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## RESOURCES: A GRAPHICAL-MECHANISTIC APPROACH TO COMPETITION AND PREDATION

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In such circumstances the question as to the causes of the victory of certain forms over others presents itself in the following aspect: By aid of what morphological and physiological advantages of the process of the individual does one plant suppress another? [G.F. Gause (1934)].

Traditional models of competition, which form the basis of much of current ecological thought and theory, are nonmechanistic. Competitive interactions are summarized in the negative effects of each species on the growth of all others, with no explicit statement of the causes of such negative effects. This limitation has been recognized since the pioneering work of Lotka (1924), Volterra (1931), and Gause (1934, see above). For instance, Gause (1932), in estimating the coefficients of the Lotka-Volterra equations, had to rely on intuition to predict how amounts of inhibitory substances might affect competition between two yeasts. The competition equations provided no guidance. Although a valid description of competition at steady state (May 1973), the Lotka-Volterra equations are more phenomenological than mechanistic and thus more descriptive than predictive.

Two main approaches have been taken to make competition theory less phenomenological: (1) the use of measures of resource utilization overlap to estimate the parameters of the Lotka-Volterra equations, and (2) the formulation of models that explicitly state the mechanisms of competition between species. The resource utilization overlap estimate of competition coefficients (e.g., Horn 1966; MacArthur and Levins 1967; Colwell and Futuyma 1971; Schoener 1974) has been hampered by lack of a strong theoretical basis for making such estimates, as May (1975) noted. On the other hand, mechanistic models of resource competition require knowledge of the mechanisms of resource acquisition and utilization by particular species. MacArthur (1972) warned that because such models would have to be designed to fit each species, they would lack the generality that was the strength of the classical approach. A comparison of several such models reveals almost as many approaches as there are workers, as shown, for example, by the models of predation by Holling (1959, 1965, 1966), Murdoch (1969), Canale (1969,

1970), Real (1977), Levin et al. (1977), and Chao et al. (1977), or the models of competition by MacArthur (1972), Maguire (1973), Stewart and Levin (1973), Peterson (1975), Taylor and Williams (1975), Hsu et al. (1977), and Tilman (1977).

All these models share two elements. The first is an emphasis on consumer-resource interactions. The second is an acknowledgment that there are different categories of both consumers and resources. In this paper I first offer a way to classify resources and consumers. The classification is an extension of microeconomic theory, which was introduced to ecology by Rapport (1971) and Covich (1972), and which has been employed in the papers of Covich (1974), Leon and Tumpson (1975), and Rapport and Turner (1975, 1977). The shape of the resource-dependent growth isocline of a species is used to classify resources as either (1) essential, (2) substitutable, or (3) hemi-essential. Essential resources are further classified as being either interactive or noninteractive. Substitutable resources are classified as being either complementary, perfectly substitutable, antagonistic, or switching.

I then derive a simple graphical technique that allows prediction of the outcomes of consumer-resource interactions when numerous species compete for two resources. The approach requires information on (1) resource class, (2) resource consumption rates (resource preferences), (3) resource supply rates, and (4) species-specific mortality rates. The approach is used to explore the qualitative patterns of species dominance and coexistence that can result from competition between several species for two resources. The analysis suggests that the type of resource for which competition occurs may greatly influence the patterns of species diversity in communities.

This is not meant to be a complete or exhaustive treatment of resource-based approaches to population and community ecology. I present these ideas partly to demonstrate the importance of knowing the type of resource for which competition occurs and to show the range of questions which can be addressed with a simple, graphical mechanistic theory of interspecific interaction. I stress the applicability of this work to both competition and predation because predator-prey interactions are a subset of consumer-resource interactions. Although a living prey is a more complex resource than an inorganic nutrient, the central interaction between several predators and several prey may be expressed in the terminology of the consumer-resource approach. I limit the mathematics presented in the main text to algebra and graphical techniques. More thorough treatments of specific cases may be found in the Appendix of this paper, and in Taylor and Williams (1975), Leon and Tumpson (1975), and Maguire (1973). Although I consider only two resources at a time, the approach is easily extended to any number of resources.

#### WHAT ARE RESOURCES?

If only one factor were to be considered, the answer to the question "What is a resource?" would be straightforward. A resource is a factor which, through some range of availabilities, leads to higher population growth rates as its availability is increased and which is consumed, in the broad sense, by the population.

If several factors are considered, the question is more difficult. The availability of one factor may influence the growth response of a population to a second factor. There may be some ranges of availability of one factor for which changes in the availability of a second factor do not lead to changes in a population's growth rate. However, I contend that it is useful to consider two factors to be resources if each meets the definition offered above for some availability of the other factor. The dependence of population growth on the joint availability of two resources is the basis for a pairwise classification of resources.

Consider a set of generalized equations:

$$\begin{aligned}\frac{dN_i}{N_i dt} &= f_i(R_1, R_2, \dots, R_k) - m_i, \quad \text{and} \\ \frac{dR_j}{dt} &= g_j(R_j) - \sum_{i=1}^n N_i f_i(R_1, \dots, R_k) h_{ij}(R_1, \dots, R_k),\end{aligned}\tag{1}$$

where  $N_i$  is the population density of species  $i$ ;  $R_j$  is the availability of resource  $j$ ;  $m_i$  is the mortality rate of species  $i$ ;  $f_i$  is the functional relationship between the availabilities of all resources and the per capita rate of population change for species  $i$ ;  $g_j$  is the function describing the supply rate of resource  $j$ ;  $h_{ij}$  is the function describing the amount of resource  $j$  required to produce each new individual of species  $i$ ; for a total of  $n$  species competing for  $k$  resources.

These equations show that the dynamics of consumer-resource interactions depend on the functions describing resource-dependent growth, resource supply, resource consumption, and on the mortality rate experienced by each species.

These equations embody two critical assumptions. First, they assume that species interact only through their use of resources. For all cases considered,  $\partial f_i / \partial N_j = 0$  for all  $i$  and  $j$ . If any of these partial derivatives were not zero, it would indicate direct interaction either within or between species, rather than pure resource competition. Secondly, these equations assume that resources are not interactive, i.e., that  $(\partial g_i / \partial R_j)^* = 0$  for  $i \neq j$ , where the asterisk means the function is to be evaluated at equilibrium. This latter assumption is valid for many types of resources, but may be invalid for resources which are themselves interacting organisms (Lynch 1978) if their mechanism of interaction is not directly included in the model.

The function  $f_i(R_1, R_2)$  is the basis for a pairwise classification of resources. I class as essential those pairs of resources for which  $f_i(R_1 = 0, R_2) \leq 0$  for all  $R_2$  and  $f_i(R_1, R_2 = 0) \leq 0$  for all  $R_1$ . Essential resources are both required for growth, with no growth possible if either one is lacking. This is easily illustrated in the  $R_1, R_2$  resource quarter plane (fig. 1) by showing the locus of points of  $R_1$  and  $R_2$  for which the consumer has a given value of  $f_i(R_1, R_2)$ , i.e., a given reproductive rate. The curves of figure 1 are the values of  $R_1$  and  $R_2$  for which  $f_i(R_1, R_2) = \gamma$ , and may be called the  $\gamma$ -growth isolines. Note that  $\gamma$  is the rate of reproduction in the absence of mortality ( $m_i$ ). Essential resources have isolines which never intersect either the  $R_1$  or  $R_2$  axis, as their definition demands. Assuming that neither resource is inhibitory at high availabilities, these isolines can have one of two shapes. They may form a perfect right-angle corner (fig. 1A), in which case I call

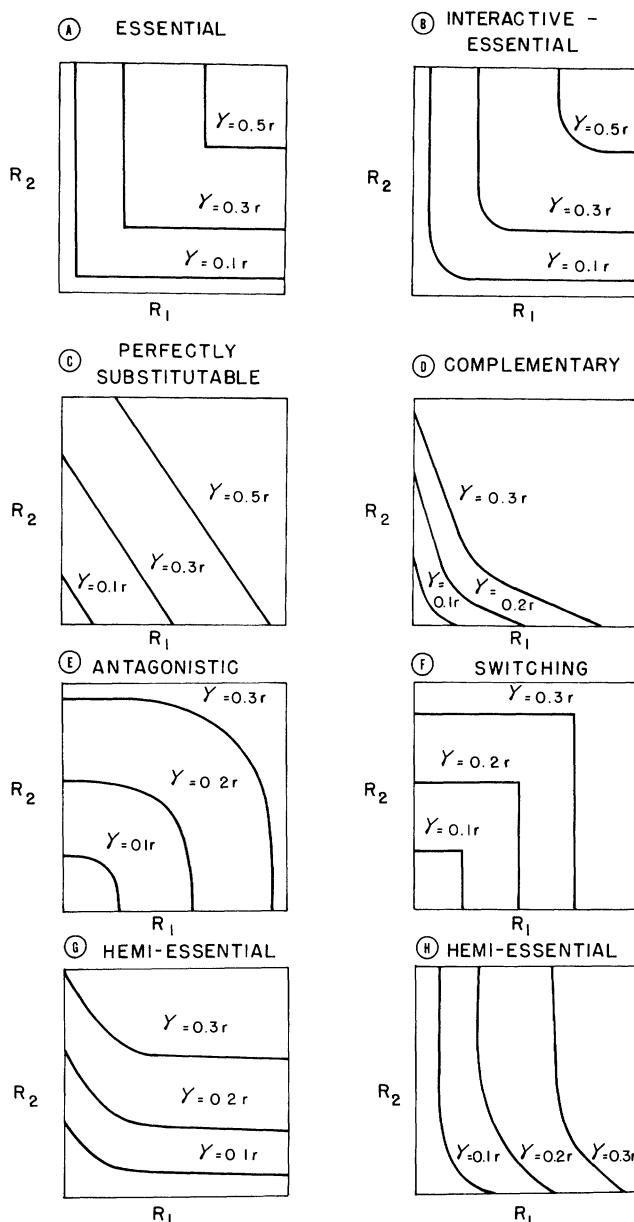


FIG. 1.—Growth isoclines for different classes of resources. The curves of each figure show amounts of two resources ( $R_1$  and  $R_2$ ) that a species requires in order to have the specified per capita reproductive rate ( $\gamma$ ). In all cases shown, increases in one or both resources will lead to increases in growth rate, up to the maximal rate  $r$ . Cases C, D, E, and F illustrate the four types of substitutable resources. See text.

them noninteractive essential resources, or they may have a rounded corner (fig. 1B), in which case I call them interactive essential resources.

I class as substitutable those resources for which  $f_i(R_1 = 0, R_2) > 0$  for some  $R_2$  and for which  $f_i(R_1, R_2 = 0) > 0$  for some  $R_1$ . They are substitutable for each other because each can sustain reproduction when the other is lacking. Their  $\gamma$ -growth isoclines will intersect both axes, as shown (fig. 1C, 1D, 1E, 1F). If the isoclines form a straight line (fig. 1C), the resources are perfectly substitutable. If the isoclines bow in toward the origin (fig. 1D), they are complementary. If they bow away from the origin (fig. 1F), they are antagonistic, with a right angle curve representing perfectly antagonistic resources (fig. 1F), which I term switching.

I class as hemi-essential those pairs of resources for which  $f_i(R_1 = 0, R_2) \leq 0$  for all  $R_2$  but for which  $f_i(R_1, R_2 = 0) > 0$  for some  $R_1$ . A pair of resources are hemi-essential if one resource is required for and can sustain reproduction on its own, and the second resource can partially substitute for the first, but is not in itself capable of sustaining growth in the absence of the first element. They are a pair, one of whose members is required or essential—hence, the term hemi-essential. If a pair of resources are hemi-essential, the  $\gamma$ -growth isoclines will intersect the axis of the nutritionally complete resource and will not touch the other axis. The nutritionally complete resource in figure 1G is  $R_2$ , and  $R_1$  is the nutritionally complete resource in figure 1H.

I have presented these classifications of resources with little biological justification. I will now discuss each type in more depth, suggest what resources will fall into each category, justify the categories nutritionally and ecologically, and suggest some expressions for  $f_i(R_1, R_2)$ . Although the resource consumption preferences of a species should be closely related to the shape of its growth isoclines (Rapport 1971), I do not explore this question in this paper. Rather, assumptions about consumption preferences for each class of resource are presented with brief justification because such assumptions are not important in the analysis of resource competition.

### *Essential Resources*

All organisms require an energy source and various forms of N, P, C, O, H, S, Fe, etc., in order to live. Autotrophs most often obtain these elements separately from their environment. Heterotrophs, being direct or indirect consumers of autotrophs, obtain several basic nutritional elements in the same food item. For this reason it is likely that the majority of resources potentially limiting to autotrophic plants will be essential, whereas those limiting heterotrophs are more likely hemi-essential or substitutable. The resources that I call essential were termed “perfectly complementary” by Leon and Tumpson (1975). Because complementarity is a property of substitutable resources, I prefer to call these essential resources, emphasizing the growth requirement for both. This terminology is consistent with that used in plant and animal nutrition.

Numerous studies have demonstrated that inorganic plant nutrients are essential (see any introductory plant physiology text, such as Salisbury and Ross 1969). A few recent experiments have indicated that plant nutrients may be noninteractive essential resources. Droop (1973) proposed that essential resources should be

multiplicative, a special type of interactive essential resource. Droop (1974) tested this hypothesis using a marine alga, grown with vitamin B-12 and phosphate as limiting nutrients, and found that his results fit the noninteractive model better than the interactive model. Rhee (1978) similarly demonstrated that phosphate and nitrate are noninteractive essential resources for a freshwater green alga. Because the available experimental evidence indicates that plant nutrients are noninteractive essential resources, I shall consider only this category for the rest of this paper, and shall call noninteractive essential resources simply "essential resources." However, as Taylor and Williams (1975) noted, this distinction is of slight ecological importance.

Not all pairs of plant nutrients will be essential with respect to each other. Consider  $N_2$ ,  $NO_2^{-2}$ ,  $NO_3^{-1}$ ,  $NO_4^{+1}$ —four forms of nitrogen each of which can be used by some plants as the sole source of nitrogen, and  $PO_4^{-3}$ .  $PO_4^{-3}$  is essential relative to  $NO_2^{-2}$  or  $NO_3^{-1}$  or  $NH_4^+$ , but these forms of nitrogen may be substitutable relative to each other.  $N_2$  can only be used as a nitrogen source by nitrogen-fixing organisms. Because of the high energetic cost of reducing atmospheric  $N_2$  and because of the need to induce specialized systems to do this, it might be that  $N_2$  will be found to be antagonistic or even switching relative to the reduced forms of nitrogen which may be used by nitrogen-fixing organisms. Thus, not all pairs of plant nutrients are likely to be essential resources. All usable forms of nitrogen-containing compounds are likely to be essential relative to all usable forms of phosphorus-containing compounds. Such considerations allow the pairwise definitions offered here to be extended to groups of resources.

For a pair of essential resources, the growth rate of a species will be determined by either one or the other resource, whichever is more limiting. The region of values of  $R_1$  and  $R_2$  in which a species is limited by one or the other resource is defined by a curve from the origin through the corners of all the growth isoclines (fig. 2A). The slope of this curve at any particular growth rate is the ratio of resources which is required for growth at that rate. This curve of optimum proportion of the two resources may bend as shown or be a straight line.

At a particular growth rate, the consumption rate of  $R_1$  and  $R_2$  might be proportional to the tangent to this curve at that growth rate. This is to say, resources might be consumed in the proportion they are required for steady-state growth. If one resource were consumed in excess of this proportion, there would be no gain in current growth rate (unless excess consumption were detrimental to a competitor or resource availability fluctuated), and there might be a loss if such excess consumption had a reproductive cost. However, resource consumption and growth isoclines cannot be considered independently. As will be discussed, a change in consumption may affect both the position and shape of the growth isoclines. For this presentation I assume consumption of essential resources is proportional to requirement. Such instantaneous rates of consumption are shown with vectors in figure 2A.

As Leon and Tumpson (1975) noted, and as used by Tilman (1977), essential resources may be easily modeled. In the absence of mortality, the growth relationship is

$$\frac{dN_i}{N_i dt} = \min_{j=1,k} [f_i(R_j)]. \quad (2)$$

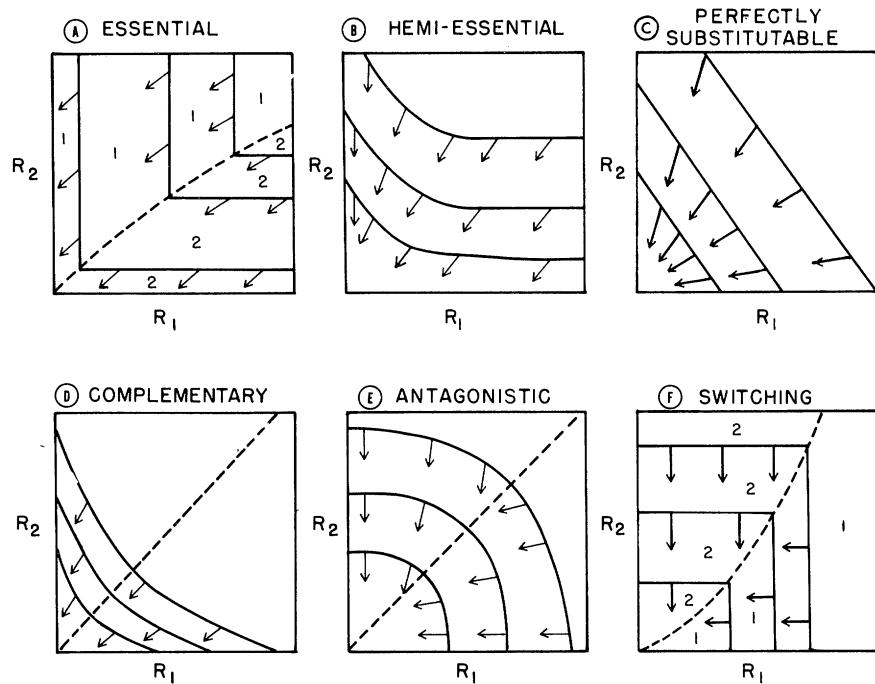


FIG. 2.—Consumption vectors. The vectors shown represent the proportion of  $R_1$  and  $R_2$  consumed by a species at a particular growth rate. The slope of each vector is the rate of  $R_2$  consumption divided by the rate of  $R_1$  consumption. The length of each vector can symbolize the per capita rate of resource consumption, but no biological significance should be attached to the lengths of the consumption vectors in this figure.

The form of  $f_i(R_j)$  for all resources defines the shape of the optimal proportion line and the placement of the  $\gamma$ -growth isoclines. Experimental work to date indicates that  $f_i(R_j)$  has the shape of the Monod function (Monod 1950; e.g., Tilman and Kilham 1976) or the type I, II, III curves of Holling (1959). High levels of some resources may inhibit growth, in which case the growth isoclines may form closed curves (Maguire 1973).

#### *Hemi-essential Resources*

A pair of resources will be hemi-essential if one is nutritionally complete and the other lacks some nutritional element or elements available in relative excess in the first resource.

For an herbivore, some fruits may be hemi-essential relative to foods such as seeds. Many fruits are rich in carbohydrates, fats, or oils, but lack one or more nutritionally required amino acids. No reproduction would be possible on a long-term diet of only such fruit. However, the caloric content of the fruit would allow it to supplement a diet of other foods which were relatively rich in protein, as are many seeds and animals.

The rate of consumption of two hemi-essential foods should depend on their absolute availabilities and on the extent of hemi-essential complementarity. In figure 2B, I show with vectors a guess as to how an optimally foraging organism might consume two such resources. In the absence of  $R_1$  (the incomplete food) the diet would be totally  $R_2$ , since  $R_2$  by itself can sustain growth. As more  $R_1$  is available,  $R_1$  would increase in the diet in some compromise between at least two factors: (1) consumption in proportion to abundance or ease of capture; (2) consumption in the proportion that gives maximal use of the two foods. For very high availabilities of  $R_1$ ,  $R_1$  and  $R_2$  would be consumed purely in that proportion which leads to equal limitation by the nutritional elements which complement each other.

#### *Substitutable Resources*

Resource items that can each support growth on their own are substitutable relative to each other. Most of the dietary items of herbivores and carnivores are probably substitutable. Substitutability only defines the end points of the growth isoclines, stating that all growth isoclines must touch both the  $R_1$  and  $R_2$  axes. The shape of the curve joining these two points is the basis for the definition of types of substitutable resources.

*Perfectly substitutable resources.*—Two resources are perfectly substitutable if the two can be substituted for each other with equal effect at all abundances of the two resources. This would mean that an amount of resource 2,  $R_2$ , would be equivalent to an amount of  $C_1R_1$  of resource 1, for all values of  $R_2$ , with  $C_1$  a constant (i.e.,  $R_2 = C_1R_1$  and  $R_1 = R_2/C_1$ ). Thus,  $f_i(R_1, R_2) = f_i(R_1 + R_2/C_1, 0) = f_i(0, R_2 + C_1R_1)$  for all values of  $R_1$  and  $R_2$ . Considering the nutritional complexity of most foods, I doubt if many foods would be perfectly substitutable for each other. However, this often may be a useful approximation.

For a homogeneous environment in which the chance of an encounter between a consumer and a resource is proportional to the abundance of the resource, assuming that the consumer is not limited by various components of handling time, consumption should be proportional to the abundance of the resources. This is shown with the vectors in figure 2C. Such vectors always point toward the origin. It is easy to devise situations for which this would not be the case (Rapport 1971), but for brevity I will not consider them in this paper.

Growth isoclines and consumption vectors are intimately related to each other. For instance, even if two resources were nutritionally perfectly substitutable, a growth isocline would only be a straight line if the resources were consumed in particular proportions. To illustrate this with an extreme case, consider the growth isocline of a species that did not consume any of one resource until its availability exceeded a certain limit. Such an isocline could not be a straight line. Optimal foraging in homogeneous environments may give straight-line growth isoclines for nutritionally perfectly substitutable resources, but would not give such straight isoclines in a heterogeneous environment, as will be discussed shortly.

*Complementary resources.*—Two resources, each containing different propor-

tions of two nutritionally essential elements, may, when consumed together, give a higher growth rate than predicted for a linearly weighted sum. Such complementarity has been noted for many foods of herbivores, and has been the subject of much research for both livestock and humans. For instance, humans eating certain types of beans with rice can increase the usable protein content of their food 40% over the sum of the usable protein of beans and rice eaten separately because beans are rich in lysine, an essential amino acid in low abundance in rice; rice is rich in sulfur-containing amino acids, which are relatively lacking in beans (Lappé 1971). Such nutritional complementarity occurs only if two foods are consumed within a short time of each other, an important restraint on optimization of diet.

If two resources are complementary, there will be a proportion which leads to maximal complementarity at any growth rate. This is shown with a dotted line in figure 2D. The vectors of figure 2D show a compromise between consumption equal to optimal proportion and consumption proportional to abundance or ease of capture.

*Antagonistic resources.*—Antagonistic resources are nutritionally substitutable, but have growth isolines which bow away from the origin (figs. 2E, 2F). This means that, when these resources are consumed together, an organism requires more than the linearly weighted total in order to attain a given reproductive rate. Such a phenomenon could be caused by synergistic effects of toxic compounds. For instance, Janzen et al. (1977) demonstrated that nonprotein amino acids, such as D,L-pipecolic acid and djenkolic acid, had no significant effect on growth of a bruchid beetle if they were consumed separately, but had a significant synergistic effect if consumed together. Thus, if one seed contained D,L-pipecolic acid and another djenkolic acid, less growth might be possible from consumption of the two seeds than from a linearly weighted consumption of either the one seed or the other. Janzen et al. (1977) noted several other cases of synergism which could lead to antagonistic resources. Although it is dangerous to argue by analogy, the known synergisms of various drugs (many being secondary plant compounds) used in human medicine suggest that nutritional antagonisms may occur. However, spatial heterogeneity may be a more likely cause of resource antagonism, as will be discussed shortly.

If two resources are antagonistic, a diet biased toward mainly one or the other, i.e., specialization, would seem beneficial. Intermediate combinations would lead to greater antagonistic effects, requiring greater absolute food consumption to achieve the same per capita reproductive rate. Given certain availabilities of two resources, each of which would lead to a particular reproductive rate if consumed alone, the diet should mainly consist of the one resource that would lead to the greater reproductive rate. Inclusion of the other resource might depend on the ease with which it would be obtained and the magnitude of the antagonistic effect. The actual tradeoffs involved, and the time scale over which they are operative, are important questions, but outside the realm of this paper. Figure 2E shows one such set of consumption vectors for antagonistic resources. The broken line represents the proportion of the two resources that leads to maximal antagonism

at particular growth rates. Above the broken line, in region 2, the diet should heavily favor  $R_2$ ; below it, in region 1, the diet should be biased toward  $R_1$ .

*Switching resources.*—The greater the antagonistic effect for two resources, the greater is the extent of bowing of the growth isoclines with respect to the origin. I define two resources as perfectly antagonistic (switching) if the growth isoclines form a right angle (fig. 2F). Switching resources are easily modeled. For the case with no mortality,

$$\frac{dN_i}{N_i dt} = \max_{j=1,k} [f_i(R_j)]. \quad (3)$$

For switching resources, growth rate is determined solely by the availability of the one resource which leads to the largest reproductive rate.

The broken line of figure 2F indicates the proportion of  $R_1$  and  $R_2$  at which both resources lead to the same reproductive rate. Above this line, in the area labeled 2, only  $R_2$  would be consumed, because  $R_2$  leads to the higher growth rate. In region 1, only  $R_1$  would be consumed. These consumption vectors are shown. The consumer switches from specializing on one resource to specializing on the other resource as the availabilities of the two resources change. Using the terminology of Murdoch (1969), all antagonistic resources are consumed in a switching manner. For this paper I prefer to use switching to mean perfect switching, in which the diet in any small period of time is composed of only one or the other resource.

Even in the absence of nutritional antagonism, selection for optimal foraging may lead to near perfect switching. Consider a species foraging for two resources which are nutritionally perfectly substitutable, but which occur in a spatially heterogeneous environment. If each resource occurs in a pure patch, a consumer will be able to forage for only one of the resources within any small period of time. An optimal forager might choose to forage in the patch with resource availability that led to the higher net reproductive rate. The net reproductive rate could include patch to patch differences in probabilities of mortality. When patches of this resource were depleted, it would switch to the patches of the other resource. Such behavior is embodied in the growth isoclines and consumption vectors given for switching resources. Foraging behavior approaching this and relevant theory has been reported by Murdoch (1969, 1971), Murdoch and Marks (1973), and Murdoch et al. (1975).

Similarly, if different behavioral or physiological traits are required to forage for or process different resources, a species may respond to the resources in a switching manner. Heinrich (1976a, 1976b) has documented such switching behavior (majoring and minoring) for individual bumblebees. The phenomenon of sequential utilization of sugars (diauxy) by bacteria is also a form of switching, caused by the need for different enzymes to use each sugar.

Switching resources illustrate the interdependence of growth isoclines and consumption vectors. Specific rates of resource consumption lead to specific growth isoclines. Other consumption vectors would lead to other positions or shapes for growth isoclines. For instance, if resources were nutritionally perfectly substitutable, and were distributed in a heterogeneous way in the environment, an

organism that consumed them in proportion to their abundance (traveling from patch to patch to do so) would have a straight-line growth isocline. If such movement had a reproductive cost, the species' growth isocline would be always outside the growth isocline of a switching individual. As will be shown, such an individual would be at a competitive disadvantage with respect to the switcher.

These categorizations of resources are offered as a starting point for research. Experimental determinations of the relationships between resource type and the consumption characteristics of various species are definitely needed.

#### CONSUMER-RESOURCE INTERACTIONS

A major purpose of this paper is to explore how resource type may influence interspecific interactions. I limit this discussion to interactions between no more than five consumers of two resources. It could be easily extended to include more resources and more consumers. Cases in which two consumers respond to the resources in the same way are considered first, then cases in which two resources are of one type to one species and of another type to a second species are considered, and finally cases in which three or more species compete for two resources are discussed.

As the generalized equations offered at the beginning of this paper imply, four pieces of information are needed to predict the equilibrium outcome of interspecific resource competition: (1) resource supply rates; (2) mortality rates; (3) consumption rates; and (4) growth responses. The growth response of each species is represented by its growth isoclines. The growth isocline at which reproductive rate is equal to mortality rate is the one at which  $dN/dt = 0$ , and is called the zero net growth isocline, or ZNGI.

For graphical purposes, I assume that the resource supply process,  $g_j(R_j)$ , is equable, *sensu* Stewart and Levin (1973). This implies that, in the absence of consumption,

$$\frac{dR_1}{dt} = a_1(_0R_1 - R_1) \quad \text{and that} \quad \frac{dR_2}{dt} = a_2(_0R_2 - R_2).$$

Here,  $_0R_1$  and  $_0R_2$  are the maximal amounts of resource 1 and 2 that can exist in the environment, analogous to a carrying capacity. I assume that  $a_1 = a_2 = a$ , i.e., that the rate of return toward  $_0R_1$  and  $_0R_2$  is the same for both resources.

Graphically this assumption is shown in figure 3. A given point in the resource plane,  $(_0R_1, _0R_2)$ , represents the maximal possible amounts of  $R_1$  and  $R_2$  that can occur in the environment at steady state. It is called a resource supply point. If the environment were perturbed to levels of  $R_1$  and  $R_2$  greater or less than  $_0R_1$  and  $_0R_2$ , respectively, it would tend to return toward  $_0R_1$  and  $_0R_2$ . The rate of return would be proportional to the magnitude of the deviation from  $(_0R_1, _0R_2)$ . Consider point  $A$ , which represents a particular resource supply point,  $(_0R_1, _0R_2)$ . If the actual availabilities of these resources were at the point  $A'$ , then the rate of supply of resource 1 would be  $dR_1/dt = a(_0R_1 - R'_1)$  and the rate of supply of resource 2 would be  $dR_2/dt = a(_0R_2 - R'_2)$ . These are shown as vectors drawn with a broken line. The total resource supply vector is  $\vec{U} = a[(_0R_1 - R_1), (_0R_2 - R_2)]$ . The

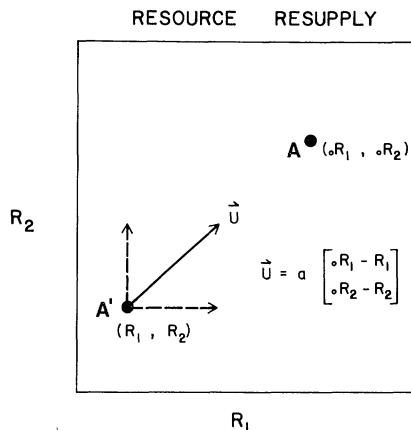


FIG. 3.—Resource supply function. For the graphical treatment presented in this paper, it is assumed that the rate of supply of a resource is proportional to the deviation of the ambient resource level,  $R_1$  and  $R_2$ , away from the maximal amounts of these resources in the environment,  $oR_1$  and  $oR_2$ . The resource supply vector is thus a vector that points from the ambient resource point,  $A'$ ,  $(R_1, R_2)$ , to the resource supply point,  $A$ ,  $(oR_1, oR_2)$ , with a magnitude proportional to the deviation. This vector is labeled  $\vec{U}$ , and its two component parts, the supply rates of  $R_1$  and  $R_2$ , are shown with broken arrows.

magnitude of this vector is proportional to the deviation from the resource supply point. Because I assume that the supply rate constants of the two resources are identical, i.e.,  $a_1 = a_2$ , supply vectors always point toward the supply point. Each point in the  $R_1, R_2$  quarter plane can thus be considered to represent a unique resource supply point. Using this notation, it is possible to ascertain what resource supply points lead to dominance or coexistence of consumers. As any given habitat has specific resource supply process, all such habitats are included in the  $R_1, R_2$  quarter plane.

The interactions between one consumer and two resources can now be considered. All cases assume consumption vectors as in figure 2. For a consumer experiencing a given mortality rate, there will be a particular combination of availabilities of the resources at which a species has a reproductive rate equal to its mortality rate. These zero net growth isolines (ZNGI) for three such cases are shown in figure 4. Any habitat which has a resource supply point,  $(oR_1, oR_2)$ , that falls inside the ZNGI will provide insufficient resources to maintain a stable population. Resource supply points which are outside the ZNGI lead to a positive population size for the consumer. Resources will be consumed in increasing quantities as the population grows. Eventually a population size will be reached at which total resource consumption by the population is equal to the resource supply rate, and at which mortality equals resource-dependent population growth (fig. 4). This steady state will be a point on the ZNGI at which the population consumption vector is opposite in direction, but equal in magnitude, to the supply vector.

For any  $(oR_1, oR_2)$  outside the ZNGI, the resource equilibrium for essential

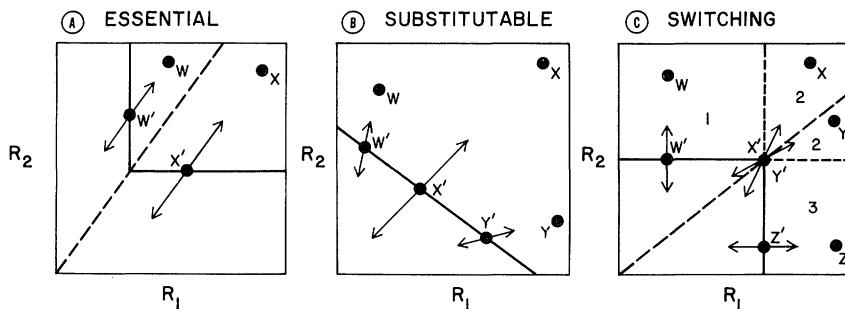


FIG. 4.—One species–two resource equilibrium. For each section of this figure, each point labeled with a nonprimed letter represents a supply point. Each primed point represents the equilibrium point for a species consuming these two resources. The vector pointing in the general direction of the origin is the total rate of consumption of the resources by the species, and the vector pointing toward the supply point is the supply vector. The equilibrium point always falls on the ZNGI, the isocline along which per capita reproductive rate equals per capita mortality rate.

resources (fig. 4A) will occur at the point at which a line through  $(_0R_1, _0R_2)$  and parallel to the consumption vector intersects the ZNGI. For a habitat with resource supply point  $W$ , for instance, the equilibrium will occur at point  $W'$ , at which point the consumption vector is opposite in direction from the supply vector. Population density will change until the total consumption rate equals the supply rate. Similarly, supply point  $X$  leads to an equilibrium at  $X'$ . Above the broken line, the species is limited by  $R_1$ ; below it, by  $R_2$ . Supply points inside the ZNGI lead to extinction.

For perfectly substitutable resources, with consumption proportional to abundance, the consumption vector points toward the origin. The equilibrium point occurs where a line running through the origin and  $(_0R_1, _0R_2)$  intersects the ZNGI. Figure 4B shows three such cases, for three different supply points.

For switching resources, three regions of the resource plane (fig. 4C) must be considered. A supply point in region 1 leads to an equilibrium on the ZNGI at the point at which a line through  $(_0R_1, _0R_2)$ , parallel to the  $R_2$  axis, intersects the ZNGI (points  $W$  and  $W'$ ). The equilibrium point is similarly determined in region 3 (points  $Z$  and  $Z'$ ). Any  $(_0R_1, _0R_2)$  in region 2 leads to an equilibrium at the kink in the ZNGI. For supply points in this region, the consumer switches from one resource to the other, consuming the one resource which leads to higher growth rate. The long-term net effect is an average consumption vector that is equal in magnitude and opposite in direction to the supply vector from the kink in the ZNGI. For two points in region 2,  $X$  and  $Y$ , the two consumption vectors are shown, as are the supply vectors.

#### *Interspecific Competition*

This graphical resource theory is easily extended to two species competing for two resources. If the ZNGI of the two species do not touch or cross, no two

species equilibrium is possible, and one species should be competitively dominant, completely displacing the other from all habitats in which either species can survive (see fig. 6). Every point in the resource plane at which the ZNGI of two species touch or cross is a resource equilibrium point at which both species can potentially coexist. It is necessary to determine (1) if an equilibrium point is locally stable and (2) what set of resource supply points ( ${}_0R_1$ ,  ${}_0R_2$ ) could lead to that equilibrium point.

For the general case of two species competing for two resources (fig. 5) in which the ZNGI do cross, let the equilibrium point be  $(R_1^*, R_2^*)$ . There are two distinct ways that the ZNGI and consumption vectors of two species may fall relative to each other (without regard to the labeling of the species) at the resource equilibrium point, as inspection of figure 5A and B demonstrates. For both cases of figure 5, the ZNGI of species A is more horizontal than the ZNGI of species B. In figure 5A, the consumption vectors of species A and B are consistent with the assumptions embodied in figure 2. In figure 5B the consumption vectors have been reversed.

For figure 5A, the ZNGI relationship implies that, compared to species B, the growth rate of species A is limited more by  $R_2$ , than by  $R_1$ . Comparably, it means that, compared to species A, the growth rate of species B is limited more by  $R_1$  than by  $R_2$ . The consumption vectors of figure 5A mean that, compared to each other, species A consumes relatively more  $R_2$  and that species B consumes relatively more  $R_1$ . Thus, for the case of figure 5A, each species consumes proportionately more of the resource that more limits its own growth rate. The linear stability analysis in the Appendix demonstrates that this case is locally stable no matter what class of resources is involved.

The equilibrium point of figure 5B is locally unstable. The only difference between figure 5A and 5B is the change in the consumption vectors. At the resource equilibrium point of figure 5B, each species consumes relatively more of the resource which less limits its own growth rate. Compared to species B, species A is more limited by  $R_2$ ; but compared to species B, it consumes relatively more  $R_1$ .

As is demonstrated in the Appendix, there are two necessary conditions for a stable two-species equilibrium. These conditions apply to competition for any two resources, and may be considered a generalization of the criterion presented by Leon and Tumpson (1975) for perfectly substitutable and essential resources. These two conditions are stated in the rigorous language of partial derivatives in the Appendix. For a two-species—two-resource equilibrium point to be locally stable, it is necessary that the following conditions hold.

**CONDITION A.** For two species to stably coexist on two resources, each species must, relative to the other species, consume proportionately more of the one resource which more limits its own growth rate.

**CONDITION B.** The amounts of each resource consumed by individuals of each species may change only slightly in response to small changes in the availability of each resource.

Given that an equilibrium point is stable, it is possible to ascertain what particular resource supply points will lead to the equilibrium, i.e., what set of  $({}_0R_1$ ,

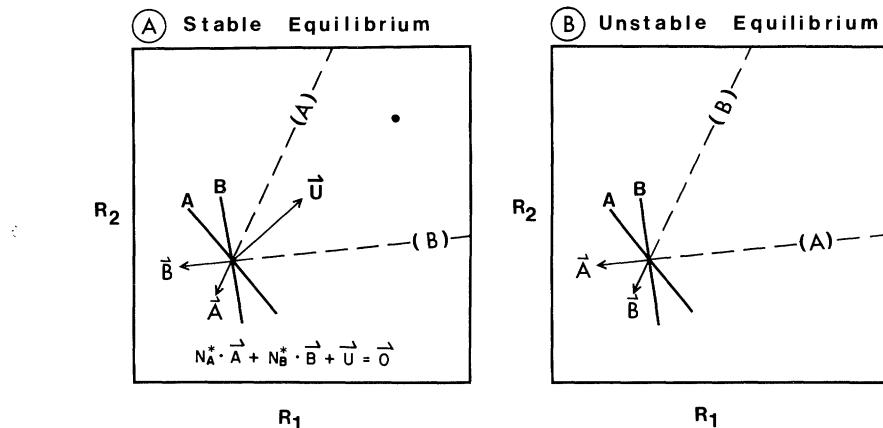


FIG. 5.—Stable and unstable equilibrium points. For both parts of this figure, the two heavy lines through the equilibrium point,  $(R_1^*, R_2^*)$ , are the zero net growth isoclines (ZNGI) for species A and species B. The vectors  $\vec{A}$  and  $\vec{B}$  are the consumption vectors for species A and B, and the vector  $\vec{U}$  is the supply vector for the supply point,  $(_0R_1, _0R_2)$ . For part (A) of this figure, the equilibrium point is locally stable (see text and Appendix for details). Any habitat with a supply point within the region bounded by the two broken lines will eventually lead to this equilibrium point. The vector equation describes the density of species A ( $N_A^*$ ) and species B ( $N_B^*$ ) at steady state. At steady state, the total consumption rate of  $R_1$  and  $R_2$  equals the supply rate. For part (B), the ZNGI of the two species are the same, but the consumption vectors are reversed. This equilibrium point is unstable. Any supply points within the region bounded by the broken lines would lead to one or the other species being competitively dominant, with the outcome dependent on initial conditions.

$_0R_2$ ) will result in coexistence or dominance of one or the other species. For ease of mathematics, I will translate the origin to  $(R_1^*, R_2^*)$ . To do this, let  $S_1 = _0R_1 - R_1^*$  and  $S_2 = _0R_2 - R_2^*$ . Let  $C_{A1}$  and  $C_{A2}$  be the steady state per capita consumption rates of  $R_1$  and  $R_2$  for individuals of species A. Thus,  $C_{A2}/C_{A1}$  is the slope of the consumption vector for species A. Let  $C_{B1}$  and  $C_{B2}$  be similarly defined for species B. With  $N_A^*$  and  $N_B^*$  the steady-state population sizes for species A and B, respectively,

$$a \begin{bmatrix} S_1 \\ S_2 \end{bmatrix} - N_A^* \begin{bmatrix} C_{A1} \\ C_{A2} \end{bmatrix} - N_B^* \begin{bmatrix} C_{B1} \\ C_{B2} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix},$$

at equilibrium, where  $C_{ij}$  is positive for all  $i, j$ . Solving these equations for  $N_A^* > 0$  and  $N_B^* > 0$  for the case of figure 5A (and case 3 of fig. 6) gives

$$\frac{C_{A2}}{C_{A1}} > \frac{S_2}{S_1} > \frac{C_{B2}}{C_{B1}}.$$

This is easily interpreted graphically. The resource supply points that lead to coexistence (i.e., to  $N_A^* > 0$  and  $N_B^* > 0$ ) must fall within the region bounded by the broken lines through  $(R_1^*, R_2^*)$  on figure 5A. Each of these two broken lines goes through the equilibrium point and has the slope of the consumption vector of each species. Any resource supply points,  $(_0R_1, _0R_2)$ , outside this region will lead to one

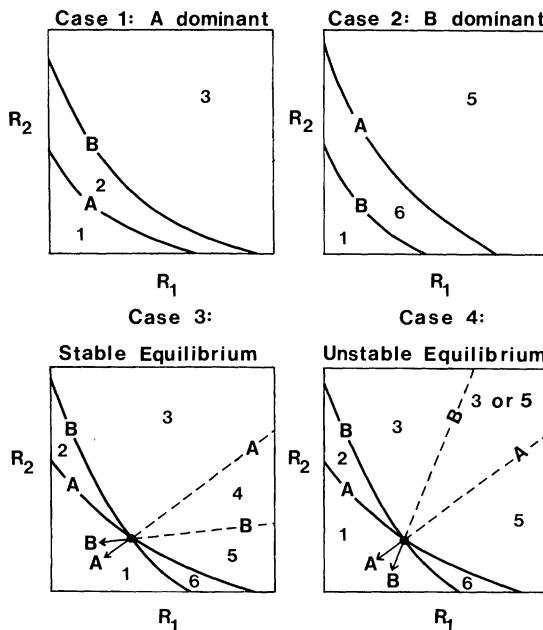


FIG. 6.—The four cases of resource competition. These four cases are directly analogous to the four cases of the Lotka-Volterra competition equations. The outcomes of competition are labeled consistently in all four parts of this figure: 1 = neither species able to survive for resource supply points in this region; 2 = only species A able to survive; 3 = species A competitively displaces species B; 4 = stable coexistence of both species; 5 = species B competitively displaces species A; 6 = only species B able to survive. Case 1: Because the ZNGI (zero net growth isocline) of species A is inside that of species B, species A will always competitively displace species B. Case 2: Because the ZNGI of species B is always inside that of species A, species B will always win in competition with species A. Case 3: This equilibrium point is locally stable. Any resource supply points in region 4 will lead to both species stably coexisting at the resource equilibrium point. Case 4: This two-species resource equilibrium point is locally unstable. Any resource supply point in the region labeled "3 or 5" will eventually result in the competitive exclusion of either species A or B. The outcome of competition in this region depends on the starting conditions.

or the other species being dominant at steady state. This analysis holds regardless of the resource type for which competition occurs. It is easily modified for any resource supply function besides that used in this paper. If an equilibrium point is stable, two species will coexist in a particular habitat only if the resource supply vector from the equilibrium point falls within the region defined by the consumption vectors of the two species.

*The four cases of resource competition.*—Assuming that the ZNGI of two species cross or touch in at most one place (i.e., at one two-species equilibrium point), there are four distinct cases of two-species competition for two resources. These cases are directly analogous to the four cases of the Lotka-Volterra compe-

tition equations (Slobodkin 1961), and are shown in figure 6 using complementary resources. Species A will always competitively displace species B if the ZNGI of species A is always inside that of species B (case 1). Similarly, species B will always displace species A if the ZNGI of species B is always inside that of species A (case 2). For case 3, the ZNGI cross, and the consumption vectors are such that the equilibrium point is stable. For this case, there are resource supply regions for which species A is dominant (regions 2 and 3), a resource supply region (4) in which both species stably coexist, and resource supply regions (5 and 6) in which species B is dominant. For case 4, the resource equilibrium point is locally unstable. As shown, this happens because excess amounts of  $R_2$  are consumed by species B (which is relatively more limited by  $R_1$ ), thus destabilizing the equilibrium point. The region labeled "3 or 5" is not a region of stable coexistence. Resource supply points in this region will not lead to an equilibrium at the point of intersection of the ZNGI, but will lead to an equilibrium in which either species A or species B is dominant. The outcome of competition in this region depends on the starting conditions.

In consuming excess quantities of  $R_2$ , species B competitively displaces species A from a region of resource supply space in which both species could coexist if species B consumed the resources in the proportions shown in case 3. Such excess consumption may be called hoarding or luxury consumption. It may be an important strategy for competition. Hoarding, considered a form of interference competition, may be directly included in resource-based competition theory.

*Two species—two resources.*—Figure 7 shows six different cases of competition for two resources. In all cases, the consumption vectors reflect the assumptions of figure 2. For essential resources (fig. 7A), habitats with  $(_0R_1, _0R_2)$  in region 1 lead to the extinction of both species. For habitats with supply points in region 2, species A will be able to maintain a stable population, but species B will not be able to do so. In region 3, species A will competitively displace species B, both species being limited by  $R_1$ . In region 3', species A will again be dominant, even though species A is limited by  $R_2$  and species B by  $R_1$ . Any supply points within region 4 will lead to stable coexistence of both species, as the application of the stability criterion easily demonstrates. In region 5' each species is limited by a different resource, but species B is dominant. Species B is dominant in region 5, for which habitats both species are limited by  $R_2$ . Only species B can survive in region 6.

A similar diagram for hemi-essential resources (fig. 7B) uses this same notation to label the regions of dominance by one species or coexistence. Again, note that both species should stably coexist in the region of resource space labeled 4, with species A dominant in regions 2 and 3, and species B dominant in regions 5 and 6. Neither species can live in environments with supply points that fall in region 1.

Four cases are shown for substitutable resources (figs. 7C, 7D, 7E, and 7F). In three of these four cases, the resource plane is divided into regions in which one species is dominant, both species coexist, or neither species can maintain stable populations, again labeled as before. However, the assumption that perfectly substitutable resources are consumed in direct proportion to their abundance causes the resource consumption vectors of both species to fall exactly on top of

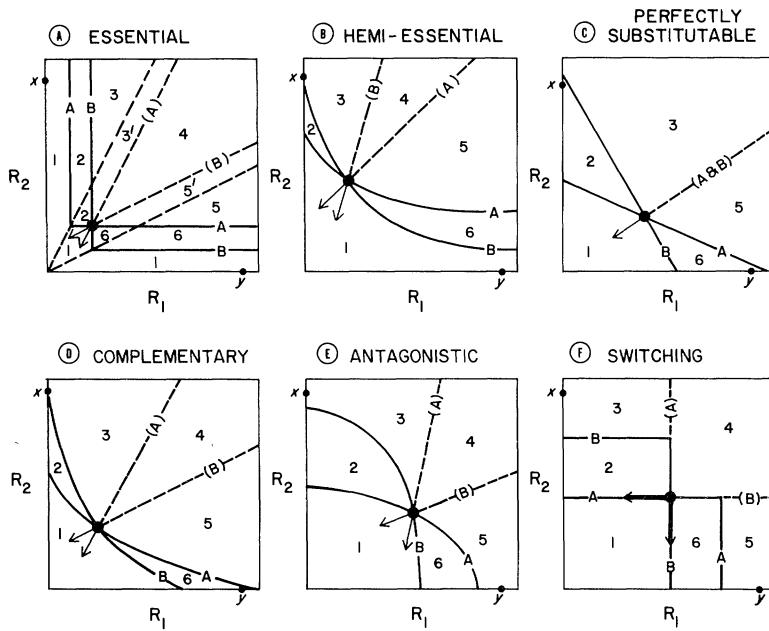


FIG. 7.—Two species—two resource competition. The outcomes of competition between two species competing for two resources are shown for six resource types. The unbroken lines labeled A and B are the ZNGI for these two species. For all parts of this figure, the outcomes of competition are labeled as in fig. 6, with the addition of 3' = species A competitively displaces species B even though both are limited by different resources, and 5' = species B competitively displaces species A even though each species is limited by a different resource. The broken lines labeled A and B are lines through the equilibrium point with the same slope as the consumption vectors of species A and B.

each other. This means that coexistence occurs only on the infinitely thin line that divides region 3 from region 5 of figure 7C. Clearly, any factors that would cause the diets of the two species to deviate could lead to a region of coexistence. Such differences in foraging strategies could be caused by spatial structure, which could open up a region of coexistence (figs. 7E, 7F).

**Resource gradients.**—Natural habitats often differ in the availability of various resources. A convenient way to summarize such differences is to order habitats according to the relative abundance of the two resources. Such an ordering results in what has been termed a resource gradient. A resource gradient may actually exist in a continuous manner in nature, such as the gradients in soil moisture and nutrient availability that occur on slopes, or it may be a convenient way to summarize the heterogeneity of an area, i.e., the relative resource supply that occurs in an area. Whittaker (1967) has discussed the pattern of species distributions along some natural gradients. A transect from point *x* to point *y* on figures 7A, 7B, 7D, 7E, and 7F gives a resource ratio gradient along which the distribution of species A and species B is qualitatively similar to that of figure 8A. For perfectly substitutable resources (fig. 7C), the distribution along a gradient would be as shown in figure 8B.

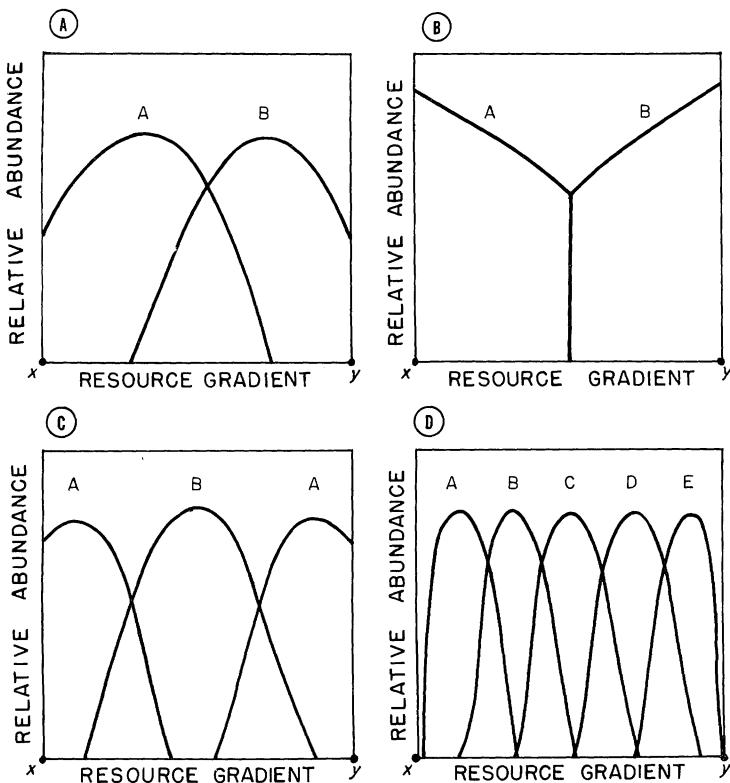


FIG. 8.—Competition along a resource gradient. *A*, The approximate relative abundance of species A and B along a gradient from point *x* to point *y* of fig. 7*A*, *B*, *D*, *E*, and *F*, i.e., for two species with a stable equilibrium when competing for essential, hemi-essential, complementary, antagonistic, and switching resources. *B*, Similar diagram for perfectly substitutable resources, as shown in fig. 7*C*. *C*, For the cases shown in fig. 9*A*, 9*B*. *D*, For fig. 9*C*, a case of five species competing for two essential resources.

*Mixed resource competition.*—So far I have only considered competition in which two species compete for the same types of resources. It is easy to imagine cases for which two species would respond to the same resources in different ways. I will present a few of the possibilities. Consider two resources which for species A are perfectly substitutable, but which are complementary for species B. There are several ways these curves could fall. One such way is shown (fig. 9*B*). Note the pattern of species dominance. There is a region in which species A is dominant, followed by a region of coexistence, a region of dominance by species B, another region of coexistence, and another region in which species A is dominant. Figure 9*B* shows a case in which two resources are perfectly substitutable for species B but are switching for species A. As already discussed, this might occur if the two species foraged differently for nutritionally substitutable resources. A pattern similar to that of figure 9*A* occurs in this case. A region of resource supply in which species A is dominant is followed by a region of

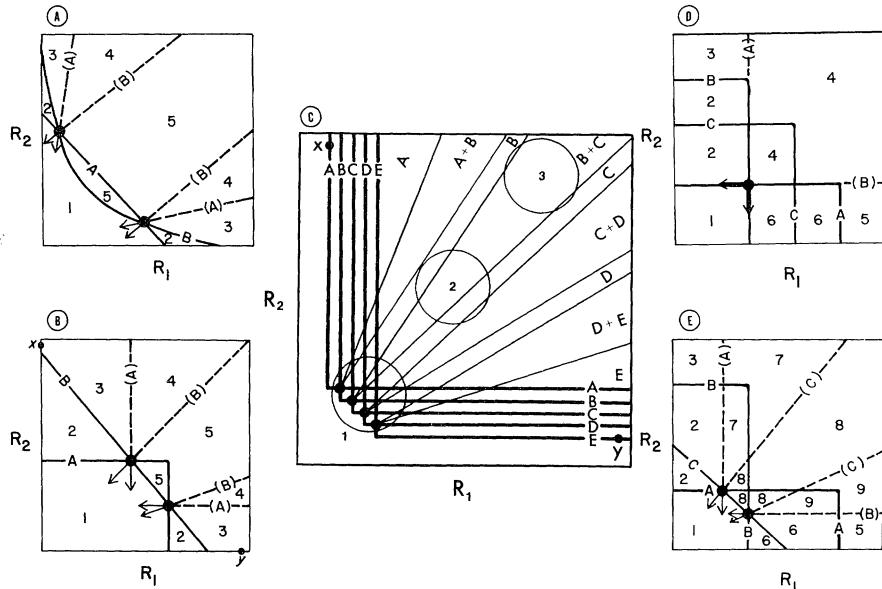


FIG. 9.—*A*, Two stable two-species equilibria occur for this case. The resources are perfectly substitutable for species A and complementary for species B. Regions are labeled as in fig. 6. *B*, For species A the resources are switching; for species B, perfectly substitutable. Both equilibria are stable. Regions are labeled as in fig. 6. *C*, Five species competing for essential resources. The four stable, two-species equilibria are marked with dots. Regions of coexistence are labeled, for example, with “C+D” meaning that resource supply points in this region lead to the stable coexistence of species C and D. The circles (labeled 1, 2, and 3) represent spatial heterogeneity around the habitat average resource supply point. See text for more details. *D*, Three species competition for switching resources. The two-species equilibrium point marked with a dot is stable. Regions are labeled as in Fig. 6. *E*, The resources are switching for species A and B and are perfectly substitutable for species C. In region 7, species A and C stably coexist; in region 8, species C displaces species A and B; in region 9, species B and C stably coexist. The other regions are labeled as in fig. 6.

coexistence, a region of dominance by species B, a second region of coexistence, and a second region of dominance by species A. A resource gradient from point  $x$  to point  $y$  of figure 9B would give a distributional pattern as shown in figure 8C. A similar pattern occurs for the case of figure 9A. In both cases there are two, two-species equilibrium points. Multiple two-species equilibrium points may also occur when species compete for antagonistic, complementary, and hemi-essential resources.

*Multi-species competition.*—The graphical approach just presented is readily applied to multi-species competition for two resources. Figure 9C shows five species competing for two essential resources. The species rank in ability to grow under limitation by  $R_1$  with  $A > B > C > D > E$ , and in ability to grow under limitation by  $R_2$  with  $E > D > C > B > A$ , where “ $>$ ” is read “is a superior competitor to.” The ZNGI for these five species cross in 10 places, of which the four stable, two-species equilibrium points are shown with dots. If any number of

species competing for essential resources are so ranked, there will be regions in the resource supply plane in which various pairs of species will coexist (fig. 9C). The approximate distribution of these five species along a resource gradient from point  $x$  to point  $y$  of figure 9C is shown in figure 8D. This illustrates that these five species could coexist in a habitat with the range of relative resource availabilities which occurs along the resource gradient of figure 8D. The effect of spatial heterogeneity on species composition in a community is better illustrated by using both the average rate of nutrient supply (the average resource supply point) and spatial variance in resource supply within a habitat. For instance, the number 3 of figure 9C might show the average resource supply point for a habitat, and the circle around the number 3 could include the range of microhabitat to microhabitat variation of the resource supply point in that habitat. The closed curve (assumed to be a circle) showing the spatial variation in resource supply in habitat 3 includes regions in which species B and C can maintain stable populations (fig. 9C). The same amount of spatial heterogeneity in the more resource-poor habitat 2 would include regions in which species B, C and D could maintain stable populations. All five species could co-occur in the equally heterogeneous but even more resource-poor habitat 1 (fig. 9C). This suggests that a given amount of spatial heterogeneity will lead to maximal species diversity in moderately resource-poor habitats. Thus, a graph of species diversity against resource richness would give a humped curve.

A case of three-species competition for switching resources is shown in figure 9D. Of the three points of intersection of the ZNGI, only one is a stable, two-species equilibrium point. Species A and B coexist at this equilibrium point, reducing  $R_1$  and  $R_2$  to equilibrium levels below that required for the existence of species C. Species A will be dominant in regions 2 and 3, both species will coexist in region 4, species B will be dominant in regions 5 and 6, and no species will be able to exist in region 1. Species C is excluded from all habitats.

This raises a question related to plant-pollinator community structure. No matter how the ZNGI are arranged for three or more species consuming two switching resources (excluding the unlikely case of exact coincidence of the ZNGI), there is only one stable, two-species equilibrium point. This equilibrium point allows the coexistence of only two of these species. All others are competitively excluded from all regions of the  $R_1, R_2$  resource plane. This means that, no matter how spatially heterogeneous the distribution of numerous resources might be, there can be no more species responding to them in a switching manner than there are resources. Thus, there should be a one-to-one relationship between the number of co-occurring species of switching pollinators and the seasonal average number of distinct, vector-pollinated species in flower at any given time.

This does not hold for species which do not respond to resources in a switching manner. In figure 9E, species A and B respond to  $R_1$  and  $R_2$  in a switching manner, but the resources are perfectly substitutable for species C. Species A will be dominant in regions 2 and 3, species B will be dominant in regions 5 and 6, and species C will be dominant in region 8. Species A and C will coexist in region 7, and species B and C will coexist in region 9. For a third species, like species C in this example, to be able to invade a community in which resources are consumed in a switching manner, the third species must have a range of resource availabilities for which it is a superior competitor to both of the switching species.

A comparison of competition for essential resources with competition for switching resources demonstrates some of the qualitative effects of resource class on competition. For a group of species to be able to coexist along a resource gradient when competing for essential resources, they must be ranked in competitive ability for one resource in reverse order of their competitive ranking for the second resource, as shown in figure 8D. However, such a ranking will lead to the coexistence of only two species if they are competing for switching resources. The criterion for coexistence of species on an essential resource gradient is not sufficient to predict coexistence of species competing along a gradient of complementary, antagonistic, or hemi-essential resources. Thus, there are qualitative differences in competition for different classes of resources. The class of resource for which competition occurs determines the criteria for coexistence along a resource gradient.

#### APPLICABILITY OF THEORY

I am familiar with few studies of interspecific interaction which were done in a way that would allow them to be directly analyzed using the methods described here. Droop (1974) and Rhee (1978) demonstrated that plant nutrients are noninteractive essential resources, but did not use this information to predict the outcome of interspecific competition.

I (Tilman 1977) reported the results of competition experiments between two freshwater algae under conditions in which phosphate or silicate should have been the limiting factors, comparing the results with predictions based on nutrient utilization information reported by Tilman and Kilham (1976). Figure 10 presents these results in the notation developed in this paper. The ZNGI shown are for a mortality rate of  $0.25 \text{ day}^{-1}$ , approximately 30% of the maximal growth rate for both species. Competition experiments were performed for several  $(_0R_1, _0R_2)$  at this mortality rate. The  $(_0R_1, _0R_2)$  which led to dominance by *Asterionella* are shown with a star, those that led to dominance by *Cyclotella* are shown with a diamond, and those that led to coexistence are shown with a dot. Note the close agreement of predictions and results. Resource competition theory was used to predict relative abundance of these two species in Lake Michigan. In so doing, it was necessary to assume that both species experienced the same mortality rates, and that the ambient (measured) concentrations of phosphate and silicate were near steady state. Even with these restrictive assumptions, over 70% of the variance in the relative abundance of these two species along a natural resource gradient in Lake Michigan was explained by the model (Tilman 1977).

Studies of the response of freshwater algae to various nutrient additions also seem to be qualitatively consistent with a theory of competition for essential resources. Particular nutrient additions seem to favor certain species (see, for instance, Menzel et al. 1963; Schindler 1977). Stoermer et al. (1978) demonstrated a close agreement between those species that have a growth response to additions of nitrogen or phosphorus and those that tend to become dominant in areas with anthropogenic additions of these nutrients.

Levin et al. (1977) used a mechanistic model to explore the interactions of limiting resources (sugars), consumers (different strains of *Escherichia coli*), and a

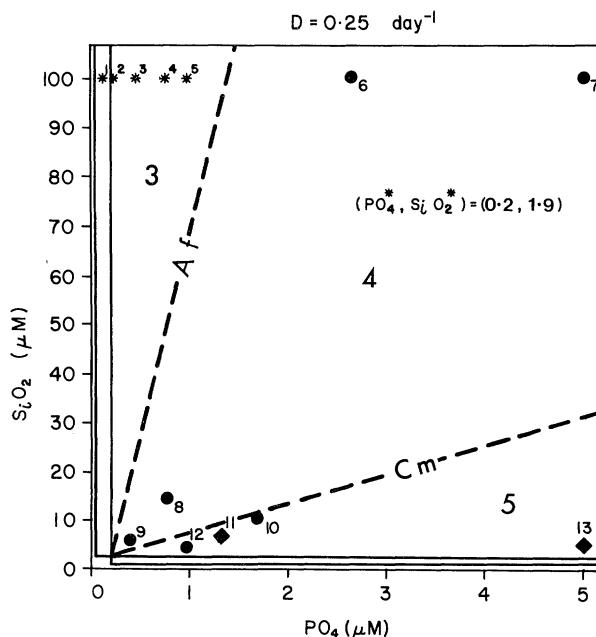


FIG. 10.—Predicted and observed outcomes of competition for phosphate and silicate by *Asterionella formosa* and *Cyclotella meneghiniana* at a mortality (flow) rate of 0.25 day<sup>-1</sup>. The two-species equilibrium point occurs at 1.9 μM SiO<sub>2</sub> and 0.2 μM PO<sub>4</sub>. The consumption vectors (from Tilman 1977) have a slope (Si/P) of 87 for *Asterionella* and of 6.2 for *Cyclotella*. For resource supply points in the region labeled 3, *Asterionella* should be dominant. For resupply points in region 4, both species should coexist. *Cyclotella* should be dominant in region 5. Experiments (Tilman 1977) for which *Asterionella* was dominant are shown with an asterisk; those for which *Cyclotella* was dominant are shown with a diamond, and those for which both species coexisted are shown with a dot. A supply point off the graph (9.8 μM PO<sub>4</sub>, 15 μM SiO<sub>2</sub>) was dominated by *Cyclotella*, as predicted. For this analysis, the observed maximal growth rates, reported in Tilman and Kilham (1976), were used even though the maximal rates under PO<sub>4</sub> and SiO<sub>2</sub> limitation for each species differed. The boundaries shown differ slightly from those of Tilman (1977) because of this difference in maximal rates.

predator (the bacteriophage T<sub>2</sub>). Although their model predicted diverging oscillations for the case of one resource, one consumer, and one predator, they observed a stable equilibrium. One resource, two consumers, and one predator stably coexisted as predicted by their model. In terms of the classification of resources presented here, the model that Levin et al. (1977) developed assumed that the resources used by *E. coli* were perfectly substitutable, a reasonable assumption for sugars.

Platt and Weis (1977) studied a guild of fugitive prairie plants, for which they believed that soil moisture and open (disturbed) sites were two limiting resources. Their graphs of the soil moisture and disturbance requirements of several species are comparable to zero net growth isolines. If Platt and Weis had expressed the disturbance requirements of the prairie plants as an absolute requirement for open space instead of the inverse (distance between disturbances), their curves would

have been directly comparable to the ZNGI for essential resources. This suggests that space may be considered an essential resource. With estimates of the supply rates and consumption rates of these resources, it would be possible to predict the abundances of various fugitive species along the natural gradients in soil moisture and disturbance rate that Platt and Weis observed. This would allow an equilibrium analysis of competition in disturbed habitats.

Competition for nutrients may be an important process in terrestrial plant communities. Numerous studies have found a correlation between soil nutrients and species composition (e.g., Zedler and Zedler 1969; Milton 1940; Ellis 1971; Beadle 1966). For instance, Zedler and Zedler (1969) studied a 1.5 m elevational gradient in an old field in Wisconsin. This slight elevational change correlated significantly negatively with a soil moisture gradient ( $r = -.60$ ;  $n = 320$ ;  $P < .01$ ). Soil moisture was significantly positively correlated with phosphorus ( $r = +.16$ ;  $n = 320$ ;  $P < .01$ ) and significantly negatively correlated with soil potassium ( $r = -.13$ ;  $n = 320$ ;  $P < .01$ ). Of the eight major species on this gradient, three were absent at one end of the gradient and increased along the gradient, three other species were at peak density when the first three species were absent and decreased in density along the gradient, and two species had peak density near the middle of the gradient. Not one of the species was dominant at both ends of the gradient and rare in the middle, an observation that is consistent with the predictions of a model of competition for two essential resources. Whittaker (1967) reported that the distribution of plants along elevational gradients has a similar pattern. Although these observations are consistent with the hypothesis that resource competition may be an important factor determining the structure of this plant community, this hypothesis has not yet been experimentally tested.

At any given point along a resource gradient, plant species which are coexisting should be limited by different nutrients. If nutrients are essential resources and if resource competition is occurring, the addition of a given nutrient should favor the species limited by it. Plants which increase in density after the addition of one nutrient in a particular locality should not increase with the addition of any other nutrient. Willis (1963) fertilized the vegetation of the sand dunes of Braunton Burrows with only nitrogen (N), only potassium (K), only phosphorus (P), or with all nutrients except N, P, or K. Of the 10 plant species that were detectable above trace levels, four increased relative to controls when N was added, one when P was added, and one when K was added. None of these six species increased in response to more than one of the three single nutrient additions during the 2-yr period of the experiment.

#### *Testability of Resource Theory*

A major advantage of resource-based theory over classical theory is the testability of the predictions made by resource-based theory. Resource theory can make qualitative and quantitative predictions from both lower to higher and from higher to lower levels of organization. For qualitative predictions, consider a terrestrial plant community for which it would be a straightforward, if tedious, matter to collect the following four pieces of information: (1) the resource re-

quirements (growth responses) of each major species for each of the potentially limiting resources; (2) the outcome of competition experiments between the major species performed under conditions of controlled supply of various resources; (3) the distribution in the field of these major species in relation to the distribution of the potentially limiting resources; and (4) the effect on the abundance of these species in the field of additions of various resources or combinations of resources. The first piece of information could be used to predict the next three, providing three opportunities to falsify the hypothesis of the importance of competition for resources. Similarly, any one of the four pieces of information necessarily places constraints on the other three if the theory is correct. Similar multiple predictions are made by resource-based models for any class of resource. Resource-based theory is robust not only in providing multiple chances for falsification, but also in making predictions both from lower level to higher level phenomena, and from higher level to lower level phenomena. Quantitative predictions can also easily be made. Again the mechanistic element of the theory allows prediction of several measurable items from a small data base. For instance, the information collected for item 1 above can be used to predict the population dynamics of particular species and the absolute abundances of particular resources under conditions in which the nutrient supply process is known, such as it would be in laboratory competition experiments.

As I hope that this paper has demonstrated, attempts to build mechanistic, resource-based theory may prove more fruitful if different resource classes are considered. For plants consuming inorganic elements, a model of competition based on essential resources may be most appropriate. For herbivores, resources may prove to be hemi-essential or substitutable. If they are substitutable, argument by analogy with livestock nutrition studies indicates that the resources of herbivores are likely to be complementary, in the absence of either synergistic effects of secondary compounds or spatial structure. The resources of carnivores are likely to be perfectly substitutable in unstructured environments, but antagonistic or switching in spatially or temporally heterogeneous environments.

These differences in the category of resource for which competition occurs can greatly influence the interactions between species, and thus should be included explicitly in models of resource competition. The question of species packing (see, for instance, MacArthur and Levins 1964; MacArthur 1969, 1970; May 1973; Yoshiyama and Roughgarden 1977) is often phrased in terms of competition for resources which may be ranked along a "resource gradient." The resource gradient of the species packing literature is different than that of this paper. The former is a convenient way to summarize all the resources available in a particular environment; the latter a way to summarize all the relative availabilities of two resources in a series of microhabitats. However, whether explicitly or implicitly, the species packing models make an assumption about the class of resource for which competition occurs. In all the work done to date, the resources have been assumed to be perfectly substitutable for each other. If the resources were not perfectly substitutable, the definition of the competition coefficient, alpha, would have to be changed, because the alpha derivable from resource-based models depends on the type of resource for which competition occurs.

In terms of the resource gradients presented in this paper, it can be seen (figs. 8 and 9) that resource type determines the patterns of species dominance and coexistence that can occur. For instance, with essential resources, a species can only be dominant at one point on a resource gradient; whereas with substitutable resources, a species may be dominant at both ends, and absent in the middle of a gradient. (cf. figs. 8C and 8D).

Although in this paper I have mostly discussed cases in which resources are consumed as hypothesized in figure 2 and are supplied in a equitable mode, the method of analysis is not restricted to these cases. The technique presented allows prediction of the outcome of consumer-resource interaction even if the growth functions, resource supply functions and resource consumption functions are unknown. As figures 5 and 6 illustrate, it is only necessary to know (1) the position of the ZNGI for each species, (2) the steady-state consumption characteristics of each species, and (3) the steady-state supply rates of each resource. These supply rates give the vector  $\bar{U}$  of figure 5. Applying the criteria for stability to these three pieces of information, it is possible to determine in which habitats given species should be dominant or coexist with other species.

It is possible to imagine many shapes for resource growth isolines other than those shown in this paper, including closed curves caused by inhibition of high levels of a resource (Maguire 1973). I have presented and discussed the classes of essential, hemi-essential, and substitutable resources, and the subclasses of substitutable (complementary, perfectly substitutable, antagonistic, and switching) because I believe that they are of the greatest ecological significance. Much further work needs to be done to determine the extent to which organisms of different trophic status can be categorized as to resource class, and to determine how well such information can predict the outcome of consumer-resource interactions.

#### SUMMARY

The growth response of a population to the resources in a particular environment is used to classify pairs of resources as being either (1) essential, (2) hemi-essential, (3) complementary, (4) perfectly substitutable, (5) antagonistic, or (6) switching. Although nutrition is one important factor determining resource type, the growth response of a population to resources also depends on the interaction between a species' foraging methods and the spatial distribution of the resources. For example, two resources which are nutritionally perfectly substitutable may be operationally switching, antagonistic, or complementary because of spatial heterogeneity.

A graphical, equilibrium theory of resource competition allows prediction of the outcome of interactions between several consumers for the various classes of resources. The technique requires information on (1) resource type (growth isolines), (2) resource preference, (3) resource supply processes, and (4) mortality rates for all species. For all resource types, the major criterion for stable coexistence is that each species consume relatively more of the one resource which more limits its own growth rate.

The patterns of species dominance and coexistence in a community are shown to depend on the types of resources for which competition occurs. For instance, it is theoretically possible for an unlimited number of species competing for essential resources to stably coexist in a spatially heterogeneous environment, but only two species competing for two switching resources may stably coexist in an equally heterogeneous environment. However, the latter community is susceptible to invasion by other species which respond to these same resources in a non-switching manner.

#### ACKNOWLEDGMENTS

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#### APPENDIX

This Appendix explores the local stability characteristics of the two-species equilibrium point which can occur when two species compete for two resources. If such an equilibrium point is found to be locally stable, both species should return to the equilibrium after small perturbations in any of the variables. In this case, the variables are the densities of both species and the availabilities of both resources. Linear stability analysis is now a common technique in mathematical ecology, and I refer interested readers to May (1973) for an elaboration of its assumptions, principles, and validity.

For an equilibrium point to be locally stable, the eigenvalues of the Jacobian matrix,  $J$ , must all have negative real parts. The Jacobian is a matrix of the partial derivatives of the rates of change of variables, evaluated at equilibrium. For two species competing for two resources, it is a  $4 \times 4$  matrix. For notational convenience, I will use  $u_{ij} = (\partial N_i / \partial N_j)^*$ ,  $v_{ij} = (\partial N_i / \partial R_j)^*$ ,  $w_{ij} = -(\partial R_i / \partial N_j)^*$ , and  $x_{ij} = -(\partial R_i / \partial R_j)^*$ , where the asterisk means the expression is to be evaluated at equilibrium. For all the models of resource competition presented in this paper,  $u_{ij} = 0$  for all  $i, j$ . For all cases, the Jacobian matrix has the general form

$$J = \begin{bmatrix} 0 & 0 & v_{11} & v_{12} \\ 0 & 0 & v_{21} & v_{22} \\ -w_{11} & -w_{12} & -x_{11} & -x_{12} \\ -w_{21} & -w_{22} & -x_{21} & -x_{22} \end{bmatrix}.$$

The eigenvalues,  $\lambda$ , are determined by the characteristic equation,  $\det(J - \lambda I) = 0$ . Letting, for notational convenience,  $q_1 = w_{11}v_{11} + w_{12}v_{21}$ ,  $q_2 = w_{11}v_{12} + w_{12}v_{22}$ ,  $q_3 = w_{11}v_{12} + w_{12}v_{21}$ , and  $q_4 = w_{21}v_{12} + w_{22}v_{22}$ , the characteristic equation for this matrix is

$$\begin{aligned} \lambda^4 + (x_{11} + x_{22})\lambda^3 + (q_1 + q_4 + x_{11}x_{22} - x_{12}x_{21})\lambda^2 \\ + (x_{11}q_4 + x_{22}q_1 - x_{12}q_3 - x_{21}q_2)\lambda + (q_1q_4 - q_2q_3) = 0. \end{aligned}$$

This characteristic equation has the general form  $\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$ . The Rough-Hurwitz criteria for stability with such a characteristic equation (see May 1973) are (1)  $a_1 > 0$ ; (2)  $a_3 > 0$ ; (3)  $a_4 > 0$ ; and (4)  $a_1a_2a_3 - a_1^2a_4 - a_3^2 > 0$ .

I will first present a general model, and then discuss specific cases. The general model which will be considered is derived from the one presented earlier in the main text. It is explicitly a model of competition for two resources which are resupplied as shown in figure 3. The form of  $f_i$  and  $h_i$  determines the type of resource for each species.

$$\frac{dN_i}{dt} = N_i[f_i(R_1, R_2) - m_i], \quad \text{for } i = 1, 2,$$

and  $\frac{dR_j}{dt} = a(R_j - R_j) - \sum_{i=1}^2 N_i h_{ij}(R_1, R_2) f_i(R_1, R_2), \quad \text{for } j = 1, 2.$

Terms are defined as in the main text of this paper. For notational convenience, let the following partial derivatives, all evaluated at equilibrium (\*), be represented as follows:

$$\begin{aligned} \left(\frac{\partial f_1}{\partial R_1}\right)^* &= P_1; & \left(\frac{\partial f_1}{\partial R_2}\right)^* &= P_2; & \left(\frac{\partial f_2}{\partial R_1}\right)^* &= P_3; & \left(\frac{\partial f_2}{\partial R_2}\right)^* &= P_4; \\ \text{and } \left(\frac{\partial h_{11}}{\partial R_1}\right)^* &= G_1; & \left(\frac{\partial h_{11}}{\partial R_2}\right)^* &= G_2; & \left(\frac{\partial h_{12}}{\partial R_2}\right)^* &= G_3; & \left(\frac{\partial h_{12}}{\partial R_1}\right)^* &= G_4; \\ \left(\frac{\partial h_{21}}{\partial R_1}\right)^* &= G_5; & \left(\frac{\partial h_{21}}{\partial R_2}\right)^* &= G_6; & \left(\frac{\partial h_{22}}{\partial R_2}\right)^* &= G_7; & \left(\frac{\partial h_{22}}{\partial R_1}\right)^* &= G_8. \end{aligned}$$

Note that  $(f_i)^* = m_i$  and let  $(h_{11})^* = c_1$ ;  $(h_{12})^* = c_2$ ;  $(h_{21})^* = c_3$ ; and  $(h_{22})^* = c_4$ .

For all cases to be considered in this Appendix,  $P_1, P_2, P_3$ , and  $P_4 \geq 0$ , i.e., a small increase in the availability of either  $R_1$  or  $R_2$  will not lead to a decreased growth rate for either of the species. Similarly,  $c_1, c_2, c_3$ , and  $c_4 \geq 0$ , i.e., the competing species do not release or create resources. Also,  $G_1, G_3, G_5$ , and  $G_7 \leq 0$ , i.e., the per capita consumption rate of a particular resource does not decrease if that resource is slightly increased. And  $G_2, G_4, G_6$ , and  $G_8 < 0$ , i.e., the per capita consumption rate of a particular resource does not increase if the other resource is slightly increased. Note that  $a, m_1, m_2, N_1^*, N_2^* > 0$ . The Jacobian matrix for this model contains the following elements:

$$\begin{aligned} v_{11} &= N_1^* P_1, & v_{12} &= N_1^* P_2, \\ v_{21} &= N_2^* P_3, & v_{22} &= N_2^* P_4, \\ w_{11} &= c_1 m_1, & w_{12} &= c_3 m_2, \\ w_{21} &= c_2 m_1, & w_{22} &= c_4 m_2, \\ x_{11} &= a + N_1^* (G_1 m_1 + c_1 P_1) + N_2^* (G_5 m_2 + c_3 P_3), \\ x_{12} &= N_1^* (G_2 m_1 + c_1 P_2) + N_2^* (G_6 m_2 + c_3 P_4), \\ x_{21} &= N_1^* (G_4 m_1 + c_2 P_1) + N_2^* (G_8 m_2 + c_4 P_3), \\ x_{22} &= a + N_1^* (G_3 m_1 + c_2 P_2) + N_2^* (G_7 m_2 + c_4 P_4). \end{aligned}$$

Given these coefficients it is a straightforward, (but tedious) algebraic process to determine under what conditions each of the four stability criteria will be met. These will be considered in order.

*Criterion 1:  $a_1 > 0$ .*—As stated earlier,  $a_1 = x_{11} + x_{22}$ . Thus, for criterion 1 to hold,  $x_{11} + x_{22} > 0$ . This will be the case if

$$2a + N_1^* (G_1 m_1 + G_3 m_1 + c_1 P_1 + c_2 P_2) + N_2^* (G_5 m_2 + G_7 m_2 + c_3 P_3 + c_4 P_4) > 0.$$

Because all the terms in the left-hand side of this inequality are greater than or equal to zero, the inequality always holds. Thus, criterion 1 is met for all cases considered.

*Criterion 2:  $a_3 > 0$ .*—After some algebra, the value for  $a_3$  is found to be

$$\begin{aligned} a_3 = & a[m_1 N_1^* (c_1 P_1 + c_2 P_2) + m_2 N_2^* (c_3 P_3 + c_4 P_4)] \\ & + (m_1 + m_2) N_1^* N_2^* (c_1 c_4 - c_2 c_3) (P_1 P_4 - P_2 P_3) \\ & + m_1^2 N_1^{2*} [c_1 (P_1 G_3 - P_2 G_4) + c_2 (P_2 G_1 - P_1 G_2)] \\ & + m_1 m_2 N_1^* N_2^* [c_1 (P_1 G_7 - P_2 G_8) + c_2 (P_2 G_5 - P_1 G_6) \\ & + c_3 (P_3 G_3 - P_4 G_4) + c_4 (P_4 G_1 - P_3 G_2)] \\ & + m_2^2 N_2^{2*} [c_3 (P_3 G_7 - P_4 G_8) + c_4 (P_4 G_5 - P_3 G_6)]. \end{aligned}$$

Consider the last three terms of  $a_3$ .  $G_b > 0$  for  $b = 1, 3, 5, 7$  and  $G_d < 0$  for  $d = 2, 4, 6, 8$ ;  $P_i > 0$  for all  $i$ . Each of the terms of the form  $(P_a G_b - P_c G_d)$  has  $b$  as an odd number and  $d$  as an even number. These terms are thus positive. The first term in the expression for  $a_3$  is always positive. Thus,  $a_3$  will be greater than zero only if  $(m_1 + m_2) N_1^* N_2^* (P_1 P_4 - P_2 P_3) (c_1 c_4 - c_2 c_3) > 0$ . Because  $m_1, m_2, N_1^*$ , and  $N_2^* > 0$ , this simplifies to  $(P_1 P_4 - P_2 P_3) (c_1 c_4 - c_2 c_3) > 0$ . Both factors must be either positive or both negative for this inequality to hold. In terms of the original variables, for stability to occur, criterion 2 requires either

$$\text{I. } \frac{(\partial f_1 / \partial R_1)^*}{(\partial f_1 / \partial R_2)^*} > \frac{(\partial f_2 / \partial R_1)^*}{(\partial f_2 / \partial R_2)^*} \text{ and } \frac{h_{11}^*}{h_{12}^*} > \frac{h_{21}^*}{h_{22}^*}$$

$$\text{or } \text{II. } \frac{(\partial f_1 / \partial R_2)^*}{(\partial f_1 / \partial R_1)^*} > \frac{(\partial f_2 / \partial R_2)^*}{(\partial f_2 / \partial R_1)^*} \text{ and } \frac{h_{12}^*}{h_{11}^*} > \frac{h_{22}^*}{h_{21}^*}.$$

These conditions are easily interpreted biologically. If condition I holds, the growth rate of species 1, relative to the growth rate of species 2, is more limited by resource 1 than by resource 2, and species 1, relative to species 2, consumes proportionately more of resource 1. If condition II holds, the growth rate of species 1, relative to the growth of species 2, is more limited by resource 2 than by resource 1; and species 1, relative to species 2, consumes proportionately more of resource 2. Criterion 2 thus has the following as a necessary condition for the stable coexistence of two species utilizing two resources.

**CONDITION A.** For two species to stably coexist on two resources, each species, relative to the other, must consume proportionately more of the one resource which more limits its own growth rate.

This is shown in figure 5. For figure 5A, the growth isolines and consumption vectors are such that, assuming nearby growth isolines are approximately parallel to the ones shown, species A is more limited by  $R_2$ , compared to species B, and species A consumes relatively more  $R_2$  than  $R_1$ , compared to species B. The case of figure 5A meets a necessary condition for stability. The case of figure 5B does not. The reversal of the consumption vectors from figure 5A means that each species, compared to the other, consumes proportionately more of the resource which less limits its own growth rate. This equilibrium must be unstable.

*Criterion 3:  $a_4 > 0$ .*—From the characteristic equation derived earlier,  $a_4 = q_1 q_4 - q_2 q_3$ . Substituting in the variables for  $v$  and  $w$  gives  $a_4 = m_1 m_2 N_1 N_2 (P_1 P_4 - P_2 P_3) (c_1 c_4 - c_2 c_3)$ . Clearly for  $a_4 > 0$ , it is sufficient that criterion 2 hold. For the models considered in this paper, criterion 2 and criterion 3 both require that condition A be met before a stable equilibrium is possible.

*Criterion 4:  $a_1 a_2 a_3 - a_1^2 a_4 - a_3^2 > 0$ .*—This criterion is algebraically the most cumbersome.

If expanded in terms of the general variables of the characteristic equation (i.e.,  $q_i$  and  $x_{ij}$ ), it reduces to:

$$\begin{aligned}
 & (q_1 - q_4)^2 x_{11} x_{22} \\
 & + q_2 q_3 (2x_{11} x_{22} - 2x_{12} x_{21} + x_{11}^2 + x_{22}^2 - x_{21}^2 + x_{12}^2) \\
 & + (q_2 x_{21} + q_3 x_{12}) (x_{22} - x_{11}) (q_1 - q_4) \\
 & + q_1 (x_{11}^2 x_{22}^2 + x_{11} x_{22}^3 - x_{11} x_{12} x_{21} x_{22} - x_{12} x_{21} x_{22}^2) \\
 & + q_2 (x_{11} x_{12} x_{21}^2 + x_{12} x_{21}^2 x_{22} - x_{11}^2 x_{21} x_{22} - x_{11} x_{21} x_{22}^2) \\
 & + q_3 (x_{11} x_{12}^2 x_{21} + x_{12}^2 x_{21} x_{22} - x_{11}^2 x_{12} x_{22} - x_{11} x_{21} x_{22}^2) \\
 & + q_4 (x_{11}^3 x_{22} + x_{11}^2 x_{22}^2 - x_{11}^2 x_{12} x_{21} - x_{11} x_{12} x_{21} x_{22}) > 0.
 \end{aligned}$$

After substituting in the variables represented by  $q_i$  and  $x_{ij}$ , the fully expanded form of this inequality occupies several pages. Some of the terms cancel. Others can be matched such that, given that condition A holds, a negative term is paired with a positive term of greater absolute value. However, I could not show the inequality to hold unless I added one more restriction: that the  $m_j G_j$  of  $x_{11}$ ,  $x_{12}$ ,  $x_{21}$ ,  $x_{22}$  are all about zero, i.e., that  $G_j \approx 0$  for all  $j$ . Because  $G = (\partial h / \partial R)^*$ , this requires, for a given species, that the consumption vectors near an equilibrium point (as in fig. 5) be almost parallel to the consumption vectors at the equilibrium point. If  $G_j = 0$  for all  $j$ , criterion 4 always holds if condition A is met. However, if  $G_j \neq 0$  for some  $j$ , criterion 4 requires that condition B be met in addition to condition A.

**CONDITION B.** The amounts of each resource consumed by individuals of each species may change only slightly in response to small changes in the availability of each resource.

Condition A is an exact statement of one necessary condition for stability. Condition B is a qualitative statement of a second condition which, if also met, will assure local stability. A restriction less rigorous than that of condition B may also allow stability, but I could not uncover it in the pages of algebra associated with criterion 4.

Condition B is always met for all of the cases considered in this paper, unless an equilibrium point occurs at the switching point for antagonistic resources. For both essential resources and for perfectly switching resources (but not at the switching point), consumption vectors in the vicinity of an equilibrium point will be exactly parallel, assuring that  $G_j \approx 0$ . For the other cases, the consumption vectors change only slightly in response to changes in  $R_1$  and  $R_2$ . Thus, of the two conditions, condition A is the more restrictive, at least for the cases considered in this paper.

#### LITERATURE CITED

- Beadle, N. C. W. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophyllly. *Ecology* 47:992–1007.
- Canale, R. P. 1969. Predator-prey relationships in a model for the activated process. *Biotechnol. Bioeng.* 11:887–907.
- . 1970. An analysis of models describing predator-prey interactions. *Biotechnol. Bioeng.* 12:353–378.
- Chao, L., B. R. Levin, and F. M. Stewart. 1977. A complex community in a simple habitat: An experimental study with bacteria and phage. *Ecology* 58:369–378.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567–576.
- Covich, A. 1972. Ecological economics of seed consumption by *Peromyscus*—a graphical model of resource substitution. *Trans. Conn. Acad. Arts Sci.* 44:71–93.
- . 1974. Ecological economics of foraging among coevolving animals and plants. *Ann. Mo. Bot. Gard.* 61:794–805.

- Droop, M. R. 1973. Some thoughts on nutrient limitation in algae. *J. Phycol.* 9:264–272.
- . 1974. The nutrient status of algal cells in continuous culture. *J. Mar. Biol. Assoc. U.K.* 54:825–855.
- Dugdale, R. C. 1967. Nutrient limitation in the sea: dynamics, identification, and significance. *Limnol. Oceanogr.* 12:685–695.
- Ellis, R. C. 1971. Growth of *Eucalyptus* seedlings on four different soils. *Aust. For.* 35:107–118.
- Gause, G. F. 1932. Experimental studies on the struggle for existence. I. Mixed population of two species of yeast. *J. Exp. Biol.* 12:44–48.
- . 1934. The struggle for existence. Hafner, New York.
- Heinrich, B. 1976a. Resource partitioning among some eusocial insects: bumblebees. *Ecology* 57:874–889.
- . 1976b. The foraging specializations of individual bees. *Ecol. Monogr.* 46:105–128.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entomol.* 91:293–332.
- . 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:5–60.
- . 1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48:1–86.
- Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *Am. Nat.* 100:419–424.
- Hsu, S. B., S. P. Hubbell, and P. Waltman. 1977. A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM (Soc. Ind. Appl. Math.) J. Appl. Math.* 32:366–383.
- Janzen, D. H., H. B. Juster, and E. A. Bell. 1977. Toxicity of secondary compounds to the seed-eating larvae of the bruchid beetle *Callosobruchus maculatus*. *Phytochemistry* 16:223–227.
- Lappé, F. 1971. Diet for a small planet. Ballantine, New York.
- Leon, J. A., and D. B. Tumpson. 1975. Competition between two species for two complementary or substitutable resources. *J. Theor. Biol.* 50:185–201.
- Levin, B. R., F. M. Stewart, and L. Chao. 1977. Resource-limited growth, competition, and predation: a model and experimental studies with bacteria and bacteriophage. *Am. Nat.* 111:3–24.
- Lotka, A. J. 1924. Elements of physical biology. Williams & Wilkins, Baltimore.
- Lynch, M. 1978. Complex interactions between natural coexploiters—*Daphnia* and *Ceriodaphnia*. *Ecology* 59:552–564.
- MacArthur, R. H. 1969. Species packing, or what competition minimizes. *Proc. Natl. Acad. Sci. USA* 64:1369–1375.
- . 1970. Species packing and competitive equilibrium for many species. *Theor. Popul. Biol.* 1:1–11.
- . 1972. Geographical ecology. Harper & Row, New York.
- MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proc. Natl. Acad. Sci. USA* 51:1207–1210.
- . 1967. The limiting similarity, convergence, and divergence of co-existing species. *Am. Nat.* 101:377–385.
- Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. *Am. Nat.* 107:213–246.
- May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, N.J.
- . 1975. Some notes on estimating the competition matrix,  $\alpha$ . *Ecology* 56:737–741.
- Menzel, D. W., E. M. Hulbert, and J. H. Ryther. 1963. The effects of enriching Sargasso Sea water on the production and species composition of the phytoplankton. *Deep-Sea Res.* 10:209–219.
- Milton, W. E. J. 1940. The effect of manuring, grazing, and cutting on the yield, botanical and chemical composition of natural hill pastures. I. Yield and botanical section. *J. Ecol.* 28:326–356.
- Monod, J. 1950. La technique de culture continue; theorie et applications. *Ann. Inst. Pasteur (Paris)* 79:390–410.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39:335–354.

- . 1971. The developmental responses of predators to changes in prey density. *Ecology* 52:132–137.
- Murdoch, W. W., S. Avery, and M. E. B. Smyth. 1975. Switching in predatory fish. *Ecology* 56:1094–1105.
- Murdoch, W. W., and J. R. Marks. 1973. Predation by coccinellid beetles: experiments on switching. *Ecology* 54:160–167.
- Petersen, R. 1975. The paradox of the plankton: an equilibrium hypothesis. *Am. Nat.* 109:35–49.
- Platt, W. J., and I. M. Weis. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. *Am. Nat.* 111:479–513.
- Rapport, D. J. 1971. An optimization model of food selection. *Am. Nat.* 105:575–587.
- Rapport, D. J., and J. E. Turner. 1975. Feeding rates and population growth. *Ecology* 56:942–949.
- . 1977. Economic models in ecology. *Science* 195:367–373.
- Real, L. A. 1977. The kinetics of function response. *Am. Nat.* 111:289–300.
- Rhee, G. Y. 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnol. Oceanogr.* 23:10–25.
- Salisbury, F. B., and C. Ross. 1969. *Plant physiology*. Wadsworth, Belmont, Calif.
- Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. *Science* 195:260–262.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Slobodkin, L. B. 1961. *Growth and regulation of animal populations*. Holt, Rinehart & Winston, New York.
- Stewart, F. M., and B. R. Levin. 1973. Partitioning of resources and the outcome of interspecific competition: a model and some general considerations. *Am. Nat.* 107:171–198.
- Stoermer, E. F., B. G. Ladewski, and C. L. Schelske. 1978. Population responses of Lake Michigan phytoplankton to nitrogen and phosphorous enrichment. *Hydrobiologia* 57:249–265.
- Taylor, P. A., and J. L. Williams. 1975. Theoretical studies on the co-existence of competing species under continuous-flow conditions. *Can. J. Microbiol.* 21:90–98.
- Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58:338–348.
- Tilman, D., and S. S. Kilham. 1976. Phosphate and silicate growth and uptake kinetics of the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semicontinuous culture. *J. Phycol.* 12:375–383.
- Volterra, V. 1931. Variation and fluctuations of the number of individuals in animal species living together. In R. N. Chapman, ed. *Animal ecology*. McGraw-Hill, New York.
- Whittaker, R. 1967. Gradient analysis of vegetation. *Biol. Rev.* 42:207–264.
- Willis, A. J. 1963. Braunton Burrows: The effects on the vegetation of the addition of mineral nutrients to the dune soils. *J. Ecol.* 51:353–374.
- Yoshiyama, R. M., and J. Roughgarden. 1977. Species packing in two dimensions. *Am. Nat.* 111:107–121.
- Zedler, J. B., and P. H. Zedler. 1969. Association of species and their relationship to microtopography within old fields. *Ecology* 50:432–442.