behavior. Similarly, relatively large organisms generally exhibit a higher degree of partitioning than small organisms. Large animals would be expected to have a high T value relative to small organsims, so that the present model is consistent with this observation as well. The best available evidence relevant to the predictions made here seems to be the studies of Vance (1972a,b) and Nyblade (1974) on the hermit crabs of Puget Sounds, since the basic assumption of the model is clearly met for these invertebrates. The three species of intertidal crabs studied by Vance show very distinct segregation by level in the intertidal in which they occur. Subtidally, there are a

larger number of species (13), and Nyblade's data (Nyblade, 1974) suggests that overlap both with respect to habitats used and shells used within a habitat are higher than in the intertidal. There is fairly good evidence that the species compete for shells, and it seems reasonable that shells leave the intertidal at a faster rate than the subtidal. In the intertidal, shells which are not used are generally washed out of the system, while subtidally, shells remain in the system until they are buried by sediment or overgrown by encrusting organisms. Difficulties in sampling the subtidal community make results on niche overlap tentative. Further work on these and other hermit crab communities could do much to further our understanding of resource partitioning in general.

The Effect of Predation and Environmental Variability on Species Diversity

This section considers predation that acts in a relatively density independent manner on each of the competing species. It is clear that a predator which concentrates on the most abundant species (a predator which exhibits switching behavior) may allow competitors to coexist even if overlap in resource utilization is complete (May, 1974c). Similarly, if each competitor population is limited by a different predator, coexistence with complete overlap in resource utilization is possible. If the predators are limited by

some factor other than the population density of the competing prey populations, or if there is only a single predator, then this stabilizing density dependence will not be present, and the basic effect of predation will be to reduce population densities below the level which they would otherwise attain. It is this type of "density independent" predation which will be examined here. Predation may be density dependent in the sense of increasing as the total population of all prey species increases. What is important is that none of the competitor populations is limited by a predator.

It is simple to modify the system considered in the first section of this article to include the effect of predation by adding a term -aP to the expression for the per capita rate of increase of the populations. Here P represents the predator density and a represents the per capita consumption rate of prey by predators. Thus,

$$\frac{dN_i}{dt} = N_i \left[f_i \left[g_i (N_1 \cdots N_n) \right] - aP \right] \tag{17}$$

Since f(g) is an increasing function, it is clear that the addition of the predation term is effectively equivalent to increasing the value of T, the per capita share of resources necessary for maintenance and replacement of the species. Thus the effect of predation is to increase the minimum niche separation necessary for coexistence. In the sort of

community to which this model is applicable, predation that
is density independent will reduce species diversity.

This conclusion seems to be the opposite of the
traditional view of the effect of predation on the degree
of resource partitioning necessary for coexistence. This
traditional view has been stated by MacArthur (1972):

> *If abundant predators prevent any*
> *species from becoming common, the*
> *entire picture changes. Resources*
> *are no longerof any concern, and our*
> *equations (1) and (2) are irrelevant.*
> *More correctly, resources are still*
> *a concern, but their manner of sub-*
> *division is irrelevant.*

Along a similar vein, Connell (1971) states: "An alternative
hypothesis to explain such coexistence is that potentially
competing prey populations are kept at such low numbers by
very efficient predators that competition is greatly reduced.
The prey coexist because no species reaches high enough
density to exclude another in competition," and that, "Of
course, it has long been recognized that predators can keep
potential competitors so rare that they do not compete"
(Connell, 1975).

The fact that the minimum separation required
for coexistence increases as the level of predation increases
suggests that a simple reduction in competitor population
sizes does not reduce competition in this model. In fact,
it can be shown that several measures of the intensity of
competition increase as predation becomes greater. For

example, assume that competition is measured by the effect of species two on the per capita growth rate of species one divided by the effect of species one on its own growth rate (Gill (1974) has also suggested this quantity as a generally applicable measure of competition). This quantity, which will be labelled α_{12}, may be calculated by the following formula,

$$\alpha_{12} = \frac{\frac{\partial}{\partial N_2} \text{ (per capita growth rate of species 1)}}{\frac{\partial}{\partial N_1} \text{ (Per capita growth rate of species 1)}} \tag{18}$$

For the present model,

$$\alpha_{12} = \frac{F_2/(Q + \hat{N}_1 + \hat{N}_2)^2}{F_1/(Q + \hat{N}_1)^2 + F_2/(Q + \hat{N}_1 + \hat{N}_2)^2} \tag{19}$$

where $\hat{N}_1$ and $\hat{N}_2$ are the equilibrium numbers N_1 and N_2 attain when the two species are sympatric. Assume for simplicity that $T_1 = T_2 = T$, so that $\hat{N}_1 = \hat{N}_2 \doteq \hat{N}$. The derivative of α_{12} with respect to $\hat{N}$ is,

$$\frac{\partial \alpha_{12}}{\partial \hat{N}} = \frac{-\left\{ \dfrac{2F_1 F_2 Q}{(Q + \hat{N})^3 (Q + 2\hat{N})^3} \right\}}{\left\{ \dfrac{F_1}{(Q + \hat{N})^2} + \dfrac{F_2}{(Q + 2\hat{N})^2} \right\}^2} \tag{20}$$

Since this quantity is negative, α_{12} increases as equilibrium population numbers decrease. The increase in T brought about by predation will decrease $\hat{N}$, and therefore increase α_{12}, so by this measure of competition, predation increases the intensity of competition.

The same effect may be seen by comparing population densities of a species in the presence and absence of its competitor. Again assuming equations (5) with $T_1 = T_2 = T$, the equilibrium density of a species in the absence of its competitor is $N^* = ((F_1 + F_2)/T) - Q$. In the presence of the competitor, the equilibrium density is

$$\hat{N} = \frac{2F_1 + F_2 - 3TQ + \sqrt{T^2Q^2 + (2F_1 + F_2)^2 - 4TQF_1 + 2TQF_2}}{4T} \quad (21)$$

The ratio of $N^*/\hat{N}$ is another possible measure of the intensity of interspecific competition. This ratio is an increasing function of T. If T is very small, the ratio approaches $(F_1 + F_2)/(F_1 + .5F_2)$. As T approaches $(F_1 + F_2)/Q$, the ratio $N^*/\hat{N}$ approaches $(F_1 + 2F_2)/(F_1 + F_2)$. Thus, for a given degree of overlap, the fractional decrease in a population brought about by its competitor is greater when levels of predation are higher. Again, predation increases the level of competition.

It should be noted that even though competition is higher when T is higher, there is little change in the observed resource utilization patterns with the addition of

a competitor (when T is high). The proportion of species

one's diet that consists of shared resources is,

$$\frac{F_2/(Q + N_1 + N_2)}{F_1/(Q + N_1) + F_2/(Q + N_1 + N_2)} \tag{22}$$

when the species are sympatric, and $F_1/(F_1 + F_2)$ when they

are allopatric. If Q is large relative to N_1 and N_2 (this

will be true if T is large), the proportion of the diet

that consists of overlapped types of food will not change

much if N_2 is increased from zero to equilibrium levels.

On the other hand, if equilibrium population levels are

much larger than Q, the proportion of a species' diet that

consists of types of resources taken by both species will

decrease when the species are sympatric. This phenomenon

is not a niche shift in the sense used earlier, since con-

sumption rates per unit resource do not change. Vandermeer

(1972) has suggested that this type of change in resource

utilization when the species are sympatric can be used as

evidence of intense competition, an idea which is not sup-

ported by this analysis.

Experimental and field evidence on the effects of

predation on species diversity often, though by no means

always, show predation increasing species diversity. Darwin

noted over a century ago that more species of grasses per-

sisted on lawns that were grazed or mown. More recently,

Harper (1969) has summarized experiments on the effect of

predation on species diversity in plant communities, and
has concluded that predation can either increase or decrease
species numbers depending upon the selectivity of the
predator. Paine's (1966) experiment in which removal of a
starfish from intertidal plots resulted in decreased species
numbers is often cited as evidence supporting the hypothesis
that predation increases species diversity in competitive
communities. More recently, Addicott (1974) has studied
the effect of predatory mosquito larvae on protozoan-rotifer
communities in pitcher plants, and has found that predation
always resulted in decreased species numbers.

Of course, the present model is not applicable
to competition for space, so that Darwin's and Paine's
observations are not necessarily relevant here. However,
even in these cases it is not clear that coexistence is simply
due to reduction of all population sizes. It seems more
likely that increased diversity in both cases was due to
selective predation on the competitive dominant(s). Although
it is not yet possible to determine whether the present
model is adquate for the protozoan community studied by
Addicott, this system is clearly much closer to the type
discussed here than in Paine's. It is interesting to note
that the Lotka-Volterra model also predicts that predation
should reduce diversity in a competitive community (see
(Chapter 2).

Environmental Variability and the Limiting Similarity

Environmental variability may take a number of different forms, and it is necessary to specify something about what is varying before drawing any conclusions about how environmental variability will influence niche overlap (see Chapter 2). In the present section we consider those sorts of environmental fluctuations which act so as to reduce population sizes. This would occur when the organisms are optimally adapted to average physical conditions (e.g. temperature, salinity, etc.) and increasing amplitude or frequency of variations will lead to a decline in the population size. Here, a more variable environment is harsher, and the effect of environmental variations is similar to that of predation. A more variable environment results in a higher value of T, the share of resources needed for maintenance and replacement. Thus, the maximum overlap consistent with coexistence decreases as environmental variability increases. This conclusion is independent of the nature of cross correlations in the effect of the environmental factor on the per capita rates of growth of the different species in the guild (i.e. whether the species react similarly or differently to a given change in the environmental factor). A similar conclusion may be drawn using a Lotka-Volterra model of competitive interactions, if increased environmental variability implies a lower average rate of increase. Any factor which acts to reduce population sizes will increase

the niche separation required for coexistence, and, other things being equal, will result in reduced species diversity. This is consistent with most field observations which show decreased species diversity in variable (harsh) environments. It is also consistent with Cody's (1974) observation that overlap in horizontal habitat in bird communities was less in environments with lower climatic predictability, although other factors can explain this.

The fact that the predictions of the current model are consistent with most data on the effects of environmental variability on species diversity, but not with data on predation may be explainable on the basis that most natural predators tend to selectively prey on the competitive dominant(s), whereas the effect of environmental variability is generally less selective. Of course, further work is needed before it is possible to determine whether the present model is applicable to those cases for which data is available.

General Discussion: How General is the Model?

There are basically two questions about the generality of the model analyzed here.

> (1)   Do the major results derived for
> equations (5) also pertain to the
> more general case given by (4)?

(2) Do results derived for (4) and (5)
apply to all cases where the major
assumption (that the consumers do
not influence the rate at which
resources are supplied to the system)
is met?

Unfortunately, it is difficult to give a very rigorous answer
to either of these questions. However, in this section it
is argued that the results derived here are likely to be
reasonably general.

Question (1)

The fact that there is a clear division between
shared and exlusive resources in (5) is not essential to
the analysis presented earlier. If, for example, model (5)
was changed to the form below, numerical analysis shows that
the same conclusions emerge about the relationship between
the efficiency of exploitation and the maximum overlap which
will permit coexistence.

$$g_1 = \frac{F_1}{Q + N_1 + \beta N_2} + \frac{F_2}{Q + N_1 + N_2} + \frac{\beta F_1}{Q + \beta N_1 + N_2}$$

$$\beta \ll 1 \qquad (23)$$

$$g_2 = \frac{F_1}{Q + N_2 + \beta N_1} + \frac{F_2}{Q + N_1 + N_2} + \frac{\beta F_1}{Q + \beta N_2 + N_1}$$

Here there are no truely exclusive resources. Each species
utilizes the resource refuge of the other to a limited
extent.

Similarly, it is not necessary that the shared and exclusive resources have the same Q value. It is difficult to derive a value for the minimum separation necessary for coexistence for a situation where there are many consumers and many resources. However, an indication of the general behavior of such a system may be seen by examining the minimum size of the resource refuge (i.e. the entry rate of exclusive or almost exclusive resources) necessary to maintain a species assuming that competitors obtain most of the overlapped resources. If F_1 is the entry rate of resources exploited only by species i, species i will be able to persist using these resources alone when F_1 is greater than QT. (Or equivalently, if p_{min} is greater than QT/F_t). Therefore, the minimum size of the resource refuge increases as Q or T increases or as F_t decreases). This suggests that the conclusions about the effect of Q and T on the minimum separation necessary for coexistence in the two species-three resource case are applicable to most of the cases covered by (4).

Question (2)

This question is more difficult than the previous one. The approach adopted here is simply to illustrate that a number of plausible alterations in the model do not alter the basic conclusions.

Nonlinear Functional Reponse. The model analyzed here was derived assuming a more or less linear functional response; i.e. the rate at which consumers consumed resources was a linear function of resource density. This is probably reasonably accurate over a range of resource densities for many real consumers. However, if resource densities become high enough, the rate of consumption must decline if for no other reason than the finite handling time involved in consuming a resource (Holling, 1965). Factors such as predation which lower consumer population density will result in relatively high resource densities, and hence low per capita rates of consumption per unit resource. This effectively increases the value of Q in model (5) at low consumer densities. As noted earlier, a higher value of Q results in a larger niche separation being required for coexistence. Therefore, this type of alteration in the form of the functional response will not alter the basic conclusion that factors which reduce consumer population densities result in a requirement for greater resource segregation.

Utilization Patterns Contract at Low Densities. If population densities decline (due to predation or environmental harshness) many species contract their utilization patterns so as to only make use of the optimal types of resources. If this is the case, predation or environmental fluctuations may decrease the level of competition if two

competitors have different optimal resources. Alternatively, if they have the same optimal set of resources, competition will be increased when population densities are reduced. Which of these phenomena occurs more often is important in determining whether predation is likely to increase species diversity in a given situation. However, this type of behavior is not directly relevant to the determination of the maximum tolerable overlap of competitors under predation. In addition, the analysis of niche shift presented earlier argues that at low population densities, the presence or absence of a competitor has little effect on determining whether a given resource is worth exploiting. Therefore there does not seem to be any a priori reason to believe that competitors are much more likely to have different optimal resources rather than the same optimal resource. This suggests again that predation is likely to decrease species diversity.

Rate of Increase a Function of Population Density Independent of g(N). The present analysis has assumed that resources were the only important factor in determining the per capita rate of increase of a population. However, social facilitation and interference competition are important in determining the population dynamics of many species. This section outlines the ways in which these two phenomena may alter the analysis.

Many organisms experience difficulty finding mates and therefore have lowered fitness at low densities. In this case, an increase in population density may actually increase the per capita rate of increase of a species.

A necessary condition for the stable coexistence of two competitors is that the product of intraspecific competition terms $\left(\frac{\partial f_1}{\partial N_1} \cdot \frac{\partial f_2}{\partial N_2}\right)$ (where f_i is a function giving the per capita rate of increase of species i as before) is less than the product of the interspecific competition terms $\left(\frac{\partial f_1}{\partial N_2} \cdot \frac{\partial f_2}{\partial N_1}\right)$ (e.g. Maynard Smith, 1974). Social facilitation has the effect of offsetting intraspecific exploitative competition at low population densities, so that the product $\frac{\partial f_1}{\partial N_1} \cdot \frac{\partial f_2}{\partial N_2}$ becomes very small. As a result, a stable equilibrium (coexistence) is possible only if interspecific competition is slight (i.e. niche overlap is low). Thus the effect of social facilitation at low densities is to make the effect of predation on species diversity even more pronounced. Predation should cause a significant increase in the minimum separation required for coexistence of competitors.

Behaviors such as pack-hunting or flocking may result in social facilitation at higher densities. Little can be said about the effect of these behaviors on the present analysis without knowing the quantitative nature of the benefits derived from them. It is certainly possible for some types of flocking to reverse the conclusions drawn from equations (5).

Since many different types of interference competition are possible, it is again difficult to make any generalizations about the way this phenomenon would alter our analysis. It is necessary to know the relationships describing the effect of interference on the per capita growth rate of a species and on its competitor before it is possible to determine the effect of reduction in population density on the limiting similarity. Roughly, if the ratio of interspecific interference to intraspecific interference increases as population densities decrease, then a larger niche separation will be required for coexistence when there is relatively high predation. If this ratio decreases as population densities decrease, then predation may allow closer species packing.

Resources do not Leave System at a Constant Rate.

If, instead of assuming that resources leave the system at a constant rate, it was assumed that resources left after a fixed residence time, τ, the number of resources leaving at time t will be equal to $F(t - \tau)\exp(-a\int_{t-\tau}^{t} Ndt)$, where F is the rate of entry of resources and a is the per capita consumption rate. Assuming $F(t)$ is constant, and that the numbers of consumers do not change significantly during the residence time, the change of resource density in a one-consumer-one resource system is given by

$$\frac{dR}{dt} = F\left(1 - e^{-a\tau N}\right) - aNR, \tag{24}$$

which is analogous to equation (2). Assuming the resources
are at equilibrium with respect to consumer density gives

$$g(N) = \frac{F(1 - e^{-a\tau N})}{N} \tag{25}$$

In this model, a small value of $a\tau$ or a small value of $\hat{N}$
represents inefficient exploitation. In the two species
case analogous to (5),

$$g_1 = \frac{F_1(1 - e^{-a\tau N_1})}{N_1} + \frac{F_2(1 - e^{-a\tau(N_1 + N_2)})}{N_1 + N_2} \tag{26}$$

If N_1 and N_2 are very large, or if $a\tau$ is large enough, this
expression approaches $F_1/N_1 + F_2/(N_1 + N_2)$, and so is equiva-
lent to (5) for Q close to zero. For small values of a or
τ or large values of T (which result in small values of $\hat{N}$),
a larger value of $F_1/(F_1 + F_2)$ will be required to allow
coexistence, since the exponential terms are larger. Thus,
the behavior of the limiting similarity for this model is
substantially the same as for the model studied earlier.
It is easy to show that the analysis of when niche shift
will be advantageous is similar as well.

Another possibility is that resources leave the
system in a density dependent manner. For example, fruit
may become unavailable due to attack by a fungus, which

proliferates faster when the density of fruit is relatively
high. In this case, the parameter Q in (5) will become larger
at low population densities of the consumer. This simply
reinforces the effect of predation in requiring a larger niche
separation among competitors.

Change in Searching Effort with Population Density.
The parameter Q in (5) is inversely proportional to the per
capita encounter rate between consumer and resource. The
encounter rate is in turn a function of searching effort.
If higher searching effort were favorable in the presence
of a predator, predation would reduce Q and possibly allow
higher overlap than in the absence of predation. However,
search effort represents a balance between the risks of
being eaten while consuming resources vs. the gain in repro-
duction and survival from consuming more. Thus it seems
more likely that the presence of predators would favor reduced
searching effort, resulting in a larger value for Q, and a
greater separation required for coexistence.

Spatial Heterogeneity. The present model has
assumed a spatially homogeneous sytem, although many natural
systems are heterogeneous. Levin (1974) has shown that
spatial heterogeneity can allow coexistence where it would
otherwise be impossible when there is a priority effect.
(In a two species system, a priority effect occurs when it

is possible for species one to exclude species two or vice versa depending upon initial numbers. More generally, a priority effect will exist in a many species system when there are several alternative stable equilibria.) In the model investigated here, a priority effect is not possible, so that it seems unlikely that spatial heterogeneity will substantially alter the conclusions. This is shown in Appendix III.

Age Structure. In many organisms, resource utilization is a function of age, and the nature of competitive interactions will depend on the age-specific pattern of resource utilization. If predation or environmental fluctuations significantly alter age structures, competition may be reduced or increased depending upon the age-specific patterns of resource utilization and of mortality for the species involved, so caution should be used in extending the conclusions drawn here to situations where overlap in resource utilization changes significantly with the age and/or size of the competing species.

The preceding discussion was meant to suggest that the results derived here are general enough to often be used as an initial hypothesis about the effect of predation (or environmental fluctuations) on the limiting similarity of competitors, given that the basic assumption of the model

is satisfied. However, as indicated, social interactions,
group foraging, and age structure may alter the results of
this analysis. It is likely that there are other factors
that may reverse the conclusions reached here. Regardless
of the generality of the model, it does suggest that the
intensity of competition can be severe even when populations
of the competitors are at low levels. It is common practice
to avoid these types of systems in studies of competition,
since high population densities and scarcity of resources
are often taken as indicators of intense competition (e.g.
Connell, 1975; Vance, 1972a). For the type of system
described here, competition will be most intense (for a given
degree of overlap in resource utilization) when resources
are relatively abundant and population levels are low. It
is hoped that the present analysis will stimulate the study
of competition in these sorts of systems.

In addition, the present analysis has provided
evidence for the need to extend competition theory beyond
the Lotka-Volterra equations. Since the Lotka-Volterra
equations assume that the effect of one species upon another
is independent of density, many of the features revaled in
the present model, such as the role of predation and environ-
mental fluctuations in increasing the intensity of competition,
could not be deduced from studying these equations. In addi-
tion, the fact that the Lotka-Volterra model does not incor-
porate parameters specifying overlap in resource utilization

has resulted in a number of proposed schemes for relating

α to overlap (Vandermeer, 1972; Roughgarden, 1972; MacArthur

and Levins, 1967), without much discussion of when each method

will be applicable, and without very convincing arguments

that they are ever accurate. An understanding of resource

partitioning requires an investigation of models which incor-

porate resource overlap explicitly. Gill (1974) and Case

and Gilpin (1974) have argued using the Lotka-Volterra models

that interference competition is more likely to be favored

when α_{ij} without interference is relatively high. The present

model suggests that the efficiency of exploitation plays the

major role in determining whether interference competition

will be selected for. If T or Q in the present model is high,

competition as measured by several indices may be very high,

but there will be no selective advantage to interference

against members of the competing species. These point should

serve to show the kinds of phenomena that can be understood

by a study of alternative simple models of competition.

Chapter 4

CONCLUSIONS

These general conclusions have emerged from the
preceding analysis:

(1) The generalization that competing species
which partition resources in a one-dimensional manner need
utilization curves which are separated by a distance greater
than the standard deviation of the curves does not seem to
be generally valid. It is most likely to be true when re-
sources at a given position on the resource axis consist
of only one type.

(2) Contrary to the generalization that niche
overlap must be lower in more variable environments, many
forms of environmental fluctuations do not set limits to the
similarity of competitors. Specifically, if the competing
species react to the environmental fluctuations in the same
way, the maximum tolerable variability is similar for systems
with a high or low level of competition (niche overlap).
Environmental varability may limit niche overlap when species

react to environmental factors in an uncorrelated or an
opposite fashion, or when increased environmental variability
is correlated with lower average rates of increase.

(3) For a simple model of competition in which
the competitors do not alter the rate at which resources
become available to them, the limiting similarity is usually
smaller (the maximum permissible overlap is greater) in those
cases where exploitation is relatively efficient. If exploi-
tation is inefficient, greater niche separation is generally
required for coexistence. Density independent predation or
environmental fluctuations which reduce population levels
will increase the niche separation required for coexistence.
Therefore, these two factors should be correlated with lower
species diversity in systems where the model is applicable.

The type of models which have been studied here
are designed to help understand patterns of overlap in
resource utilization observed in competitive communities.
Although the models are not likely to be accurate descrip-
tions of any specific communities, they do suggest possible
explanations for observed phenomena in a wide variety of
communities. Assume for example, that one is interested in
explaining the difference in average overlap in diet in two
geographically separated groups of competitors. Without any
model of the competitive process, this type of question would
be virtually unanswerable. It would only be possible to

document differences between the two groups of competitors,
and to try to manipulate randomly chosen factors which differ
between the two communities. Alternatively, it would be
possible to construct a detailed simulation model of the
competitors, and manipulate various parameters in the simu-
lation model to determine their impact on the maximum tolerable
overlap. Although this would certainly be more feasible than
manipulating real communities, it is potentially a laborious
and costly procedure. In addition, one would be unlikely
to have any real appreication of the generality of the
results obtained from an analysis of the simulation.

A reasonably complete understanding of the question
is most likely to come from a combination of simple models,
complex models, and field manipulations. Simple models
serve an important function in suggesting plausible explana-
tions for a given phenomenon. These explanations should
initially be tested by constructing more realistic models
of the system under investigation, to determine whether any
specific feature of the real community is likely to alter
the predictions made by the simple model. This procedure
will ideally yield hypotheses which have a reasonably high
probability of being correct, and which are therefore worth
testing by experiments in the field if such are feasible.

The model described in Chapter 3 seems to provide
a possible explanation for the differences in overlap in
two hermit crab communities (see Chapter 3). An understanding

of this system would be furthered by constructing more detailed models and performing experiments to determine whether empty shells do turn over more quickly in the intertidal, as postulated.

As May (1973a) has pointed out, simple models are also valuable in that they sharpen discussion of issues. Chapter 1 suggests the need to specify resource utilization patterns in more detail than implied by a simple "utilization curve" if one is to understand the limits to resource overlap of competitors. Chapter 2 illustrates the need to specify the nature of environmental variability in dealing with the question of whether environmental fluctuations will limit the similarity of competitors. Chapter 3 demonstrates that the intuitive notion that a reduction in competitor numbers reduces the intensity of competitive interactions is wrong in at least one common type of system.

In a more general way, the three studies presented here demonstrate the importance of studying a number of models of ecological processes. The range of different processes included under general headings such as competition or predation is such that predictions based upon one model or one set of assumptions are not likely to be accurate for more than a small portion of biologically realized situations. Because of this, simple models are more likely to be useful in explaining differences between communities, rather than establishing general principles. The first two parts

of this investigation show that even for the simplest possible
model of competition - the Lotka-Volterra - previously
suggested generalities are dependent on particular assumptions
which are often not reasonable. In order to understand
resource partitioning in competitive communities, it is
important to study models which incorporate explicitly the
degree of overlap of the competing populations. It is hoped
that the model presented in Chapter 3 will show the value of
this approach, and stimulate the study of other models.

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APPENDIX I

DERIVATION OF α FOR SCHOENER'S MODEL

The equilibrium population levels of the two species may be found by setting the per capita rates of increase equal to zero. Since we have assumed, in effect, that the two species have equal equilibrium populations, this equation becomes,

$$\frac{I_E}{\hat{N}} + \frac{I_0}{2\hat{N}} = C \qquad or \qquad N = \frac{2I_E + I_0}{2C} \qquad (I.1)$$

The derivatives of the per capita rates of increase of species 1 ($P_1 = (I_E/N_1) + (I_0/(N_1 + N_2)) - C$) are,

$$\frac{dP_1}{dN_2} = \frac{-I_0}{(N_1 + N_2)^2} \qquad \frac{dP_1}{dN_1} = \frac{-I_E}{N_1^2} + \frac{-I_0}{(N_1 + N_2)^2} \qquad (I.2)$$

Substituting (I.1) in (I.2), and taking the ratio $(dP_1/dN_2)/(dP_1/dN_1)$, one arrives at,

$$\alpha = \left. \frac{dP_1}{dN_2} \middle/ \frac{dP_1}{dN_1} \right|_{\hat{N}_1, \hat{N}_2} = \frac{I_0}{4I_E + I_0} \qquad (I.3)$$

APPENDIX II

CONDITIONS FOR INVASION ASSUMING EQUAL CARRYING CAPACITIES

The formula for $L(d)$ referred to below is given in chapter one. If the utilization curves are not separated then $L(0) = 1$, since $\alpha(0) = 1$. If $L(d)$ is a decreasing function of d for all values of d, then there will be no limiting similarity, since $L(d)$ will be less than one for any positive value of d. Differentiating $L(d)$ we obtain

$$L'(d) = \frac{2\alpha'(d) + 2\alpha'(d)\alpha(2d) - 4\alpha(d)\alpha'(2d)}{(1 + \alpha(2d))^2} \qquad (II.1)$$

Noting that $\alpha(d)$ is a decreasing function, the requirement that the derivative of $L(d)$ be less than zero translates into

$$\alpha'(d)(1 + \alpha(2d)) < 2\alpha(d)\alpha'(2d),$$

or

$$\alpha'(d) < \left[\frac{2\alpha(d)}{1 + \alpha(2d)}\right] \alpha'(2d) \, . \qquad (II.2)$$

At d = 0, the derivative of L(d) is equal to zero. For d slightly greater than zero, $2\alpha(d)/(1 + \alpha(2d)) = 1$, so that condition (II.2) is satisfied if the second derivative of $\alpha(d)$ is greater than zero (i.e. if the curve $\alpha(d)$ is concave upward).

The next step is to consider what formulae for $\alpha(d)$ and what utilization curves give an $\alpha(d)$ curve which is concave upward. Here it is useful to restrict our attention to the three expressions for α we are considering here. Roughgarden (1974) has already analyzed expression (1), and for the utilization curves which he analyzed, $\alpha(d)$ has a negative second derivative near d = 0 resulting in a limit to the closeness of the resident species consistent with successful invasion by a species with an equal carrying capacity. Formula (3), on the other hand, can be shown to generate $\alpha(d)$ curves which are everywhere concave upward for any unimodal resource utilization curve. If the utilization curves are normalized, formula (3) may be written as

$$\alpha(d) = 2\int_{d/2}^{\infty} U(x)dx$$

assuming the curves have the same shape (for convenience the utilization curve U(x) has been assumed to have a maximum at x = 0). Differentiating this expression twice results in $\alpha''(d) = -U(d/2)/2$. If U(x) is unimodal, its derivative will be negative for x greater than zero, so that the second derivative is always positive. For the limiting case of rectangular curves, $\alpha(d)$ is linear. A

similar analysis may be used to show that expression (6) also generates $\alpha(d)$ curves which are concave upward for any unimodal utilization curve.

APPENDIX III

NO PRIORITY EFFECT FOR TWO COMPETITOR MODEL

This analysis assumes a slightly more general version of (5), given by the following equations:

$$g_1 = \frac{F_1}{Q_1 + N_1} + \frac{F_2}{Q_2 + N_1 + CN_2}$$

$$g_2 = \frac{F_3}{Q_3 + N_2} + \frac{F_2}{Q_2 + CN_2 + N_1}$$

In order for species one to be able to exclude species two and vice versa, it is necessary that $g_1(0, \hat{N}_2) < T_1$, and $g_2(\hat{N}_1, 0) < T_2$. The following substitutions are made in the above inequalities:

(1) $$g_1(0, \hat{N}_2) + \frac{F_1}{Q_1} + \frac{F_2}{Q_2 + C\hat{N}_2}$$

(2) $$g_2(0, \hat{N}_1) + \frac{F_3}{Q_3} + \frac{CF_2}{Q_2 + \hat{N}_1}$$

(3) $$T_1 = \frac{F_1}{Q_1 + \hat{N}_1} + \frac{F_2}{Q_2 + \hat{N}_1}$$

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$$(4) \qquad T_2 = \frac{F_3}{Q_3 + \hat{N}_2} + \frac{CF_2}{Q_2 + C\hat{N}_2}$$

This results in,

$$(5) \qquad \frac{F_1}{Q_1} + \frac{F_2}{Q_2 + C\hat{N}_2} < \frac{F_1}{Q_1 + \hat{N}_1} + \frac{F_2}{Q_2 + \hat{N}_1}$$

$$(6) \qquad \frac{F_3}{Q_3} + \frac{CF_2}{Q_2 + \hat{N}_1} < \frac{F_3}{Q_3 + \hat{N}_2} + \frac{CF_2}{Q_2 + C\hat{N}_2}$$

Multiplying (5) by C and rearranging (5) and (6) gives

$$\frac{CF_1}{Q_1} + \frac{CF_2}{Q_2 + C\hat{N}_2} - \frac{CF_1}{Q_1 + \hat{N}_1} < \frac{CF_2}{Q_2 + \hat{N}_1} < \frac{F_3}{Q_3 + \hat{N}_2} + \frac{CF_2}{Q_2 + C\hat{N}_2} - \frac{F_3}{Q_3}$$

For this to be satisfied for any parameter values, the left hand term must be smaller than the right hand term. Cancelling $CF_2/(Q_2 + C\hat{N}_2)$ from each side,

$$\frac{CF_1}{Q_1} - \frac{CF_1}{Q_1 + \hat{N}_1} < \frac{F_3}{Q_3 + \hat{N}_2} - \frac{F_3}{Q_3}$$

Clearly, the left hand side is positive and the right hand side is negative, so it is impossible for species one to be able to exclude two and vice versa. There can be no priority effect.