Resource utilization theory has lacked a method of explicitly defining the qualitative and quantitative interrelationships between populations of species in a community. Graphical isocline analysis as a method can be used to determine the effect of the environment, including the energy input rate on a community, with the kinds of dimensions of predator-prey interactions, competition, mutualism, commensalism, and amensalism. A nonlinear mathematical model of a community with an energy resource, a plant, two competing herbivores, and a carnivore is solved graphically in order to construct the prey and predator isoclines on successive predator-prey phase planes based on the density dependent responses of the populations.

The equilibria on any of a series of predator-prey, competition, and diversity phase planes are functions of the community's energy input rate, the density of the highest predator in the trophic chain and the physical, chemical, and biological identities in the
environment of the defined system. Different conditions were found where co-existence of competitors is both possible and not possible depending on the characteristic density dependent responses of organisms in the population. The community's global stability was analyzed and found to be strongly stable. Characteristic density dependent responses of the organisms promote strongly stable isocline configurations.
A Theory of Resource Utilization

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A THEORY OF RESOURCE UTILIZATION

Resource utilization theory based on multispecies mathematical models has been inadequate in several important respects. It has limited equilibrium analysis to two-species models. Stability characteristics of the equilibrium have been determined only in the vicinity of equilibrium nodes. It has failed to show the expected increase in community stability with increased trophic complexity (May, 1973). It does not introduce in an appropriate way the impact of the community's energy resource on predator-prey interaction, competition, and diversity. It fails to include the important density dependent responses of organisms at the population level in the community's total response. And finally it has not established the important interrelationships between the different categories of species interaction: commensalism, amensalism, mutualism or symbiosis, predator-prey phenomena, and competition.

Extant graphical isocline analysis has provided a method of freeing resource utilization theory from some of the shortcomings of other modeling, but has failed so far to be useful in representation of multispecies systems. The discussion has been concerned mainly with the shape of the prey isocline and the stability of the equilibrium at the intersection of the prey and predator isoclines (Rosenzweig and MacArthur, 1963; May, 1972; Rosenzweig, 1973). Rosenzweig
(1973) expanded isocline analysis to a three-trophic level exploitative system on a three-dimensional phase space. Three-dimensional isoclines are difficult to visualize, thus limiting their usefulness. Expansion into the fourth dimension is graphically impossible.

The purpose of this thesis is to analyze a small but comprehensive community model by a quantitatively and qualitatively explicit graphical method of isocline analysis not having the above shortcomings and use it as a basis of explanation of previously inadequately represented resource utilization phenomena. The community representation in Figure 1 has the kinds of dimensions necessary to include the most important community phenomena: the community's energy resource, predator-prey interactions, competition, commensalism, amensalism, mutualism and diversity.
Figure 1. Schematic representation of the simplest community matrix in an environment with the kinds of dimensions to analyze diversity, the five distinguishable categories of interaction between species, namely predator-prey interaction (+), commensalism (-0), amensalism (-0), competition (-), and mutualism (++) and the affect of the energy input rate (+) on them. The sign in the direction of the arrow characterizes the effects of one species on the other as positive, neutral or negative depending on whether the species increase, remain unaffected or decrease due to the interaction. Competition between $H_1$ and $H_2$ occurs through the exploitation of a common prey (plants). Commensalism occurs between $H_1$ and $H_3$ and amensalism between $C_1$ and $C_2$. Mutualism occurs between $H_2$ and $H_4$ through exploitation of competing plant species ($P_1$ and $P_2$). The environment represents other communities and the physical and chemical environment interfacing with the community matrix. $R$ is the energy resource, $I$ the energy input rate, $P$ the plants, $H$ the herbivores and $C$ the carnivores. Numerical subscripts denote different species on a given trophic level. Organisms on all trophic levels will contribute organic material (OM) utilized by decomposers (D). Decomposers will produce nutrients (N) utilized by the plants.
PROCEDURE

One solution to examining multispecies multi-predator-prey models by isocline analysis, without resorting to graphical representations having more than two dimensions, is to consider predator-prey interactions on successive, interconnected, two-dimensional phase planes in which the predator on one phase plane becomes the prey on the next successive phase plane (Fig. 2). Then graphical solutions of a special set of nonlinear differential equations permits construction of the prey and predator isoclines on each successive phase plane based on the characteristic density dependent responses of the populations. In this way the isoclines can be rigorously defined, a shortcoming that Rosenzweig (1969) began to remedy by mathematically defining his humped shaped isocline. The prey isocline on each phase plane has been found to be parameterized in terms of the community's energy input rate, the predator isocline in terms of the density of the highest predator in the trophic chain, the densities of competitors in the defined community, and amensalists, commensalists, and mutualists in the environment of the defined system. Therefore, the equilibrium and its stability on any of the two-dimensional phase planes is consistent with its equilibrium and stability in the x-dimensional hypervolume. These identities, as variables on the isoclines, generate any number of transitory equilibrium nodes which
Figure 2. The prey and predator isoclines on prey-predator phase planes are derived and parameterized from the intersections of systems of gains and loss curves based on density dependent responses of prey and predator in the differential equations. On the R-P1 phase plane, the energy resource's gain rates and in turn R's prey isoclines are parameterized by different energy input rates. On successive phase planes, the prey's production rates, gain rates and prey isoclines are identified by the energy input rate. The predator isoclines on any phase plane are parameterized by the density of the predator on the next higher level, and ultimately by the predator in the highest level. Therefore the equilibriums between successive predator–prey relationships are parameterized by the energy input rate and indirectly by the TC's density. In the equations r is the recruitment rate and d is the nonpredatory loss rate. k is a density constant.
define an area on the predator and prey phase plane limited only by
the possible existence of predator and prey isoclines.

Competition phase planes can be constructed from the predator-
prey phase planes for predator populations competing for a common
prey (Fig. 3). The competition isoclines have the same dimensions
as the predator and prey isoclines and are parameterized accordingly,
thus showing what processes lead to the co-existence or extinction of
competing species.

Diversity isoclines can be derived from equilibrium conditions
on competition phase planes and are parameterized by these condi-
tions.
Equations

\[
\begin{align*}
\frac{dP_1}{dt} & = f(R) - f(H_1, d, H_2) \\
\frac{dH_1}{dt} & = f(H_1) \\
\frac{dH_2}{dt} & = f(H_2)
\end{align*}
\]

Pred - Prey Phase Plane

\[
\begin{align*}
P_1 \text{ 's Prey Isocline} & \quad f(H_1) \\
H_1 \text{ 's Pred. Isocline} & \quad f(H_2)
\end{align*}
\]

Competition Phase Plane

\[
\begin{align*}
H_1 \text{ 's Competition Isoclines} & \quad \text{Parameterized by energy input rates} \\
H_2 \text{ 's Competition Isoclines} & \quad \text{Parameterized by carnivore density}
\end{align*}
\]

Figure 3. The isoclines on the competition phase plane are derived and parameterized from those on the predator-prey phase planes. Since the competing herbivores both utilize \( P_1 \) for food, the differential equation for the plants will have a predation term for both \( H_1 \) and \( H_2 \), which results in a family of prey isoclines on the \( P_1-H_1 \) and \( P_1-H_2 \) phase planes parameterized by the energy input rates and the \( H_2 \) and \( H_1 \) densities respectively. The density dependent responses of recruitment and nonpredatory losses for each herbivore are a function of its competitor density and result in a family of predator isoclines for each carnivore density, parameterized by its competitor density. The competitor isoclines for \( H_2 \) on the \( H_1-P_1 \) phase plane and \( H_1 \) on the \( H_2-P_1 \) phase plane is constructed on the \( H_1-H_2 \) competition phase plane from the intersections of the prey and predator isoclines and parameterized by the energy input rate and carnivore density. L. I, M. I and H. I are substituted for Low I, Medium I and High I.
MATHEMATICAL FRAMEWORK

A community consisting of an energy resource \( R_j \) and population densities \( T_{ij} \) on different trophic levels, utilizing the energy resource either directly or indirectly through predation, can be defined by the set of equations:

\[
\frac{dR_j}{dt} = I_j - \sum_{j=1}^{n_0} \left[ \sum_{\ell=1}^{n_1} \frac{g_{ij\ell}}{y_{ij\ell}} \right] T_{1j}
\]

\[
\frac{dT_{ij}}{dt} = r_{ij} T_{ij} + \sum_{j=1}^{n_i} \left[ \sum_{\ell=1}^{n_{i-1}} g_{ij\ell} \right] T_{ij} - \sum_{j=1}^{n_{i+1}} \left[ \sum_{\ell=1}^{n_i} \frac{g_{i+1,j\ell}}{y_{i+1,j\ell}} \right] T_{i+1,j} - d_{ij} T_{ij}
\]

where \( t \) is time, \( n_0 \) is the total number of energy resource species, \( n \) is the total number of species on a trophic level, \( i \) is the trophic level, \( j \) is the species counter for trophic level \( i \), \( \ell \) is the species counter for trophic level \( i-1 \), \( I_j \) is the energy input rate, \( r_{ij} \) is the relative recruitment rate, \( g_{ij\ell} \) is the relative growth rate of species \( j \) on trophic level \( i \) consuming prey species \( \ell \), \( y_{ij\ell} \) represents the yield of organism \( T_{ij} \) per unit of prey \( T_{i-1,\ell} \) consumed, and \( d_{ij} \) is the relative nonpredatory death rate. The relative growth rate \( g_{ij\ell} \) of a given species \( T_{ij} \) consuming the prey \( T_{i-1,\ell} \) can be estimated from the empirical equation:

\[
g_{ij\ell} = \frac{M_{ij\ell} T_{i-1,\ell}}{k_{i-1,\ell,j} + T_{i-1,\ell}}
\]
\( M_{ij} \) is the maximum relative growth rate constant for species \( T_{ij} \) consuming the prey \( (T_{i-1,j}) \) which can be developed under a particular operational condition when the prey concentration is so high that \( g_{ij} \) is independent of the prey density. The constant \( k_{i-1,j} \) determines the curvature of a plot of \( g_{ij} \) versus \( T_{i-1,j} \) and is numerically equal to the prey density at which \( g_{ij} \) is half the value of \( M_{ij} \).

Assume for simplicity the maintenance ration of the prey is zero. I will use \( k_{ij} \) as a convenient unit for representing the density of the population on trophic level \( T_{ij} \) so that the general development of the relationships between populations on different trophic steps can be qualitative if \( k_{ij} \) is not defined and quantitative if it is defined.

Equation (3) was originated by Monod (1942) on the basis of analysis of bacterial growth curves as a function of substrate concentration. The equation is equivalent to the Michaelis-Menton equation for enzyme kinetics.

Figure 1 informally defines a community consisting of an energy resource and five populations on four trophic levels. This community in its environment can be formally defined with equations (1) and (2) by interpreting \( T_{11} \) as \( P_1 \), \( T_{21} \) as \( H_1 \), \( T_{22} \) as \( H_2 \), \( T_{31} \) as \( C_1 \) and \( T_{41} \) as \( TC \) and making the appropriate substitutions. The resulting set of equations is

\[
\frac{dR}{dt} = I - g_{P_1} \frac{P_1}{y_{P_1}} \tag{4}
\]
\[
dP_1/dt = r_p P_1 \left[ \frac{M_{p1}}{k + R} \right] P_1 - \frac{M_{h1}}{y_{h1}} \left[ \frac{P_1}{k p_1 + P_1} \right] H_1 - \frac{M_{h2}}{y_{h2}} \left[ \frac{P_1}{k p_1 + P_1} \right] H_2 - d_{p1} P_1
\]

\[
dH_1/dt = r_h H_1 \left[ \frac{M_{h1} P_1}{k p_1 + P_1} \right] H_1 - \frac{M_{c11}}{y_{c11}} \left[ \frac{H_1}{k_{h1} H_1 + H_1} \right] C_1 - d_{h1} H_1
\]

\[
dH_2/dt = r_h H_2 \left[ \frac{M_{h2} P_1}{k p_1 + P_1} \right] H_2 - \frac{M_{c12}}{y_{c12}} \left[ \frac{H_2}{k_{h2} H_2 + H_2} \right] C_1 - d_{h2} H_2
\]

\[
dC_1/dt = r_c C_1 \left[ \frac{M_{c11} H_1}{k_{h1} H_1 + H_1} \right] C_1 + \frac{M_{c12} H_2}{k_{h2} H_2 + H_2} C_1 - \frac{M_{tc}}{y_{tc}} \left[ \frac{C_1}{k_{c1} + C_1} \right] TC - d_{c1} C_1
\]

For simplicity $k_{h1}$ and $k_{h2}$ will hereafter equal $k_{h1}$ and $k_{h2}$ respectively.

The special set of equations is important because the energy input rate and TC densities as explicit variables and $P_2$, $H_3$, $H_4$ and $C_2$ as implicit variables define the community equilibrium in a field of community equilibria that are subject to change by dimensions within the system. This permits the community of x species in an x-dimensional space to be represented on a series of successive predator-prey phase planes in which the set of prey isoclines (dprey/dt=0) on every phase plane is parameterized in terms of energy input rate, and the predator isoclines (dpredator/dt=0) are parameterized in terms of the predator's consumer density, which
is indirectly related to the density of TC. The prey and predator isoclines on the two-dimensional predator-prey phase planes are projections of x-dimensional community isoclines in the phase space. Likewise, a predator-prey equilibrium is a projection of a community equilibrium. Therefore the intersections of isoclines can be examined for global stability of predator-prey interactions within the community framework without linearization assumptions. Isocline equilibria and stability conditions on successive predator-prey and competition phase planes determine the equilibrium and stability of the community for a given set of environmental conditions. A changing environment results in a continuum of community equilibria.
PREDATOR-PREY INTERACTIONS

Considering R as a prey or as a resource for $P_1$, the prey isocline for R can be determined graphically from the gain-loss graph for R (Fig. 4A). The prey isocline for R rises at low densities of R, because the rate of consumption becomes so low that greater $P$ density has little effect on the density of R (Fig. 5A). At higher densities of R, the prey isocline for R is independent of R because of the saturation growth rate of $P_1$ (given a constant utilization coefficient) and will remain so until R at very high levels becomes inhibitory to $P_1$ and the isocline starts to descend due to increased nonpredatory loss rate of $P_1$, a condition not explicitly developed here.

Considering $P_1$ as a predator or utilizer of R, the predator isocline for $P_1$ (Fig. 5A) can be determined graphically from the gain-loss graph for $P_1$ (Fig. 4B). The predator isocline for $P_1$ at zero $H_1$ density has an abscissal intercept at its maintenance value of R. The predator isocline for $P_1$ with an $H_1$ identity has an ordinate intercept at the $H_1$'s maintenance ration of $P_1$ on the R-$P_1$ phase plane. The predator isocline approaches an asymptote at high $P_1$ densities and low $H_1$ densities, due to rapidly increasing nonpredatory loss rates of $P_1$. This asymptote decreases as predatory loss rates increase with greater $H_1$ densities.

The predator and prey isoclines on the $P_1-H_1$ (Fig. 5B) and
Figure 4. The prey isoclines for the energy resource at different energy input rates are constructed on the R-P1 phase plane from the graphical solution of equation (1) in (A). The equilibrium between R and P are determined from the intersections of the gain curve at low, medium and high energy input rates with the plant consumption loss rate curves at different plant densities. The energy input rate is independent of any dimension in the system and therefore constant with respect to the energy resource. Adding resource species for the plants would result in a family of gain curves for each input rate. The plant's functional and numerical utilization response is Holling type 2 predation response. The predation isocline for the plants at different H1 densities is constructed on the R-P1 phase plane from the graphical solution of equation (2) in (B). The densities at which the plants are at equilibrium with the H1 at different R is determined from the intersections of the gain curves at different energy resource levels with the loss rate curves at different herbivore no. 1 densities. The total gain response for the plants is a summation of recruitment (assumed to be zero) and production. Production is a direct function of the amount of plants available to the herbivore, consequently the family of straight line production responses at different resource levels. The total loss rate curve is a summation of nonpredatory plant losses and predation at different H1 densities. The time track on the R-P1 phase plane from some instable point back to equilibrium can be constructed from the R-P1 gain loss graphs by solving for the resultant vector from the R and P1 component vectors. If at 1k_r and 3k_p1 for a system at equilibrium at high I and 3k_h1 the magnitude of the R component vector in (A) is the difference between the gain curve at high I and the loss curve at 3k_p1. The magnitude of the P1 component vector in (B) is the difference between gain curve at 1k_r and 3k_h1. The resultant vector constructed from the R and P1 component vectors (in Fig. 5) establishes where the next sequence of component vectors originates and eventually returns to equilibrium at high I and 3k_h1. The vectors are numbered in sequence.
Figure 5. The family of resource and utilization isoclines in Figures A, B and C express the density relationship between the resource and utilizing on successive trophic steps as determined from the graphical solution of equation (1) and (2) for the appropriate $i$. The family of resource isoclines has either low, medium or high energy input rate as an identity on each phase plane. The family of predator isoclines has different predator densities as the identity. Time tracks show how the perturbed system returns to equilibrium for different system identities. The time tracks can be approximated by connecting the end of one resultant vector to the tail of the next in sequence. The resultant vectors are constructed from the horizontal--$R$ component vector--derived from Figure 4A and from the vertical--$P_1$ component vector--derived from Figure 4B in A. The shorter the vector length the more accurate the approximation is to the actual instantaneous change of the time track.
H$_1$-C$_1$ (Fig. 5C) phase planes are constructed from the graphical solution of equation (2), which has gains due to recruitment and production and losses due to predation and other factors (Fig. 1). Recruitment is a summation of density dependent reproduction and immigration, and it represents the density dependent rate at which biomass is added to the population from all other sources except production. The reproduction rate usually rises to a peak and then declines as population density increases (Ricker, 1954; Gulland, 1967). Immigration rate is taken to be inversely related to population density. The recruitment response will take on different shapes with changing community and environmental conditions resulting in systems of recruitment curves (dashed lines as in Fig. 6C and 7C) and a consequent shift in the isocline.

The consumer production rate at different consumer densities is decomposed into the asymptotic growth response of the consumer population with respect to its prey density, and the density of the consumer population with respect to the prey as defined by the prey isocline (Warren, 1971). For example, $P_1$'s production curve (Fig. 6D) is developed from the prey isocline for $R$ on the R-$P_1$ phase plane and $P_1$'s growth response as defined by equation (3). The consumer production rate will increase rapidly as the consumer density increases, owing to high growth rate at high prey densities (low consumer densities), then peak and decline as the growth rate decreases
Figure 6. The resource isoclines for the plants are constructed on the P-H phase plane from the graphical solution of equation (2) translated for $T_1 = P_1$, $T_2 = H_1$, and $T_2 = H_2$ above. The densities at which $P_1$ are at equilibrium with $H_1$ are determined from the intersections in A of the total gain rate curves (B) at low, medium and high energy input rates with the total loss rate curves (E) at different $H_1$ densities. The total plant gains are a summation of recruitment (C) and production (D). Plant recruitment is zero but could be represented by a family of curves, as represented by dashed lines, due to competition from other plants, energy input rate, habitat or any other phenomena for the energy resource on the R-P phase plane, and the plant's growth response with respect to the energy resource levels. A family of different production curves exist for each I for every condition that modifies the plant's growth response. The total plant losses are a summation of predation by $H_1$ (F) and the nonpredatory losses (G). The predation's terms measure the consumption rate of plants at different herbivore's densities. Alternative prey could modify the predation response with increasing $H_1$ densities. The nonpredatory loss response of the plants can also be represented by a family of curves which could result from competition, inhibitory effects of high energy resource levels (i.e. 4$K_r$) or other physical, chemical, or biological phenomena. Introduction of a competitor ($H_2$) would result in an additional set of predation responses (H) at each $H_2$ density which, if added to each total loss rate curve, would create a family of total loss rates for each $H_1$ density.
Figure 7. The predation isoclines for $H_1$ are constructed on the $P-H_1$ phase plane from the graphical solution of equation (2). The densities at which $H_1$ is at equilibrium with $P_1$ and $C_1$ are determined from the intersections in (A) of the total gain rate curves (B) at different plant densities with the total loss rate curves (E) at different carnivore densities. The total gain rate curves are a summation of recruitment (C) and production (D) at different plant densities. Families of recruitment curves can exist due to different competitor densities as shown by the dashed lines in (C) as well as other phenomena such as habitat, predation or energy resources. Production is a family of straight lines due to increasing growth rates at higher plant densities with the horizontal curve representing the $H_1$ maintenance ration of plants. The total losses (E) are a summation of predation (F) nonpredatory losses (G). The carnivore's consumption rate increases as $C_1$ increases. The addition of an alternative prey such as $H_2$ for the carnivore could change its consumption response as a function of $H_1$. $H_1$'s nonpredatory loss rate is also sensitive to competition and increasing $H_2$ can shift the loss rate curve to the left, increasing the loss rates of lower $H_1$ densities. (G)
at low prey densities (high consumer densities) (Fig. 6B). Since $I$ is the identity on the prey isocline of $P_1$ on the $R-P_1$ phase plane, the production rate for $P_1$, and in turn the prey isocline of $P_1$, has $I$ as its identity. Similarly $I$ parameterizes the set of prey isoclines on all successive prey-predator phase planes.

The characteristic functional response of a predator to increasing prey (resource) density is an initial rapid rise in the case of invertebrate species (Fig. 4B and 6F) or a response lag for vertebrate species (Fig. 7F) before leveling off at high prey density (Holling, 1959). Predation together with exponentially increasing nonpredatory losses (Fig. 6G and 7G) comprise the loss curve at different $H_1$ densities (Fig. 6E) or at different $C_1$ densities (Fig. 7E). The non-predatory losses can be represented by families of curves (dashed lines in Fig. 6G and 7G) each with its own identity due to habitat, community, and environmental conditions, which lead to new isoclines as additional identities are introduced. In this way the community equilibrium is defined for a given $I$, TC, and other community environmental conditions.

The equilibrial $C_1$ density is determined from the intersection of the prey isocline at a given $I$ with a predator isocline at a given TC density (Fig. 5C). This equilibrial $C_1$ density, together with $I$, specifies the equilibrial $H_1$ density in Figure 5B which in turn determines the equilibrium on the $R-P_1$ phase plane. The time tracks in Figure 5
tend toward the equilibrium nodes for different I's and TC densities. Since TC and C\textsubscript{2} both have the same negative effect, C\textsubscript{2} could be substituted for TC in a qualitative sense.

The equilibrium due to the configurations of the predator and prey isocline is very stable, approaching in most cases the most stable configuration: a vertical prey isocline and horizontal predator isocline. The time track returning from an instable point to equilibrium can be rigorously defined from the gain-loss graphs as in Figures 6 and 7. This approach is a substantial improvement over matrix analysis of community stability for multi-species models, which can only characterize the system as stable or instable in the neighborhood of the equilibrium node.

The community as defined by Figures 4-7 from equations (4)-(8) has strongly stable predator-prey equilibriums on successive phase planes and therefore has strong, global, stable community equilibria. The system is at equilibrium for a given I and TC and/or C\textsubscript{2} density(ies). In a strongly stable community, the community's time track follows the community equilibrium as the values of the isocline identities change as a function of the community's environment.
COMPETITION

Classical competition theory based on the Lotka-Volterra competition equations has been inadequate in several important respects. It is based solely on the assumption that the system follows a logistic response through time. It does not introduce in any way interrelationships between competition and predator-prey phenomena. It fails to include density-dependent responses of organisms at the population level in the competition response. And finally it does not establish a biological basis for the competition coefficients. Conversely the competing herbivores in the community outlined in Figure 1 are competing for $P_1$ as food and being preyed upon by $C_1$. Isocline analysis provides a qualitative (if $k$ is not defined) and quantitative (if $k$ is defined) method of analysis that permits the interactions of competitors to be explicitly defined in terms of their responses to predators and prey in their environment.

Competition is dimensionalized by adding $H_2$ to the system. $H_1$ and $H_2$ will compete for the same resource ($P_1$) and have the same population of $C_1$ as a predator (Fig. 1). With the population of $H_1$ utilizing $P_1$ as resource, an additional loss term is added in the construction of $P_1$'s gain-loss graph (Fig. 6H). Summing the predatory losses due to $H_2$ density with $P_1$'s loss response at different $H_1$ densities results in a family of $P_1$ loss curves at different $H_2$
densities, each at a given $H_1$ density (not shown). Equilibrium between $H_1$ and $P_1$ is now a function of $I$, $C_1$ and $H_2$. As the $H_2$ density increases, the prey isocline of $P_1$ shifts to the left, each new prey isocline with an $H_2$ density as an identity in addition to $I$ (Fig. 8B). The shifting isoclines are not parallel but shaped as a function of the added loss response due to $H_2$. The predator isocline for $H_1$ shifts downward (Fig. 8B) as competition affects the recruitment or nonpredatory loss rate of $H_1$ (dashed lines, Fig. 7C and 7G).

The equilibrium and stability of the two herbivore species can be examined by constructing the $H_1$-$H_2$ competition phase plane. The herbivore isoclines for $H_1$ and $H_2$ competing for the same $P_1$ at a particular $I$ and $C_1$ density are constructed from the $H_1$-$P_1$ and $H_2$-$P_1$ phase planes by using the plant dimension as the common value at particular $I$'s and $C_1$ densities (Fig. 8A). The $H_1$ isocline has an intercept on the $H_1$ axis which corresponds to its density on the $H_1$-$P_1$ phase plane (Fig. 8B) for a zero $H_2$ density. The $H_2$ isocline is constructed similarly from the $H_2$-$P_1$ phase plane (Fig. 8C). Both isoclines will have $I$ and $C_1$ density as identities. Intersections of isoclines of the two herbivore species will be equilibria. $I$ and $C_1$ as variables create a continuum of $H_1$-$H_2$ equilibria bounded only of the extreme competition isoclines of $H_1$ and $H_2$.

Examination of the competitive ability of populations requires characterization of the gain and loss rates for competitors of different
Figure 8. The family of competition isoclines (A) compares how r selected (H1) and k selected (H2) competitors coexist at different H1, H2, C1 and I from the intersections of the prey isocline and predator isoclines in the P1-H1 (B) and P1-H2 (C) phase planes respectively. The competition isoclines have energy input rate of the prey isocline and carnivore density of the predator isocline as identities. Solid lines denote dh1/dt=0 and broken lines dh2/dt=0 in A. Addition of a competitor (H2) to the system results in a family of prey isoclines and in some cases a family of predator isoclines on the P1-H1 and P1-H2 phase planes each at a different H2 or H1 density respectively. The densities that each herbivore can maintain at a given energy input rate, plant density and carnivore density decrease as the competitor's density increases. When conditions exist such that H1 cannot maintain itself under increasing competition from H2, the predator isoclines no longer have an intercept on the herbivore axis, but intercept the plant's axis at higher and higher densities as H2 density increases (B). When the prey and predator isoclines no longer intersect, H1 can no longer coexist with H2 and the H1 isocline will intercept the H2 axis in A on the H2-P phase plane, H1 shifts the predator and prey isoclines but does not change their stable character because of the r and k nature of H1 and H2 respectively. There is a continuum of competition isoclines due to changing system dimensions which creates a field of equilibrium nodes bounded only by the extreme isoclines. The time tracks converge on the only equilibrium nodes shown.
types. MacArthur and Wilson (1967) and Pianka (1970, 1972) classify populations as r and k strategists on the basis of the relationships between their instantaneous rates of increase and population densities. These relationships characterize their competitive ability at different levels of intra- and inter-specific competition. The impact on the different characteristic rate terms as well as the I and $C_1$ dimensions on the equilibrium and stability of r and k selected herbivores can be analyzed by letting $H_1$ be the r strategist and $H_2$ the k strategist and selecting rate terms accordingly.

A successful competitor or k-selected organism puts a high amount of energy into its individual progeny and produces less of them. The r-selected organism expends less energy on each progeny and produces more. The r strategist has a higher maximum recruitment rate than the k strategist but its recruitment rate will peak and return to zero at a lower population density than the k strategist. A k-selected species, having greater competitive ability, has a non-predatory loss rate much less sensitive to increasing population densities than an r-selected species. Competitors that reduce their resource availability in much the same manner as other members of their own population respond not only to their own density, but also to the density of the competitor.

As $H_1$'s food density and recruitment rate decreases and the nonpredatory loss rate increases due to high densities of $H_2$, $H_1$
cannot compete and will become extinct on the $H_1$-$H_2$ phase plane (Fig. 8A). The predator isocline at some low $C_1$ density (not necessarily zero) and the prey isocline at some low $I$ no longer intersect. As $C_1$ density increases and the population densities of $H_1$ and $H_2$ are reduced, the $r$-selected $H_1$ can coexist with $H_2$. Increasing the $I$ shifts the resource isocline to the right on the $H_2$-$P_1$ phase plane which means that $H_2$ can exist at higher competitor and lower $C_1$ densities. In contrast, $H_2$, the $k$-selected herbivore, is able to survive at all densities of $H_1$ and $C_1$. Predators on one particular trophic level may promote community stability (Hutchinson, 1961; Paine, 1966; Hall, Cooper and Werner, 1970; and Connell, 1971).

Commensalism (+0), the $H_1$-$H_3$ interaction, is another category of species interaction in the environment of the community defined in Figure 1. $H_3$ can have a positive affect on $H_1$ by either increasing its gain rates ($r_{h_1}$ or $g_{h_1}$) and/or decreasing its loss rates ($g_{c_1}/y_{c_1}$ and/or $d_{h_1}$). The $H_1$ isocline (solid line) in Figure 9 would respond to an increased gain rate or lower nonpredatory loss rate by shifting $H_1$ to higher densities in relation to $H_2$. If the commensal interaction decreases the conversion ratio ($g_{h_1}/y_{h_1}$) of plants to $H_1$, then both the $H_1$ and $H_2$ isoclines would shift in the favor of $H_1$'s density. Commensal interrelationships can also be adapted to organisms from other trophic levels. Mutual (++) interactions with the organismic environment could be handled similarly.
Figure 9. The $H_1$-$H_2$ competition isoclines on the $H_1$-$H_2$ phase plane (Fig. 8A) are modified to show the effects of a commensal (+0) interaction between $H_3$ and $H_1$ for low $I$ (A) and high $I$ (B) at 0, 2, and $4k_h$. Solid lines denote $dH_1/dt=0$ and broken lines $dH_2/dt=0$. 
An indirect mutualistic bond also exists between $H_2$ and $H_4$ as shown by the addition of $H_4$ and $P_2$ to the environment of the defined community (Fig. 1). Increase in $H_4$ density lessens the negative effect of $P_2$ on $P_1$ and then increases the production rate of $H_2$. Explicit examination of the $H_2$-$H_4$ interaction would lead to a mutual phase plane constructed similarly to the competition phase plane.
DIVERSITY

The explanation of species diversity has been largely empirical and quite inadequate. A theoretical basis has not been established to dimensionalize species diversity in terms of the way species interact, the energy input rate and the physical, chemical and biological environment. Isocline analysis as developed for a system with perfect competition (system lacks prey switching dimension) can be used as the theoretical basis for qualitative and quantitative analysis of diversity by expanding the competition isocline.

The family of diversity isoclines (Fig. 10A) is parameterized in terms of carnivore predation, energy input rate and the commensal herbivore \( H_3 \). As suggested by the productivity hypothesis (Connell and Orias, 1964; Margelef, 1969), which states that greater production results in greater stability, the diversity index (Fig. 10B) increases with increasing \( I \) which, with all things equal, results in greater production rates (Fig. 6B). The hypothesis that predation increases diversity is illustrated with the upward shifting isoclines to higher levels of diversity as the carnivore density (predation pressures) increases for given \( H_3 \) densities. The amensal relationship between \( C_1 \) and \( C_2 \) decreases the diversity by reducing predation.

Diversity increases with increasing \( H_3 \) densities because the commensal interaction of \( H_1 \) and \( H_3 \) improves the competitive
Figure 10. The family of herbivore diversity isoclines in terms of the herbivores' density (A) and diversity index (B) are parameterized by the energy input rate and the magnitude of carnivore predation. The diversity isoclines in A are determined from the equilibria on the competition phase plane in Figure 9. The diversity index was calculated at equilibria of $H_1, H_2$ and the commensal $H_3$ by assuming $k_{h1} = k_{h2} = k_{h3}$, by the Shannon-Weaver equation, $\sum \frac{H_i}{H} \log \frac{H_i}{H}$ where $H = \sum H_i$. 
performance of $H_1$, the r-selected herbivore.

The addition or omission of species as it occurs in succession can now be added as a new dimension to resource utilization theory. A change in the number of herbivores in the community matrix creates families of isoclines as the addition of $H_3$ did on the diversity phase plane in Figure 10.
CONCLUSIONS

Productivity theory (Brocksen, Davis and Warren, 1970; Warren, 1971) supplied the impetus and direction for the development of a resource utilization theory. This theory postulated that families of density relationships between successive predator and prey relationships along pathways of energy and material transfer are functions of the physical, chemical and biological environment. It further suggested that relationship at one trophic step can be parameterized in terms of variables at previous steps. Therefore the problem has been not so much what to look for but how to get there.

Resource utilization theory as proposed appears to satisfy all of the criteria for the theory of productivity. The density relationships between the predator and prey are families of predator-prey isoclines, the prey isocline being a function of the dimensions that add energy and materials to the community along the pathway to the prey isocline. The predator isocline is a function of the top consumer density in the community and other dimensions that affect the density relationship between predator and prey down to the predator isocline. The intersections of the isoclines in the family of successive predator-prey relationships establish the community equilibrium. The isocline identities as variables generate families of predator and prey
isoclines limited only by their possible existence. Competition, mutualism, amensalism and commensalism are integrally related to predator-prey phenomena and cannot be considered independently.

Community stability theory does not have to be restricted to neighborhood analysis and confining approximations, but can be analyzed anywhere within the framework of the community model. The density dependent processes of species appear to make predator-prey interactions strongly stable. Only after introduction of a more efficient competitor does an instable predator-prey relationship exist. Greater community model complexity does not reduce its strongly stable condition. Introduction of optimal foraging theory as another dimension could provide added stability for populations under competitive stress by switching predation pressures to the other competitor, and in effect providing a refugium for soon-to-be extinct competitors.

The framework may now exist for examining other dimensions of diversity in addition to the supported predation and productivity hypothesis.
BIBLIOGRAPHY


