Alternatives to Lotka–Volterra Competition: Models of Intermediate Complexity

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A family of one-level differential-equation competition models in which two populations are limited by the energy flowing into the system generates the following results. For competitors on the same and only resource: 1) Purely exploitative competition leads to exclusion; which species wins depends on relative abilities to appropriate and extract energy from the resource, and the relative death and maintenance rates. 2) If conspecific interference (e.g., deaths or energy loss from fighting, cannibalism, or display) is sufficiently high relative to abilities to exploit the common resource, competition for the same resource can lead to coexistence. 3) If heterospecific interference is sufficiently high relative to abilities to exploit the common resource, competition for the same resource can lead to a priority effect, in which the outcome depends on initial population sizes. 4) Depending on whether situation (2) or (3) prevails, an increase in the amount of the common resource can convert an outcome in which one species always wins into one giving coexistence (2) or a priority effect (3). 5) If species are similar to one another in their abilities to appropriate and extract energy from the common resource and show reciprocity in intererence costs, competition can have multiple outcomes; either one species wins or the species coexist, depending on initial values.

For competition on the same resource, but with each species monopolizing an exclusive resource as well: 1) Purely exploitative competition always leads to a unique point coexistence. 2) If interference is added to the system described in (1), two points of coexistence, separated by a saddle (an "unstable equilibrium") are possible. This is favored by a) a small yield from the exclusive resources relative to the common one; and b) strong interspecific relative to intraspecific interference.

INTRODUCTION

The Lotka–Volterra or logistic model of interspecific competition, first formulated about 50 years ago (Lotka, 1932; Volterra, 1926), quickly came to occupy a prominent position in population-dynamics theory. Its great popularity is only secondarily explained by a demonstrated coincidence with the real world. Certain systems, e.g., laboratory protozoans (Gause, 1934; Vandermeer,

309

1969), yeast (Gause, 1934) or beetles (Crombie, 1946; Neyman *et al.*, 1958) are well-mimicked by logistic competition models (or discrete analogs). But others, e.g., salamanders (Wilbur, 1972), microcrustaceans (Neill, 1974), lizards (Schoener, 1974a), or *Drosophila* (Ayala *et al.*, 1973; Gilpin and Ayala, 1973), seem inadequately described by the equations according to all but the most inexacting criteria. Primarily, Lotka–Volterra equations owe their popularity to their tractability: The equations are linear at equilibrium. This allows large numbers of species to be handled in simple mathematical operations, so that a theory of ecological communities can be readily developed (e.g., Levins, 1968; May, 1974; May and MacArthur, 1972; Roughgarden, 1974; Vandermeer, 1972). The equations thus compensate for a dynamical description of erratic exactness with a manageable model of communities near equilibrium.

Recently, some ecologists have become dissatisfied with the dominant position of Lotka–Volterra equations, in part because of the detail they obscure at the population level, in part because of an unease about the generality of a community theory built solely on a logistic model. Alternatives to Lotka–Volterra competition are becoming increasingly abundant in the ecological literature. These alternatives can be dichotomized in two ways.

First, models can be contrived as a single- or a multilevel system. The Lotka–Volterra system is, of course, an example of the former, as are models of Gilpin and Ayala (1973), Ayala *et al.* (1973), and Schoener (1973, 1974a). The commonest multilevel models include a single level below the competitors, that of the resources (Armstrong and McGehee, 1975; Hubbell, in preparation; Koch, 1974; MacArthur, 1968, 1972; May, 1971; Schoener, 1974a,b). By representing the resources as a linked dynamical system, the greatly constrained nature of resource renewal assumed by the one-level models is relieved. However, the mathematical complexity for any single model is often greatly increased, as is the number of possible models. Furthermore, two-level systems at equilibrium can reduce to the same form as single-level ones. For these reasons, and because they allow a greater elaboration at the competitor level, single-level models will probably continue to be useful.

A second dichotomy is descriptive versus mechanistic. Descriptive models (e.g., Ayala *et al.*, 1973) are often extremely successful in fitting biological data (e.g., Gilpin and Ayala, 1976, for competition models, or the notorious success of power functions with island biogeographical or physiological data). This success is probably a combination of numerical tractability and a real intermediacy or flexibility of form in a biological world characterized by great diversity. Mechanistic models (e.g., Schoener, 1973, 1974a) attempt to incorporate into their structure the exact physical form of the component processes resulting in competition. These commitments to algebra can result in special models for special kinds of competition (e.g., exploitative or interference) and even for special portions of a population's growth curve. However, because

their parameters directly correspond to biological quantities, they have two enormous advantages. First, predictions can be directly made as to how variations in these quantities affect the form and outcome of competition. Second, the models can be fitted to growth or equilibrium data, and the resulting computer-calculated parameter values can be checked against independent measurements of what the parameters purport to represent.

This paper discusses one-level, mechanistic models of competition and attempts to illustrate the first advantage. The models are more complicated extensions of simpler ones presented elsewhere (Schoener, 1973, 1974a). The additional complexity gives rise to a variety of new hypotheses not generated by the simpler models, yet is still reasonably tractable. The new results include the implications of competition for homogeneous resources, the effect of interference on competition for the same resource, the effect of increasing the amount of jointly used resource on competition mediated primarily by interference, and the conditions giving rise to multiple equilibria, including alternate stable points.

THE GENERAL MODEL

In previous papers (Schoener, 1973, 1974a), I presented two schemes for representing the effects of competition on reproductive output. One, leading literally to equations of Lotka–Volterra form, is of time-limited competing individuals. The other, leading to highly nonlinear forms, is of energy-limited competitors. Only this second type is considered here.

In the previous papers the following "pure" models were discussed: An *interference* model,

$$dN_1/dt = R_1 N_1 \left[(I_{E1}/N_1) - \gamma_{11} N_1 - \gamma_{12} N_2 - C_1 \right]$$
$$dN_2/dt = R_2 N_2 \left[(I_{E2}/N_2) - \gamma_{21} N_1 - \gamma_{22} N_2 - C_2 \right],$$

(1)

and an *exploitative* model,

$$dN_1/dt = R_1 N_1 \left[I_{01}/(N_1 + \beta N_2) - C_1 \right]$$
$$dN_2/dt = R_2 N_2 \left[\beta I_{02}/(N_1 + \beta N_2) - C_2 \right].$$

(2)

The symbols are defined as:

C_i = density-independent maintenance and replacement cost of an individual of Competitor i;

I_{Ei} = rate of net energy input into the population of Competitor i of resources exclusive to that competitor;

I_{0i} = rate of net energy input into the system that is usable by both competitors, in units of net energy for Competitor i;

N_i = number of individuals of Competitor i;

R_i = number of individuals resulting from conversion of one unit net energy input for Competitor i;

β = likelihood of an individual of Competitor 2 getting an item of resource relative to an individual of Competitor 1;

γ_{ii} = cost of interaction (interference) for an individual of Competitor i with an individual of Competitor i per unit time; and

γ_{ij} = cost of interaction (interference) for an individual of Competitor i with an individual of Competitor j per unit time.

Notice that the factors outside the square brackets are identical. The terms inside those brackets have the dimensions energy/(time × number) and give the instantaneous energy an individual has available for population increase, after deletion for competitive effects (energy loss and death), maintenance, and replacement. In Eq. (1), the species have exclusive resources, each individual getting I_{Ei}/N_i utilizable units from those resources. Individuals deplete one another's energy supply by interference (e.g., aggressive display, collision, fighting, etc.), assumed proportional to population size of the interfering group. The situations that do and do not lead to this "gas-molecule" assumption are given elsewhere (Schoener, 1973); alternatives have been proposed there and will be examined in detail in a future paper. In both models, a density-independent basic metabolic cost and death rate is subsumed under C; density-dependent deaths can be subsumed under the γ's. Finally, in the second model, the species compete for the same resource, dividing it such that each individual of Species 1 gets a fraction $1/(N_1 + \beta N_2)$ of the overlapping resource, and each individual of Species 2 gets a fraction $\beta/(N_1 + \beta N_2)$. Both resource-limitation terms assume that an individual can utilize all of its resource share. This assumption matters little at equilibrium, but should usually give unrealistic dynamics for N small. It can be relaxed at a minimal cost of one or two extra parameters, and the consequences of so doing will be explained in a future paper.[1]

The zero-isoclines of the first model are nonlinear: They descend at decreasing rates from the carrying capacity and approach the axis of the competing species asymptotically (Fig. 1a). A single intersection of the isoclines always exists, and

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[1] Specifically, if resource input is fast relative to population-dynamics time, an individual searching randomly for food can be shown to obtain approximately $I_{E1}/(y_1 + N_1)$ resources per unit of time where competition is strictly intraspecific and $I_{E1}/(Y_1 + N_1 + \beta N_2)$ resources if competition is both intra- and interspecific. Y_1 or y_1 is inversely proportional to the feeding period and the rate at which an individual of Species 1 can obtain food (see also Schoener, 1973).
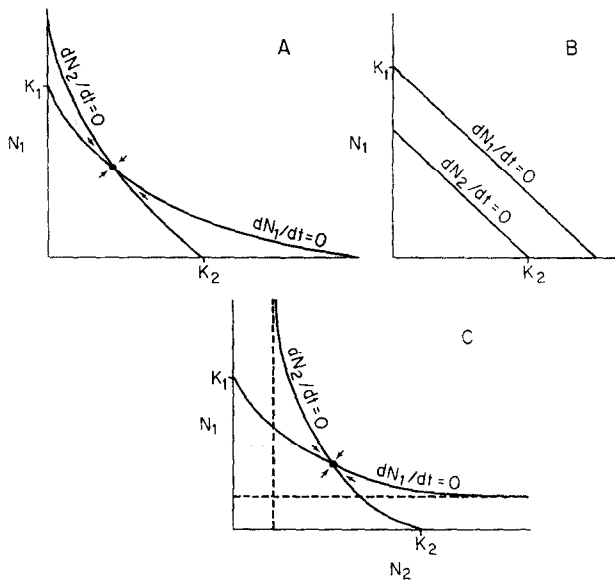
FIG. 1. Zero-isoclines for three simple competition models. (A) Interspecific competition purely interference; species have exclusive resources (Eq. (1)). (B) Interspecific competition purely exploitative; species have no exclusive resources (Eq. (2)). (C) Interspecific competition purely exploitative; species both have exclusive resources and a resource in common.

it is a stable node, so that coexistence at a unique point is always achieved. This great stability is due to the I/N terms and, in fact, may be thought an artifact of the assumption that an individual can utilize its resource share no matter how great that share is. Technically, once a species is reduced below a whole individual, it is extinct; realistically, stochastic events not in the model render an equilibrium near an axis very precarious. Thus coexistence is not certain. However, these considerations should not obscure the very stable nature of the biological process represented by I/N (or the similar term in footnote 1): The larger the population, the less resource each individual loses by the addition of another; or conversely, as population size goes down, each individual gets absolutely more and more resource to meet the exigencies of interference and to convert into offspring. This diminishing "per-individual" cost of competition is very different from a logistic model.

The zero-isoclines of the second model are linear and parallel (Fig. 1b). This means that if the inequality $\beta I_{02}/C_2 > I_{01}/C_1$ holds, Species 2 wins, whereas if the reverse holds, Species 1 wins. If everything is equal about the two species, the lines are coincident, and a whole collection of points exists at which growth ceases. Notice that both abilities to gain a unit resource (of which β is a ratio)

and abilities to utilize a resource once gained (incorporated into the I's) determine the outcome, and one may exactly counterbalance the other.

The foregoing models were reviewed in detail because they are the simplest that contain all the terms pertinent to our discussion of more complicated models. These terms are:

Term	1	2	3	4	5
For Species 1	$I_{01}/(N_1 + \beta N_2)$	I_{E1}/N_1	$-\gamma_{11}N_1$	$-\gamma_{12}N_2$	$-C_1$
For Species 2	$\beta I_{02}/(N_1 + \beta N_2)$	I_{E2}/N_2	$-\gamma_{22}N_2$	$-\gamma_{21}N_1$	$-C_2$

Terms 1–5 have dimensions energy/(time $\times$ number) and can appear in various combinations as M_i inside the square brackets of

$$dN_i/dt = R_i N_i [M_i(N_i, N_j)]. \tag{3}$$

It is M that is set equal to zero and solved for the zero-isocline. Notice also that at least one positive (1–2) and one negative (3–5) term must be present for equilibrium.

All possible versions of Eq. (3) have three major properties in common (we give them only for Species 1):

1. *The zero-isoclines monotonically decrease* $(dN_1/dN_2 < 0)$. This follows immediately upon implicitly differentiating $M_1(N_1, N_2) = 0$, the isocline equation for Species 1. For all terms included, this gives

$$-I_{01}(N_1' + \beta)/(N_1 + \beta N_2)^2 - I_{E1}N_1'/N_1{}^2 - \gamma_{11}N_1' - \gamma_{12} = 0. \tag{4}$$

For $N_1, N_2 > 0$, the sign of all terms containing $N_1' = dN_1/dN_2$ is negative, and all others are negative also. Consequently, N_1' is negative no matter what combination of terms is included in M_1.

2. *The isoclines (if not linear) are concave* $(d^2N_1/dN_2{}^2 > 0)$. Differentiating Eq. (4) implicitly,

$$[-I_{01}(N_1 + \beta N_2) N_1'' + 2I_{01}(N_1' + \beta)^2]/(N_1 + \beta N_2)^3 + [-I_{E1}N_1N_1''$$
$$+ 2I_{E1}(N_1')^2]/N_1{}^3 - \gamma_{11}N_1'' = 0. \tag{5}$$

For $N_1, N_2 > 0$, the sign of all terms including N_1'' is negative, but the sign of all other terms is positive. Hence N_1'' must be positive or zero. Concave isoclines seem a common deviation from linearity in real systems (e.g., Varley *et al.*, 1974; Gilpin and Ayala, 1973).

3. *No closed trajectories in the first quadrant can be generated by this family of models.* In particular, no semistable (or other) limit cycles exist for trajec-

tories involving N_1 and N_2 both positive. To show this, we use the Dulac extension of Bendixson's negative criterion (Andronov *et al.*, 1966): For no closed trajectories, it is sufficient to show there exists a multiplier $B(N_1, N_2)$, continuous and with continuous derivatives, such that

$$(\partial/\partial N_1)(B\,dN_1/dt) + (\partial/\partial N_2)(B\,dN_2/dt)$$

is of constant sign. Choose $B = 1/N_1N_2$. Then

$$(\partial/\partial N_1)(B\,dN_1/dt) = (R_1/N_2)(dM_1/dN_1)$$

and

$$(\partial/\partial N_2)(B\,dN_2/dt) = (R_2/N_1)(dM_2/dN_2).$$

For M containing at least one of Terms 1 or 2, both of these numbers are negative for all $N_1, N_2 > 0$.

Although having three major properties in common, the members of this family of models have differences that allow representation of diverse situations. In particular, note that concavity alone cannot tell us how many times the isoclines intersect, and the number and nature of the intersections make the models critically different. We now work our way through a series of models of increasing complexity, culminating in the model with all possible terms in M.

COEXISTENCE IN THE SIMPLEST EXPLOITATIVE MODEL

As noted for Eq. (2), competition for a uniform resource alone does not allow point coexistence. Two modifications of Eq. (2) give coexistence. We summarize the first here (for extensive discussion, see Schoener, 1974a) and the second in the next section.

Suppose each species has an exclusive resource which it uses in addition to its share of the overlapping resource. Then we have a model with Terms 1, 2, and 5 comprising M. The result is a zero-isocline that asymptotes at some non-zero value of N for each species. Hence, numbers cannot be reduced past a certain population size (that sustainable on the exclusive resource), and coexistence is guaranteed. In fact, the isoclines intersect exactly once in a stable node (Fig. 1C).

COEXISTENCE IN MODELS WITH COMPLETELY OVERLAPPING RESOURCES AND INTERFERENCE

The previous model agrees completely with our intuition concerning competition for shared and exclusive resources. While this agreement is perhaps reassuring, another less intuitive way to modify Eq. (2) toward coexistence will

now be presented. This involves the addition of only interference terms to those of Eq. (2), so that under certain circumstances exclusion resulting from competition for a single resource can be checked if interference is sufficiently high. We develop this model ($M =$ Terms $1 + 3 + 4 + 5$) by first discussing intermediate models ($M =$ Terms $1 + 3 + 5$ and $M =$ Terms $1 + 4 + 5$) as limiting cases. These intermediates preview the behavior of the full-blown model and produce some interesting results in their own right.

A. *Completely Overlapping Resources, Intraspecific Interference only (Terms 1, 4, 5)*

This model is

$$
\begin{aligned}
dN_1/dt &= R_1 N_1 \left[I_{01}/(N_1 + \beta N_2) - \gamma_{11} N_1 - C_1 \right] \\
dN_2/dt &= R_2 N_2 \left[\beta I_{02}/(N_1 + \beta N_2) - \gamma_{22} N_2 - C_2 \right].
\end{aligned}
\tag{6}
$$

The zero-isoclines are, for $dN_1/dt = 0$,

$$
\hat{N}_1 = -(C_1'/2) - (\beta N_2/2) + \{[(C_1'/2) - (\beta N_2/2)]^2 + I_{01}'\}^{1/2},
\tag{7}
$$

and for $dN_2/dt = 0$,

$$
N_1 = \beta[I_{02}' - \hat{N}_2(\hat{N}_2 + C_2')/(\hat{N}_2 + C_2')]^{1/2}.
\tag{8}
$$

where the primes indicate that the original parameter has been divided by γ_{11} (Eq. (7)) or γ_{22} (Eq. (8)). Notice we have written N_1 as a function of N_2 in both cases. Now from Eq. (4),

$$
d\hat{N}_1/dN_2 = -\beta I_{01}'/[I_{01}' + (\hat{N}_1 + \beta N_2)^2].
\tag{9}
$$

When this derivative is most negative ($N_2 = 0$), $d\hat{N}_1/dN_2 > -\beta$. From the analog for Species 2 of Eq. (4),

$$
dN_1/d\hat{N}_2 = -\beta - (N_1 + \beta \hat{N}_2)^2/\beta I_{02}'.
\tag{10}
$$

When this derivative is least negative ($N_1 = 0$), $dN_1/d\hat{N}_2 < -\beta$. Thus the slope of the isocline for Species 1 is everywhere less steep in the first quadrant than the slope for the isocline of Species 2. Hence, if the isoclines intersect in the first quadrant, they do so only once. Furthermore, it is obvious geometrically that the intersection must be a stable node (see also Fig. 2, Case 1 below).

It is easy to show the isoclines need not intersect at all for $N_1, N_2 > 0$. Note that

$$K_1 = -C_1'/2 + [(C_1'/2)^2 + I_{01}']^{1/2}$$
$$X_1 = I_{01}'/\beta C_1'$$
$$K_2 = -C_2'/2 + [(C_2'/2)^2 + I_{02}']^{1/2} \qquad (11)$$
$$X_2 = \beta I_{02}'/C_2'$$

where K_i (the carrying capacity of Species i) and X_i are the intercepts for $dN_i/dt = 0$ on the N_i and opposite axis, respectively. Then we can certainly have $K_1 > X_2$ and $K_2 < X_1$ (Species 1 wins) or vice versa. Likewise, the intercepts allow $K_1 < X_2$ and $K_2 < X_1$ (a stable node), but the reverse is impossible, as already shown geometrically and as can be proven algebraically.

This model shows that competition for the same resource can allow coexistence at a single point provided that self-inhibiting interference is great enough. Notice from Eq. (11) that, the larger the γ_{ii}'s, the smaller the K_i's, whereas the X_i's are not affected (recall that the primes signify the original parameter divided by the appropriate γ). Thus values of the γ's exist at which both K's are less than both X's, leading to coexistence. The result is analogous to that for the α's of Lotka–Volterra systems. It is perhaps not surprising in view of Haigh and Maynard-Smith's (1972) discussion for two-level models of the number of predators that can be supported on a given number of resources. However, the biological significance of the result should be underscored: Competition for a single resource can be stable given enough self-interference in the form of energy loss to the population (or of deaths). This self-interference may involve death from cannibalism or aggression, or involve energy lost in fighting, display, and even side-stepping. It will be greater, the smaller the area occupied by the population, so in that sense might reflect space as a second limiting resource. But in another sense, the interference can be considered an inevitable consequence of the need for individuals to remain in the same general area for reproduction. So long as enough energy or lives are lost in this way, coexistence must prevail.

This model also suggests how increasing the amount of the overlapping (and only) resource affects the outcome of competition. The quantities I_{01} and I_{02} include both the amount of resource available and the efficiency of its utilization once obtained. That is, $I_{0i} = \rho_i I_0$, where ρ_i is the efficiency of Species i on the resource. Increasing I_0, the amount of resource, thus increases I_{01} and I_{02} proportionately. But notice that of the four quantities in Eqs. (11), the K's increase only as the square root of I_0, whereas the X's increase linearly. This implies that any competitive situation resulting in exclusion of Species 1 or 2 can be made into one giving coexistence by increasing I_0 sufficiently, since such an increase causes both X's to exceed both K's.

B. *Completely Overlapping Resources, Interspecific Interference Only (Terms 1, 3, 5)*

This model is

$$dN_1/dt = R_1N_1\,[I_{01}/(N_1 + \beta N_2) - \gamma_{12}N_2 - C_1]$$

$$dN_2/dt = R_2N_2\,[\beta I_{02}/(N_1 + \beta N_2) - \gamma_{21}N_1 - C_2]. \tag{12}$$

The zero-isocline equations are, for $dN_1/dt = 0$

$$\hat{N}_1 = I_{01}'' - \beta N_2(N_2 + C_1'')/(N_2 + C_1''), \tag{13}$$

and for $dN_2/dt = 0$

$$N_1 = -(C_2''/2) - (\beta \hat{N}_2/2) + [(C_2''/2) - (\beta \hat{N}_2/2)^2 + I_{02}'']^{1/2}, \tag{14}$$

where the double primes indicate that the original parameter has been divided by γ_{12} (Eq. (13)) or γ_{21} (Eq. (14)). Notice the structural similarity between these equations and those for the opposite isoclines in the previous model (Eqs. (9) and (10)). From Eq. (4),

$$d\hat{N}_1/dN_2 = -\beta - (\hat{N}_1 + \beta N_2)^2/I_{01}''. \tag{15}$$

Where this derivative is least negative ($N_1 = 0$), $d\hat{N}_1/dN_2 < -\beta$. From Species 2's analog to Eq. (4),

$$dN_1/d\hat{N}_2 = -I_{02}''\beta^2/[\beta I_{02}'' + (N_1 + \beta\hat{N}_2)^2]. \tag{16}$$

Where this derivative is most negative ($N_2 = 0$), $dN_1/d\hat{N}_2 > -\beta$. Hence the slope of Species 1's isocline is everywhere more steep in the first quadrant than that of Species 2, the opposite situation from the previous model. Now the single intersection, if it exists, must be a saddle. Thus while allowing a priority effect, this model cannot give coexistence.

To show that the isoclines need not intersect in the first quadrant is again straightforward, given the intercepts:

$$K_1 = I_{01}''/C_1''$$

$$X_1 = -C_1''/2 + [(C_1''/2)^2 + (I_{01}''/\beta)]^{1/2}$$

$$K_2 = I_{02}''/C_2 \tag{17}$$

$$X_2 = -C_2''/2 + [(C_2''/2) + \beta I_{02}'']^{1/2}.$$

We can certainly have $K_1 > X_2$ and $K_2 < X_1$, or the reverse, leading to victory for one or the other species. We can also have $K_1 > X_2$ and $K_2 > X_1$, leading to a saddle, but the opposite is algebraically impossible.

In this model, a saddle or priority effect must exist, given γ_{ij}'s sufficiently large. Notice from Eqs. (17) that the K's do not change with increasing γ's (recall that the double prime signifies division by γ_{ij}), but the X's decrease. The result is analogous to that for α's in the Lotka–Volterra model: If both γ's are sufficiently large, a saddle ("unstable equilibrium") is achieved, no matter what the K's.

We also have an unambiguous result for the effect of increasing the amount of overlapping resources. As Eqs. (17) show, increasing I_0 (proportional to I_{01}'' and I_{02}'') will eventually result in the K's exceeding the X's, since the K's increase linearly with I_0, whereas the X's increase as $I_0^{1/2}$. Hence, a sufficient increase in the common (and only) resource can transform an unconditional superiority of one or the other species into a situation where the winner depends on initial population sizes.

C. *Completely Overlapping Resources, Inter- and Intraspecific Interference (Terms 1, 3, 4, 5)*

This model is

$$dN_1/dt = R_1 N_1 \left[I_{01}/(N_1 + \beta N_2) - \gamma_{11} N_1 - \gamma_{12} N_2 - C_1 \right]$$

$$dN_2/dt = R_2 N_2 \left[\beta I_{02}/(N_1 + \beta N_2) - \gamma_{22} N_2 - \gamma_{21} N_1 - C_2 \right]. \tag{18}$$

The zero-isocline equations are, for $dN_1/dt = 0$

$$\hat{N}_1 = -(C_1'/2) - (\beta N_2/2) - (\gamma_{12}' N_2/2)$$

$$+ \{[(C_1'/2) - (\beta N_2/2) + (\gamma_{12}' N_2/2)]^2 + I_{01}'\}^{1/2}, \tag{19}$$

and for $dN_2/dt = 0$

$$N_1 = -(C_2'/2\gamma_{21}') - (\beta \hat{N}_2/2) - (\hat{N}_2/2\gamma_{21}')$$

$$+ \{[(C_2'/2\gamma_{21}') - (\beta \hat{N}_2/2) + (\hat{N}_2/2\gamma_{21}')]^2 + \beta I_{02}'/\gamma_{21}'\}^{1/2}. \tag{20}$$

For this model, the isocline derivatives have no constant relation to one another, and the nature of the intersections depends on the parameters. To show this, we first take limits of the isocline equations (19) and (20). These limits depend

upon the sign of the coefficients of N in the squared quantity in the radical. This sign, in turn, depends upon the relation of β to the γ's. For the N_1-isocline,

$$\lim_{N_2 \to \infty} \hat{N}_1 = -\beta N_2 \qquad\qquad \gamma'_{12} > \beta \qquad\qquad\qquad (21a)$$

$$\lim_{N_2 \to \infty} \hat{N}_1 = -C_1' - \gamma'_{12}N_2 \qquad \gamma'_{12} < \beta \qquad\qquad\qquad (21b)$$

$$\lim_{\hat{N}_1 \to \infty} N_2 = -(C_1' + N_1)/\gamma'_{12} \qquad \gamma'_{12} > \beta \qquad\qquad\qquad (21c)$$

$$\lim_{\hat{N}_1 \to \infty} N_2 = -N_1/\beta \qquad\qquad \gamma'_{12} < \beta \qquad\qquad\qquad (21d)$$

For the N_2-isocline,

$$\lim_{N_1 \to \infty} \hat{N}_2 = -N_1/\beta \qquad\qquad \gamma'_{21} > 1/\beta \qquad\qquad\qquad (22a)$$

$$\lim_{N_1 \to \infty} \hat{N}_2 = -C_2' - \gamma'_{21}N_1 \qquad \gamma'_{21} < 1/\beta \qquad\qquad\qquad (22b)$$

$$\lim_{\hat{N}_2 \to \infty} N_1 = -(C_2' + N_2)/\gamma'_{21} \qquad \gamma'_{21} > 1/\beta \qquad\qquad\qquad (22c)$$

$$\lim_{\hat{N}_2 \to \infty} N_1 = -\beta N_2 \qquad\qquad \gamma'_{21} < 1/\beta \qquad\qquad\qquad (22d)$$
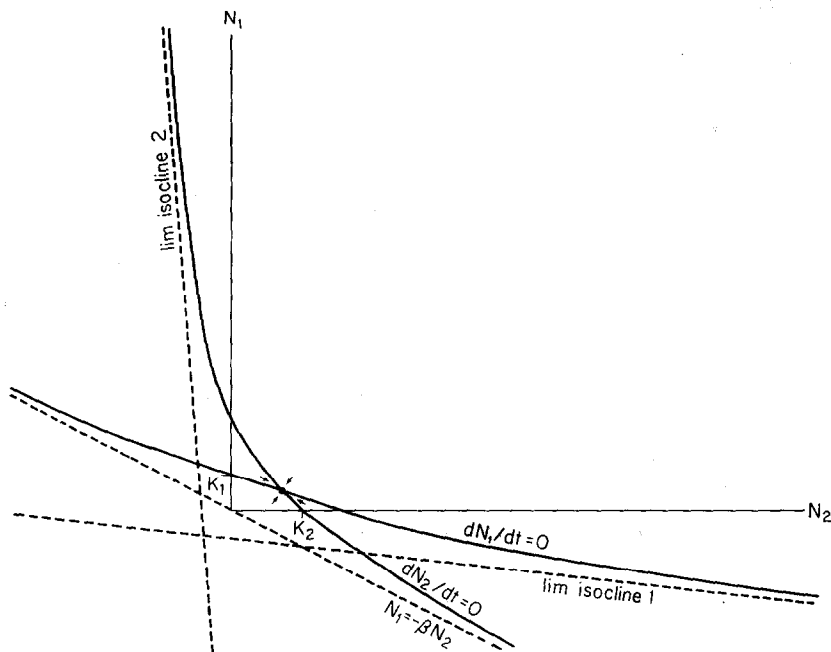

FIG. 2. Zero-isoclines for species with completely overlapping resources, inter- and intraspecific interference (Eq. (18)), Case 1: $\gamma'_{12} < \beta$; $\gamma'_{21} < 1/\beta$. A stable node occurs here if the isoclines intersect, as they do in the figure.

Combinations of the above conditions lead to four cases:

Case 1. $\gamma'_{12} < \beta$; $\gamma'_{21} < 1/\beta$. This case, of which Eq. (6) is a limiting form, is illustrated in Fig. 2. Notice that the isocline for Species 1 achieves its steepest slope $(-\beta)$ at the same value that the isocline for Species 2 has its least slope. Consequently, at most one intersection exists for $\hat{N}_1$, $\hat{N}_2 > 0$, and it is a stable node.

Case 2. $\gamma'_{12} > \beta$; $\gamma'_{21} > 1/\beta$. This case, of which Eq. (12) is a limiting form, is illustrated in Fig. 3. The configuration of its isoclines is structurally the same as Case 1, except that the species labels are reversed. This implies that the single intersection, if it exists, is a saddle.
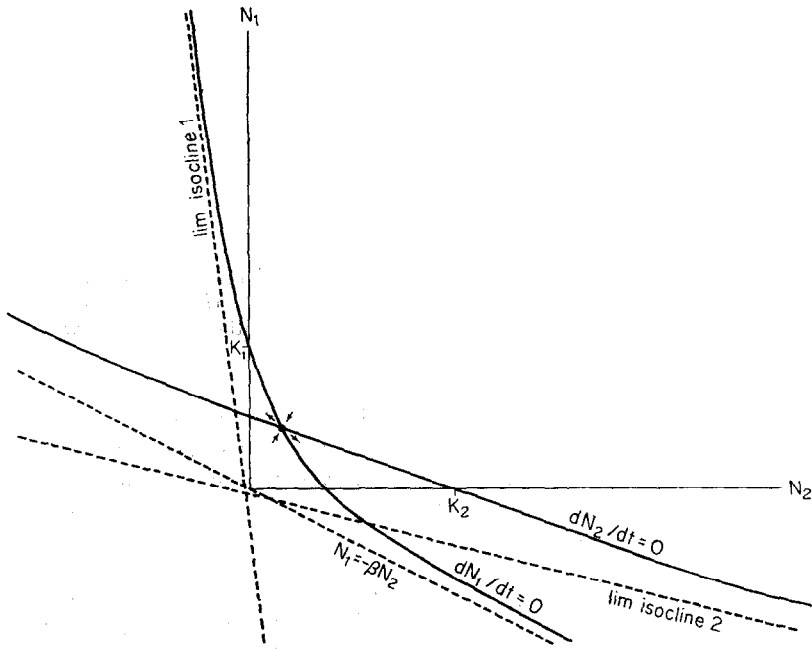

FIG. 3. Zero-isoclines for species with completely overlapping resources, inter- and intraspecific interference (Eq. (18)), Case 2: $\gamma'_{12} > \beta$; $\gamma'_{21} > 1/\beta$. A saddle (priority effect) occurs here if the isoclines intersect, as they do in the figure.

Case 3. $\gamma'_{12} > \beta$; $\gamma'_{21} < 1/\beta$. In this case, both isoclines have their least steep slope at $-\beta$ and increase to different limiting slopes (Fig. 4). Consequently, it is not obvious from the derivatives how often the isoclines can intersect. In fact, as many as *two* (but no more, as Appendix 1 shows) intersections for positive N_1 and N_2 can exist. These intersections must be a stable node and a saddle.
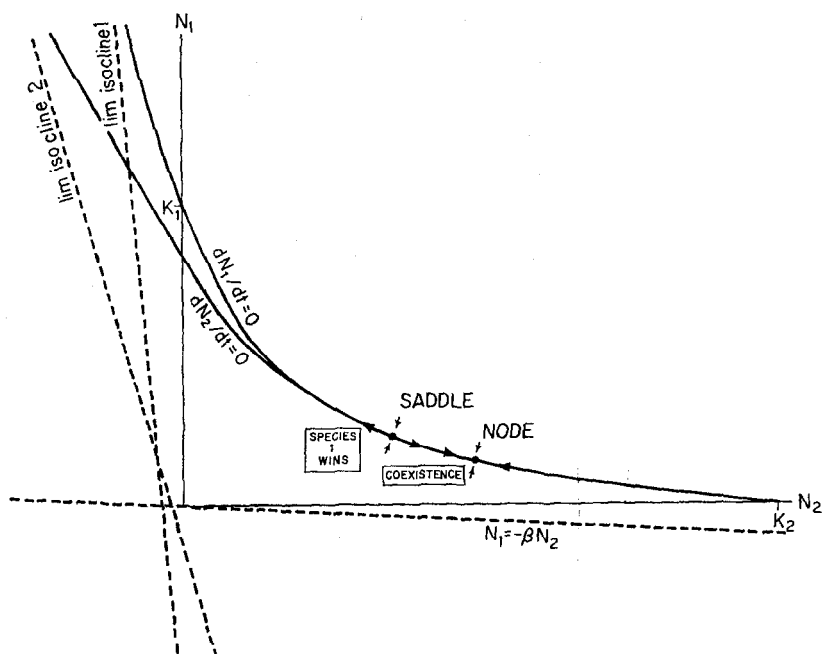
FIG. 4. Zero-isoclines for species with completely overlapping resources, inter- and intraspecific interference (Eq. (18)), Case 3: $\gamma'_{12} > \beta$; $\gamma'_{21} < 1/\beta$. Various possibilities can occur; in the figure, the isoclines intersect twice, and either Species 1 wins if it is abundant enough to start or there is coexistence.

The implication is that the phase plane is divided into regions of initial values where the outcome of competition is different: Either one species wins if abundant enough to start, or coexistence will prevail. Figure 4 gives a numerical example of this situation. Case 3 also allows a single intersection (of either variety) or no intersection at all.

Case 4. $\gamma'_{12} < \beta$; $\gamma'_{21} > 1/\beta$. If for an example of Case 3 we interchange 1's and 2's of all coefficients and set β equal to $1/\beta$, we obtain an example for Case 4 that is the mirror image of the example from Case 3. Therefore, the two cases have the same range of qualitative behavior.

Finally, the intercepts of this system are similar or identical to the less complicated intercepts of the previous two systems:

$$K_1 = -C'_1/2 + [(C'_1/2)^2 + I'_{01}]^{1/2}$$
$$X_1 = -C'_1/2\gamma'_{12} + [(C'_1/2\gamma'_{12})^2 + (I'_{01}/\beta\gamma'_{12})]^{1/2} \tag{23}$$
$$K_2 = -C'_2/2 + [(C'_2/2)^2 + I'_{02}]^{1/2}$$
$$X_2 = -C'_2/2\gamma'_{21} + [(C'_2/2\gamma'_{21})^2 + (I'_{02}\beta/\gamma'_{21})]^{1/2}.$$

This system has the following implications:

1.   The necessary conditions for stable point coexistence in Case 1 parallel these conditions in the Lotka–Volterra model. In both, the product of the α's or γ's must be less than 1. But in our nonlogistic model, the interference coefficients must be sufficiently less than the corresponding exploitative coefficients. In other words, γ'_{12} is the ratio of the per-individual interspecific cost of interference to the corresponding intraspecific cost, whereas β is the ratio of the inter- to intraspecific abilities to gain a unit of the overlapping resource (both for Species 1). Only where both interference coefficients are sufficiently small is coexistence an inevitable outcome of the isoclines intersecting. Depending upon the other parameters, the species may be too unequal for the isoclines to intersect. This is especially the case if the resource exploitation terms are very different: If one species has a much greater ability to obtain or to utilize resources, it will exclude the other regardless of the small interference costs. Thus in Eqs. (23), increasing I_{02} or β causes $K_2 > X_1$ and $X_2 > K_1$, extincting Species 1 (see also below).

2.   The conditions for a saddle in Case 2 likewise recall the Lotka–Volterra system. But here the interspecific interference costs must be large compared to the corresponding exploitative abilities.

3.   By taking limits in the isocline equations (18), we can determine for what parameters a difference can occur between the species sufficient to guarantee unconditional victory for one.

   a.   If one species has β (or $1/\beta$), the ability to gain the overlapping resource, sufficiently greater or less than the other, one will always win.

   b.   If one species has I_{0i}, the ability to utilize the overlapping resource, sufficiently greater or less than the other, one will always win. However, the cost terms are different.

   c.   If one species has γ_{ij}, the interspecific interference coefficient, maximally greater than another, it is guaranteed victory, but even if this cost for itself is zero, it may lose.

   d.   If one species has C_i, the density-independent death and maintenance rate, sufficiently less than another, it still may lose if its resource input is too small or the effect of the other species too large (this result contrasts with that for no interference, Eq. (2)). On the other hand, a sufficiently high C_i guarantees defeat.

   e.   If one species has γ_{ii}, the intraspecific interference coefficient, maximally less than another, it still may lose, for the same reason as (d). But a sufficiently high γ_{ii} guarantees defeat, again as in (d).

These results have evolutionary implications: Natural selection that increases

one of β or I_{0i} must cause an eventual lowering of community diversity, whereas selection decreasing one of the C_i's, γ_{ii}'s, or γ_{ij}'s has no necessary ultimate effect on diversity.

4. Increasing the amount of overlapping resource now has a variable effect. From Eqs. (23), we see that if the intraspecific interference coefficients are large enough, increasing I_0 will cause the K's to decrease relative to the X's. This ultimately gives a stable node. Conversely, if the interspecific coefficients are large enough, the X's will decrease relative to the K's, giving a saddle. Thus results from the simpler models (Eqs. (6) and (12)) hold under less limited conditions in the more general model. However, if the γ_{ij}/γ_{ii}'s from the two species are very unequal in their relative magnitudes, stabilization of an extinction situation is not guaranteed with an increase in I_0, and indeed the opposite may happen.[2]

5. As in Fig. 4, two intersections can occur only if the isoclines are fairly close to superimposition. Graphically, we see for Case 3 that this is favored, among other things, when the left-hand asymptotes (Eqs. (21), (22)) are similar. Thus $C_1' \cong C_2'/\gamma_{21}'$ and $\gamma_{12}' \cong 1/\gamma_{21}'$. To make the intercepts similar, we additionally must have $I_{02}'\beta/\gamma_{21}' \cong I_{01}'$. (These conditions can also be seen from the isocline equations (19) and (20).) The three conditions are favored by equality of certain parameters: the death and maintenance rates (C's), the abilities to utilize resources (I's), and the abilities to gain resources ($\beta = 1$ when these are equal). But in addition to equality, reciprocity is also involved. Thus a relatively high resource input is diminished by a high relative cost of interspecific interference (γ_{ij}/γ_{ii}). Furthermore, if the relative interference coefficients are reciprocals, coincident isoclines are favored, just as for the α's in Lotka–Volterra equations. The γ_{ij}/γ_{ii}'s are necessarily reciprocals if the intraspecific and interspecific costs are equal for each species. Of course, this is not the only way reciprocity can be met. Reciprocity will hold if individuals of one species affect conspecific and heterospecific individuals equally and greatly, while those of the other species affects both types of individuals only slightly. This situation might prevail if individuals of one species are large and aggressive, while those of the other are small and cowardly. Finally, also as for Lotka–Volterra type systems (Schoener, 1973, 1974a), changes in the intraspecific interference coefficient (γ_{ii}) affect the relative interspecific interference coefficient (γ_{ij}') and the carrying capacity in the same direction: This again favors parallel isoclines.

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[2] In particular, for Case 1, if $\rho_1/\rho_2 > \beta\gamma_{12}'$ and $\rho_2/\rho_1 > \gamma_{21}'/\beta$, an increase in I_0 can transform an extinction situation into a stable node. For Case 2, if the signs of these inequalities are reversed, an extinction situation can be transformed into a saddle. If one or the other but not both signs are reversed, various possibilities exist. In the system of Fig. 4, sufficient increase in I_0 causes the isocline of Species 1 to be everywhere above that for Species 2. Thus a situation where Species 2 can persist if abundant enough at the start is transformed into unconditional victory for Species 1.

COEXISTENCE IN MODELS WITH EXCLUSIVE AND OVERLAPPING RESOURCES
AS WELL AS INTERFERENCE (TERMS 1–5)

We now ask what happens when terms for exclusive resources are added to the model (Eq. (18)) just discussed. That is, what are the properties of the model with M (Eq. (3)) including all five possible terms?

We might suspect, by analogy with the model in Fig. 1A, that addition of exclusive resources for each species must prevent their extinction. In fact, this is so and for the same reason: The per-individual share of the exclusive resource becomes very high as the number of individuals decreases. Mathematically, this can be seen from the isoclines for each species (we can get simple explicit expressions only for one of the variables in terms of the other, because of the high degree of the system). The model is

$$dN_1/dt = R_1 N_1 \left[I_{01}/(N_1 + \beta N_2) + I_{E1}/N_1 - \gamma_{11} N_1 - \gamma_{12} N_2 - C_1 \right]$$
$$dN_2/dt = R_2 N_2 \left[\beta I_{02}/(N_1 + \beta N_2) + I_{E2}/N_2 - \gamma_{22} N_2 - \gamma_{21} N_2 - C_2 \right]. \tag{24}$$

The isocline for Species 1 is

$$N_2 = I'_{E1}/2\gamma'_{12}\hat{N}_1 - (C'_1/2\gamma'_{12}) - (\hat{N}_1/2\beta) - (\hat{N}_1/2\gamma'_{12})$$
$$+ \{[-(I'_{E1}/2\gamma'_{12}\hat{N}_1) + (C'_1/2\gamma'_{12}) - (\hat{N}_1/2\beta) + (\hat{N}_1/2\gamma'_{12})]^2 + I'_{01}/\gamma'_{12}\}^{1/2}. \tag{25}$$

The isocline for Species 2 is

$$N_1 = I'_{E2}/2\gamma'_{21}\hat{N}_2 - (C'_2/2\gamma'_{21}) - (\beta\hat{N}_2/2) - (\hat{N}_2/2\gamma'_{21})$$
$$+ \{[-(I'_{E2}/2\gamma'_{21}\hat{N}_2) + (C'_2/2\gamma'_{21}) - (\beta\hat{N}_2/2) + (\hat{N}_2/2\gamma'_{21})]^2 + \beta I'_{02}/\gamma'_{21}\}^{1/2}. \tag{26}$$

Comparison of Eq. (26) with Eq. (20) shows that they are identical except for the additional term $I'_{E2}/2\gamma'_{21}\hat{N}_2$ in Eq. (26). By taking limits, we can see that this term eventually dominates near the axes, causing the slope of the isocline to approach zero (for Species 1) or infinity (for Species 2). For the isocline of Species 1,

$$\lim_{\hat{N}_2 \to \infty} N_1 = 0 \qquad\qquad \gamma'_{12} > \beta \tag{27a}$$

$$\lim_{\hat{N}_2 \to \infty} N_1 = 0 \qquad\qquad \gamma'_{12} < \beta \tag{27b}$$

$$\lim_{\hat{N}_1 \to \infty} N_2 = -(C'_1 + N_1)/\gamma'_{12} \qquad \gamma'_{12} > \beta \tag{27c}$$

$$\lim_{\hat{N}_1 \to \infty} N_2 = -N_1/\beta \qquad\qquad \gamma'_{12} < \beta. \tag{27d}$$

For the isocline of Species 2,

$$\lim_{\hat{N}_1 \to \infty} N_2 = 0 \qquad\qquad \gamma'_{21} > 1/\beta \qquad\qquad (28a)$$

$$\lim_{\hat{N}_1 \to \infty} N_2 = 0 \qquad\qquad \gamma'_{21} < 1/\beta \qquad\qquad (28b)$$

$$\lim_{\hat{N}_2 \to \infty} N_1 = -(C'_2 + N_2)/\gamma'_{21} \qquad \gamma'_{21} > 1/\beta \qquad\qquad (28c)$$

$$\lim_{\hat{N}_2 \to \infty} N_1 = -\beta N_2 \qquad\qquad \gamma'_{21} < 1/\beta. \qquad\qquad (28d)$$

Comparison with Eqs. (21) and (22) shows the nonzero limits to be identical to those from the model (Eq. (18)) without exclusive resources. But the zero limits imply that at least one stable node will always be obtained. Let us examine the same cases as before.

Case 1. $\gamma'_{12} < \beta$; $\gamma'_{21} < 1/\beta$. Here we have exactly the same situation as in the previous model. The most negative derivative for Species 1's isocline is less negative than the least negative derivative for Species 2's isocline. Therefore, we
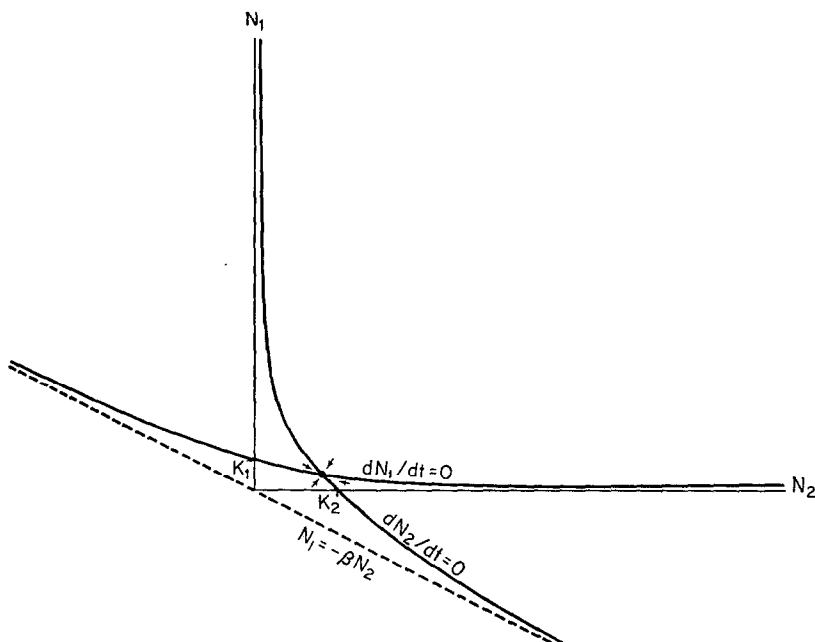

FIG. 5. Zero-isoclines for species with exclusive and overlapping resources, inter- and intraspecific interference (Eq. (24)), Case 1: $\gamma'_{12} < \beta$; $\gamma'_{21} > 1/\beta$. The isoclines must intersect exactly once, and coexistence (a stable node) results. Compare with Fig. 3.

have a stable node, and because of the asymptotic nature of the isoclines, the intersection is always at positive $\hat{N}_1$ and $\hat{N}_2$ (Fig. 5). This case thus yields a unique stable equilibrium.

Case 2. $\gamma'_{12} > \beta$; $\gamma'_{21} < 1/\beta$. This case is quite unlike the analog from the previous model. Rather than asymptote to the same line, the isoclines asymptote to opposite axes. This situation is very apt to lead to *two stable nodes*, separated by a saddle. It is easy to generate such a graph: Simply begin with the parameters giving a saddle for the simpler model (Eq. (18)) and add small exclusive-resource terms. The result is a graph nearly identical to that for the simpler model except near the axes, where the isoclines bend sharply. Figure 6A gives an example of
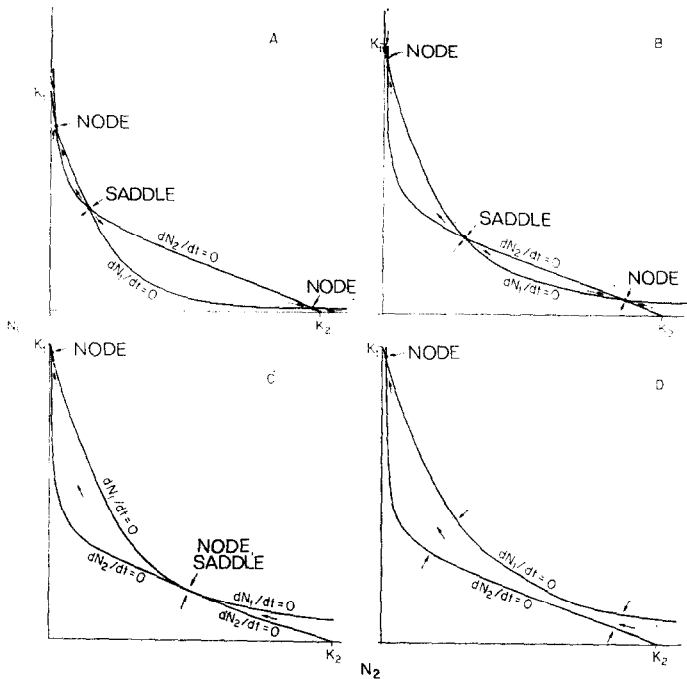

FIG. 6. Zero-isoclines for species with exclusive and overlapping resources, inter- and intraspecific interference (Eq. (24)), Case 2: $\gamma'_{12} > \beta$; $\gamma'_{21} > 1/\beta$. The isocline must intersect at least once, but may intersect three times. (A) Three intersections, two stable nodes and a saddle. Depending on initial values, one or the other stable node will be achieved, and the most abundant species to start will be the most abundant at equilibrium. Parts (B), (C), and (D) show how a gradual increase in the exclusive resource for Species 1 causes its isocline to lift almost completely above that for Species 2. The lower right stable node merges with the saddle (B, C), and eventually only the upper left node remains (D). In (D), coexistence occurs at relatively high values for Species 1, that species with the most abundant exclusive resources.

this; it is developed using parameters giving Fig. 3. (Whether more than three intersections can exist in this model is an open question; I am unable to show this analytically (explicit expressions like those in Appendix 1 do not exist) but am also unable to construct a numerical example.) Multiple stable points are favored in this model when the exclusive resources are scarce relative to the overlapping ones. As the amount of exclusive resource for one or both species increases, the one or both stable nodes migrate toward one another and eventually merge with and obliterate the saddle, giving a single stable node. Figs. 6A–D illustrates this sequence as the exclusive resource for a single species increases.

Case 3. $\gamma'_{12} > \beta$; $\gamma'_{21} < 1/\beta$. As for Case 2, situations giving two intersections for the model without exclusive resources now can give three: two stable nodes and a saddle. Figure 7 shows how two intersections for the simpler model (Fig. 4)
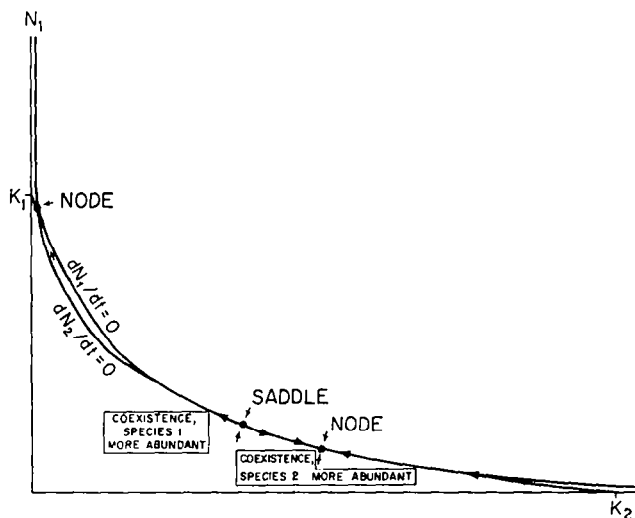

FIG. 7. Zero-isoclines for species with exclusive and overlapping resources, intra- and interspecific interference (Eq. (24)), Case 3: $\gamma'_{12} > \beta$; $\gamma'_{21} < 1/\beta$. Again, three intersections are possible. This graph was obtained from Fig. 4 by the addition of a small amount of an exclusive resource for each species.

can be changed to three: The exclusive resource "turns up" the isocline near the asymptote. This converts a phase-plane in which, depending on initial values, either Species 1 wins or coexistence is achieved, to one in which coexistence is always achieved, either at relatively high values of Species 1 or of Species 2, depending on starting numbers.

This model has the following implications.

1.   Multiple stable points are most favored when the exclusive resources are of small importance relative to resources in common. Small importance is measured as small net energy gain, either because of low resource abundance or low efficiency of energy extraction. Thus, if competition is primarily for some uniform resource, multiple stable points are likely, with the one the community settles in determined by initial values. And as the amount of exclusive resource increases, one or both stable points will coalesce with the saddle to form a single stable point.

2.   An especially likely situation for multiple stable points is one in which a strong interspecific interference component exists. Then a saddle can easily be transformed into a three-intersection system, with multiple stable points near each axis corresponding to very different relative abundances of the two species (Fig. 6A).

This increase in the amount of exclusive resources corresponds to an increase in the heterogeneity of the system, where the heterogeneity is viewed as the species discriminate it. Thus, the sequence in Fig. 6 shows how the multiple stable points of a mostly homogeneous system can change with an increase in heterogeneity to a single stable point. When that happens, the relative population sizes are determined by the structure of the heterogeneity, i.e., by the relative amounts of resource each species can monopolize.

3.   Exclusive resources in this system act exactly as would a constant level of migration. Notice that I/N, when multiplied by RN, the factor outside the square brackets of Eq. (3), gives a positive constant. This is exactly the way constant migration into a system is modeled (e.g., Schoener, 1973). Thus, instead of a small amount of exclusive resource for each species, we can interpret a small amount of migration into a homogeneous system as favoring multiple stable points. Our model is similar to the one Levin (1974) describes: Saddles are transformed into systems with multiple stable points by small migration between competition arenas. He is able to show, however, that the entire system, in which each site acts as source and recipient, can come to equilibrium, whereas in our model the source is not included.

4.   If the interference costs of competition (density-dependent energy loss and mortality) are all small relative to exploitative ones, only a single stable point will result (Case 1). In other words, the more complex model will approach the purely exploitive model given in Fig. 1C.

5.   Near coincidence of the isoclines is not necessary here for multiple intersections; e.g., the configuration of Fig. 6A is of quite noncoincident isoclines. This model contrasts with the model without exclusive resources: Its isoclines can have quite different slopes at the saddle, yet can still be bent back to intersect with one another near the axes.

These results can be compared to a real system in which multiple stable points seem to exist, the marine fouling community (Sutherland, 1974; Jackson and Buss, 1975). Sutherland and Karlson submerged ceramic plates at various months off North Carolina and monitored the relative abundances of their colonists for several years. Certain species, once established, exclude one another by a kind of priority effect: e.g., The tunicate *Styela* or the bryozoan *Schizoporella*, largely by the adults interfering with larval settlement. The system can move from one equilibrium to another under strong perturbation, such as abrupt and heavy mortality. Which equilibrium is arrived at depends on initial abundance of recruits, and is sometimes mediated by fish predation. Jackson and Buss note various interference mechanisms among space occupiers of foliaceous corals, including aggressive behavior, overgrowth, and allelo-chemical effects.

A variety of resemblances exist between the primary space occupiers of the fouling system and our model. First, competition is of course for space, a highly uniform and overlapping resource. This resource corresponds to our I_{0i} terms above and agrees with the notion that competition for a uniform resource is likely to lead to multiple stable points. (However, per-individual growth is unlikely to be proportional to $I_0/(N_1 + \beta N_2)$ initially, except near equilibrium, so the dynamics will be different.) Second, strong interspecific interference favors a priority effect as well as multiple stable points. This interference indeed exists for the fouling system. In the North Carolina experiments, already settled adults of one species apparently interfere with larval settling of another. Moreover, as in the model, the interference should most likely increase pro-portionally to the density of the interfering species, since the system is planar. Intraspecific interference may be relatively slight: A species with seasonal reproduction, once settled, is unlikely to interfere with subsequent conspecific settling because conspecific larvae are scarce or no longer exist. Hence, intra-specific interference must mainly involve the much less costly interaction among adults. Although thus complicated by differences in age structure being cor-related with differences in relative abundance, these data do suggest a kind of saddle whereby one or another species does not occur at equilibrium. Moreover, among other interpretations the "exclusive resource" terms may correspond to a small influx of immigrants from outside. In the tropical system, species produce allelochemicals they themselves resist, but which harm individuals of other species. Here again, interspecific interference is relatively great.

Thus, several characteristics of the fouling community suggest that multiple stable points should be frequent. While the North Carolina community is not known to show multiple stable points involving all the species (Sutherland, personal communication), such a situation, or one involving more than a single species, might be looked for in other fouling communities. A lack of certain species may indicate sufficient adult resistance or absence of sufficient immigra-

tion. Indeed, a complicated system of saddles "protected" by stable nodes near some axes but not others may exist.

Finally, some of the variability in this community may not be underlaid by an equilibrial system of alternative stable points. Rather, the community, which shows rapid change as space is being initially occupied, may shift into a period of much slower change. This period would begin when empty space has nearly disappeared, and the adults' resistance to displacement may cause the community to appear almost as constant as in a true population–dynamical equilibrium (see colonization models of Cohen and Schoener, in preparation). The number of possible communities during this second period is limited only by the number of possible colonization sequences, a number that could be very large indeed.

APPENDIX 1

This appendix shows that isoclines for Eq. (18) can intersect no more than twice. Let

$$Y = (\gamma'_{12} - \beta)/2 \tag{A1}$$

$$Q = [(1/\gamma'_{21}) - \beta]/2 \tag{A2}$$

$$F_1 = YN_2 + C'_1/2 \tag{A3}$$

$$F_2 = QN_2 + C'_2/2\gamma'_{21}. \tag{A4}$$

Then Eq. (19), the isocline of Species 1, is, from Eqs. (A1)–(A4)

$$\hat{N}_1 = -(C'_1/2) - N_2(\gamma'_{12} + \beta)/2 + (F_1^2 + I'_{01})^{1/2}. \tag{A5}$$

Equation (20), the isocline of Species 2, is

$$N_1 = -(C'_2/2\gamma'_{12}) - \hat{N}_2[(1/\gamma'_{21}) + \beta]/2 + (F_2^2 + \beta I'_{02}/\gamma'_{21})^{1/2}. \tag{A6}$$

Setting Eqs. (A5) and (A6) equal to one another and rearranging

$$(F_1^2 + I'_{01})^{1/2} = F - F_2 + (F_2^2 + \beta I'_{02}/\gamma'_{21})^{1/2}. \tag{A7}$$

Clearing the radicals,

$$F_1 F_2 \beta I'_{02}/\gamma'_{21} + F_1 F_2 I'_{01} - F_1^2 \beta I'_{02}/\gamma'_{21} - F_2^2 I'_{01} + (I'_{01} - \beta I'_{02}/\gamma'_{21})^2/4. \tag{A8}$$

Note that all terms of Eq. (A8) are in second or zero degree in F, so that the maximum degree in N_2 is 2. In fact, terms of first degree are also possible, as is obvious from substituting Eqs. (A3) and (A4) into Eq. (A8). Hence at most two roots of N_2 exist, corresponding to two intersections of the isoclines.

REFERENCES

ANDRONOV, A. A., VITT, A. A., AND KHAIKIN, S. E. 1966. "Theory of Oscillators," Addison-Wesley, Reading, Mass.

ARMSTRONG, R. A. AND McGEHEE, R. 1975. Coexistence of two competitors on one resource, *J. Theor. Biol.*, in press.

AYALA, F. J., GILPIN, M. E., AND EHRENFELD, J. G. 1973. Competition between species: Theoretical models and experimental tests, *Theor. Population Biol.* 4, 331–356.

CROMBIE, A. C. 1946. Further experiments in insect competition, *Proc. Roy. Soc. London Ser. B* 133, 76–109.

GAUSE, G. F. 1934. "The Struggle for Existence," Hafner, New York.

GILPIN, M. E. AND AYALA, F. J. 1973. Global models of growth and competition, *Proc. Nat. Acad. Sci. USA* 70, 3590–3593.

GILPIN, M. E. AND AYALA, F. J. 1976. Schoener's model and *Drosophila* competition, *Theor. Population Biol.* 9, 12–14.

HAIGH, J. AND MAYNARD-SMITH, J. 1972. Can there be more predators than prey? *Theor. Population Biol.* 3, 290–299.

JACKSON, J. B. C. AND BUSS, L. 1975. Allelopathy and spatial competition among coral reef invertebrates, *Proc. Nat. Acad. Sci. USA* 72, 5160–5163.

KOCH, A. 1974. Competitive coexistence of two predators utilizing the same prey under constant environmental conditions, *J. Theor. Biol.* 44, 387–395.

LEVIN, S. A. 1974. Dispersion and population interaction, *Amer. Natur.* 108, 207–228.

LEVINS, R. 1968. "Evolution in Changing Environments," Princeton Univ. Press, Princeton, N.J.

LOTKA, A. J. 1932. The growth of mixed populations: Two species competing for a common food supply, *J. Wash. Acad. Sci.* 22, 461–469.

MACARTHUR, R. H. 1968. The theory of the niche, *in* "Population Biology and Evolution" (R. C. Lewontin, Ed.), pp. 159–176, Syracuse Univ. Press, Syracuse, N.Y.

MACARTHUR, R. H. 1972. "Geographical Ecology," Harper and Row, New York.

MAY, R. M. 1971. Stability in multi-species community models, *Math. Biosci.* 12, 59–79.

MAY, R. M. 1974. On the theory of niche overlap, *Theor. Population Biol.* 5, 297–332.

MAY, R. M. AND MACARTHUR, R. H. 1972. Niche overlap as a function of environmental variability, *Proc. Nat. Acad. Sci. USA* 69, 1109–1113.

NEILL, W. E. 1974. The community matrix and interdependence of the competition coefficients, *Amer. Natur.* 108, 399–408.

NEYMAN, J., PARK, T., AND SCOTT, E. L. 1958. Struggle for existence; the *Tribolium* model: Biological and statistical aspects, *Gen. Systems* 3, 152–179.

ROUGHGARDEN, J. 1974. Species packing and the competition function with illustrations from coral reef fish, *Theor. Population Biol.* 5, 163–186.

SCHOENER, T. W. 1973. Population growth regulated by intraspecific competition for energy or time: Some simple representations, *Theor. Population Biol.* 4, 56–84.

SCHOENER, T. W. 1974a. Competition and the form of habitat shift, *Theor. Population Biol.* 6, 265–307.

SCHOENER, T. W. 1974b. Some methods of calculating competition coefficients from resource-utilization spectra, *Amer. Natur.* 108, 332–340.

SUTHERLAND, J. P. 1974. Multiple stable points in natural communities, *Amer. Natur.* 108, 859–873.

VANDERMEER, J. H. 1969. The competitive structure of communities: An experimental approach with protozoa, *Ecology* 50, 362–371.

VANDERMEER, J. H. 1972. On the covariance of the community matrix, *Ecology* 53, 187–189.

VARLEY, G. C., GRADWELL, G. R., AND HASSELL, M. P. 1974. "Insect Population Ecology," Univ. of California Press, Berkeley.

VOLTERRA, V. 1926. Variatzioni e fluttuazioni del numero d'individui in specie animali conviventi, *Mem. R. Accad. Linei Ser.* 6, II.

WILBUR, H. M. 1972. Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community, *Ecology* 53, 3–21.