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INTERFERENCE COMPETITION AND THE COEXISTENCE OF TWO COMPETITORS ON A SINGLE LIMITING RESOURCE[1]

RICHARD R. VANCE

Department of Biology, University of California, Los Angeles, California 90024 USA

Abstract. This paper proposes a mechanistic model of competition between two species for a single, nonaccumulating food resource. Actual organisms to which it may apply are sessile species like terrestrial plants and suspension-feeding benthic marine invertebrates whose energy source rains down upon them from the surrounding environment. The model's assumptions describe general functions involving population growth, resource consumption, resource availability, and interference. The population consequences of competition thereby arise in a specified way from the properties of individual organisms. The generality of the various component functions allows them to accommodate a wide range of species' morphological, physiological, and behavioral properties as well as relevant features of the physical environment. Accordingly, the overall model potentially approximates a correspondingly broad array of natural cases of competition.

This model demonstrates the theoretical possibility that two species jointly limited by the same energy resource can coexist at a globally stable equilibrium point. The proof of this assertion involves standard isocline analysis. It reveals that, in this case, coexistence depends upon species' interference as well as resource exploitation properties. In particular, the two can coexist if each species interferes less with resource acquisition by the other than with resource acquisition by itself and if this difference is great enough to overwhelm the advantage of the more efficient exploitation competitor.

The model includes the effects of space competition and abiotic disturbances. Field testing is discussed.

Key words: competition; disturbance; exploitation competition; interference competition.

INTRODUCTION

In this paper I shall show how it is possible, in principle, for two species that compete for a single limiting resource to coexist at a globally stable equilibrium point. The mechanism involves interference as well as exploitation competition. The model from which this conclusion emerges treats only a special case of resource competition, but because the model is mechanistic it provides at least a useful building block for constructing specific models for direct testing in particular natural systems. For a restricted class of competitive interactions, it may be empirically testable in its present form.

The importance of the possibility of a single limiting resource supporting multiple competitors arises from the commonplace observation that there coexist in nature many groups of apparently competing species whose differences in resource use seem too small to account for their continued persistence (Hutchinson 1959). This fact has stimulated several attempts during the past half century to find ways in which n competitors can coexist on fewer than n resources. Armstrong and McGehee (1980) review the history of these attempts, which, especially in the beginning, repeatedly produced the conclusion that such coexistence is not possible (Volterra 1928, Lotka 1932, Rescigno and Richardson 1965), although Levin (1970) proposes a slightly different view. These attempts all involve what

I call phenomenological models of competition that lack an explicit description of how consumers use resources and how they interact with each other in seeking these resources.

More mechanistic descriptions that include resource dynamics have been proposed by several authors in recent years (MacArthur 1970, 1972, Abrosov 1975, León and Tumpson 1975, Taylor and Williams 1975, Hsu et al. 1977, 1978, Case and Casten 1979, Case et al. 1979, Hsu and Hubbell 1979, Nunney 1980, Smouse 1980, Hsu 1981, Nunney 1981). Tilman (1980, 1982) reviews much of this literature. He argues from these mechanistic models that even though stable coexistence of more consumer species than resources may not be possible within any one uniform habitat, if there is sufficient spatial variability in resource abundance, then potentially many competitors can coexist regionally while exploiting even as few as two limiting resources.

Another group of authors has shown the possibility of such competitive coexistence even without spatial heterogeneity, if system properties produce a certain sort of perpetual oscillations in resource and consumer abundances (Koch 1974, Armstrong and McGehee 1976, McGehee and Armstrong 1977, Hsu et al. 1978, Nitecki 1978, Armstrong and McGehee 1980, Waltman et al. 1980, Butler and Waltman 1981). Such oscillations can arise in one-resource, two-consumer systems if the resource is itself a growing biological population. Coexistence occurs if one consumer exploits the resource more effectively when it is rare, while the other enjoys that advantage when the re-
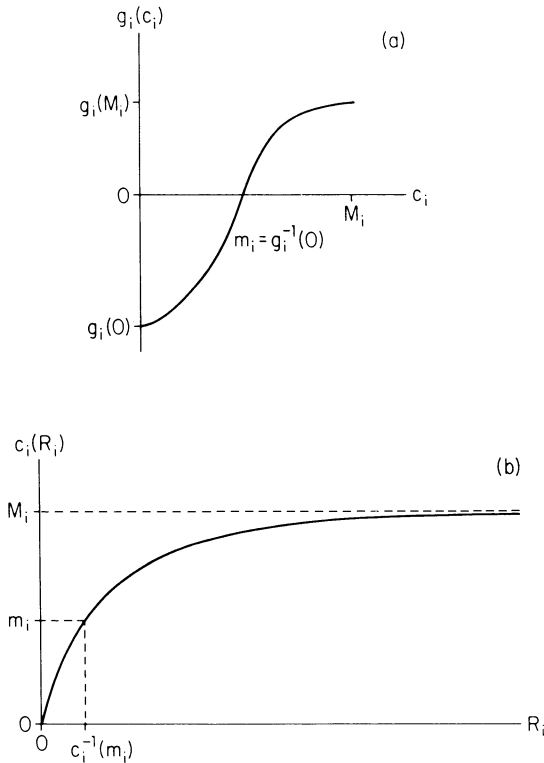
Fig. 1a. The per capita growth rate function $g_i(c_i)$. b. The per capita resource consumption function $c_i(R_i)$. All symbols are defined in assumptions 1 and 2. Selected values of the inverse functions are shown.

source is abundant. The system never approaches a stable equilibrium condition, but rather the combined exploitation by both consumers induces oscillations in resource abundance that in turn guarantee that neither competitor can drive the other to extinction.

In all of these models, the species interaction involves only exploitation competition in which each consumer affects the other solely by reducing resource abundance. Interference competition, in which each consumer alters the other's ability to exploit the resource at any abundance level, is less well understood primarily because it has not been clear how to describe it mathematically (Waltman et al. 1980). Both empirical (e.g., Connell 1961) and theoretical (Case and Gilpin 1974, Hsu 1981) work generate the impression that such direct interference between competitors strongly influences the possibility of their coexistence.

The model I shall propose describes how consumers use a resource and how they influence each others' ability to acquire this resource. To simplify the problem, I consider a special resource with two convenient properties: its input rate is not influenced by the consumer populations, and it cannot accumulate in the system. Actual resources that approximate this ideal are sunlight that comprises the energy resource for plants and the plankton that provides the energy supply for

suspension-feeding marine invertebrates that live attached to solid substrata on the bottoms and edges of large oceans. For this kind of resource, the only state variables in the competitive interaction are the abundances of the competitors themselves, because the resource can be treated as an input rather than as a state variable in the dynamical system. In this relatively simple case, resource competition between two consumers is a two-dimensional problem (Armstrong and McGehee 1980, Nunney 1980) that can be studied using the relatively straightforward but powerful technique of isocline analysis.

ASSUMPTIONS

I shall begin this section by describing the various features of the model in qualitative terms. Then I shall formalize these features as explicit assumptions, next briefly explain the content of the assumptions, and finally state the model as a dynamical system.

All resources except energy supply (sunlight, planktonic food) are assumed to occur in excess, and the population growth rate of each consumer species depends upon the rate at which individuals consume this one limiting resource. Resource consumption by each individual depends upon per capita resource availability which in turn depends upon resource input rate and the abundance and relative resource encounter rates of all consumer individuals.

Interference occurs as a reduction in the relative resource encounter rates of individuals caused by the presence of other individuals in the system. In nature, such a reduction occurs when one plant shades another because the shaded plant encounters less sunlight. Such a reduction also occurs when one filter-feeding invertebrate overgrows another. Being partly overgrown reduces an individual's ability to filter water for its contained food, and being wholly overgrown eliminates that ability altogether. (Overgrowth may also cause smothering, of course, but since starvation can produce an organism's death just as effectively as can oxygen deprivation, little realism is sacrificed by considering all interference as a reduction in the relative rate at which individuals encounter food.)

These ideas are formalized in the following assumptions. Let N_i = population size of species i, $i = 1, 2$. Denote the domain X and the range Y of a function f by $f:X \to Y$, where X and Y usually signify intervals.

Assume:

1) The per capita population growth rate of species i depends solely upon its per capita resource consumption rate c_i. It is given by $\dot{N_i}/N_i = g_i(c_i)$. The population growth rate function $g_i:[0,M_i] \to [g_i(0), g_i(M_i)]$, where $g_i(0) < 0$ and $g_i(M_i) > 0$, satisfies $g'_i(c_i) > 0$ for all c_i in the domain, and $g_i(m_i) = 0$ for some fixed m_i in the domain. (Here, m_i is the maintenance resource consumption rate, and M_i is the maximum resource consumption rate per individual of species i [Fig. 1a].)

2) The per capita resource consumption rate of species

i depends solely upon the per capita resource availability R_i to species i. It is given by $c_i(R_i)$. The consumption function $c_i:[0,\infty) \to [0,M_i)$ satisfies $c_i(0) = 0$, $c'_i(R_i) > 0$ for all R_i in the domain, and $c_i(R_i) \to M_i$ as $R_i \to \infty$ (Fig. 1b).

3) The per capita resource availability to species i is the product of two quantities. The first is the (constant) resource input rate u into the system. The second is the fraction of the resource encountered by all individuals in the community in a short time period that is encountered by a single individual of species i. The per capita relative resource encounter rate by species i is e_i; hence, the per capita resource availability to species i is $R_i = u \cdot e_i/(e_1 N_1 + e_2 N_2)$.

4) The per capita relative resource encounter rate of species i depends on the population sizes of both species. It is given by $e_i(N_1, N_2)$. The C^1 functions $e_i:[0,\infty) \times [0,\infty) \to (0,1]$ satisfy $e_i(0,0) = 1$, $e_i(N_1, N_2) > 0$, $(\partial/\partial N_j)e_i(N_1, N_2) < 0$, and $(\partial/\partial N_j)[e_1(N_1, N_2)N_1 + e_2(N_1, N_2)N_2] > 0$ for $i, j = 1, 2$ and all (N_1, N_2) in the domain, and $e_i(N_1, N_2) \to 0$ as either $N_1 \to \infty$ or $N_2 \to \infty$.

Together these assumptions describe two-species competition for a nonaccumulating resource in terms of functions that concern the morphological, physiological, and behavioral attributes of individual organisms. Assumptions 1, 2, and 4 potentially apply more generally to competition for any limiting resource.

Assumptions 1 and 2 specify consumer growth as a function of resource availability. This function is actually a composition of two functions: the growth rate depends upon consumption rate, which itself depends upon resource availability. Abrams (1980) and Nunney (1980, 1981) have also used general composition functions in this way.

Assumptions 3 and 4 together specify how exploitation and interference effects combine in the overall competitive interaction. Assumption 3 describes the exploitation component. Resource availability to each individual consumer depends on the number and species of other consumers present. Very simply, the fraction of the total resource input available to each consumer individual is equal to the fraction of the whole community's resource encounter rate that is experienced by that one individual. Without interference, i.e., with $e_i \equiv 1$, per capita resource availability is exactly equal to resource input rate per individual, $u/(N_1 + N_2)$, which can be thought of as per capita resource abundance.

Assumption 4 describes the interference component of the interaction. Individual relative resource encounter rate is 1 in very sparse populations, but it gradually declines toward 0 as populations become dense even though total community resource encounter rate increases. With these variable coefficients, per capita resource availability will generally differ from per capita resource abundance. The individuals of each species may encounter either more or less than their

proportionate share of the resource input, depending on the magnitudes of intraspecific and interspecific interference effects.

The dynamical system is:

$$\dot{N}_1 = N_1 g_1 \left\{ c_1 \left[\frac{e_1(N_1, N_2)u}{e_1(N_1, N_2)N_1 + e_2(N_1, N_2)N_2} \right] \right\}$$
$$\dot{N}_2 = N_2 g_2 \left\{ c_2 \left[\frac{e_2(N_1, N_2)u}{e_1(N_1, N_2)N_1 + e_2(N_1, N_2)N_2} \right] \right\} \qquad (1)$$

which I shall analyze in three stages.

ONE-SPECIES POPULATION GROWTH

If just one of these competitors occurred by itself, its growth equation would be:

$$\dot{N} = Ng\{c[u/N]\}, \qquad (2)$$

where I have dropped subscripts for simplicity. This basic population growth process underlies the competitive interaction of Model 1 in exactly the same way that the Verhulst-Pearl logistic equation forms the single-species basis of the Lotka-Volterra competition equations.

It is easy to show even in this very general formulation that population size approaches a unique, globally stable equilibrium point. This information is sufficient for present purposes. In Eq. 2, $\dot{N} = 0$ only if either $N = 0$ or $g\{c[u/N]\} = 0$. The monotonicity of the functions g and c guarantee that both have inverse functions. Therefore, this second condition implies that $c[u/N] = g^{-1}(0) = m$, or that $u/N = c^{-1}(m)$, where g^{-1} and c^{-1} are the inverses of the functions g and c. Hence Eq. 2 has two equilibrium points: the origin and $N^* = u/c^{-1}(m)$.

The origin is unstable, for if N is very slightly greater than zero, then $u/N \to \infty$, $c[u/n] \to M$, and $g\{c[u/N]\} \to g(M)$. Since $g(M)$ is positive, the population grows.

The composition function $g\{c[R]\}$ increases with R, and $R = u/N$ decreases with N. It follows that for positive $N < N^*$, $g\{c[u/N]\} > 0$, and the population grows. Similarly, for $N > N^*$, the population declines. Hence, the equilibrium point N^* is globally asymptotically stable.

This relatively simple argument in one dimension extends directly to the phase plane in the case of two competing species.

EXPLOITATION COMPETITION

To demonstrate the importance of interference, I shall first discuss purely exploitative competition. Without interference, all individuals experience peak relative resource encounter rates, $e_1 = e_2 \equiv 1$. Per capita resource availability is equal to per capita resource abundance, and Model 1 collapses to:

$$\dot{N}_1 = N_1 g_1 \{c_1[u/(N_1 + N_2)]\}$$
$$\dot{N}_2 = N_2 g_2 \{c_2[u/(N_1 + N_2)]\}. \qquad (3)$$

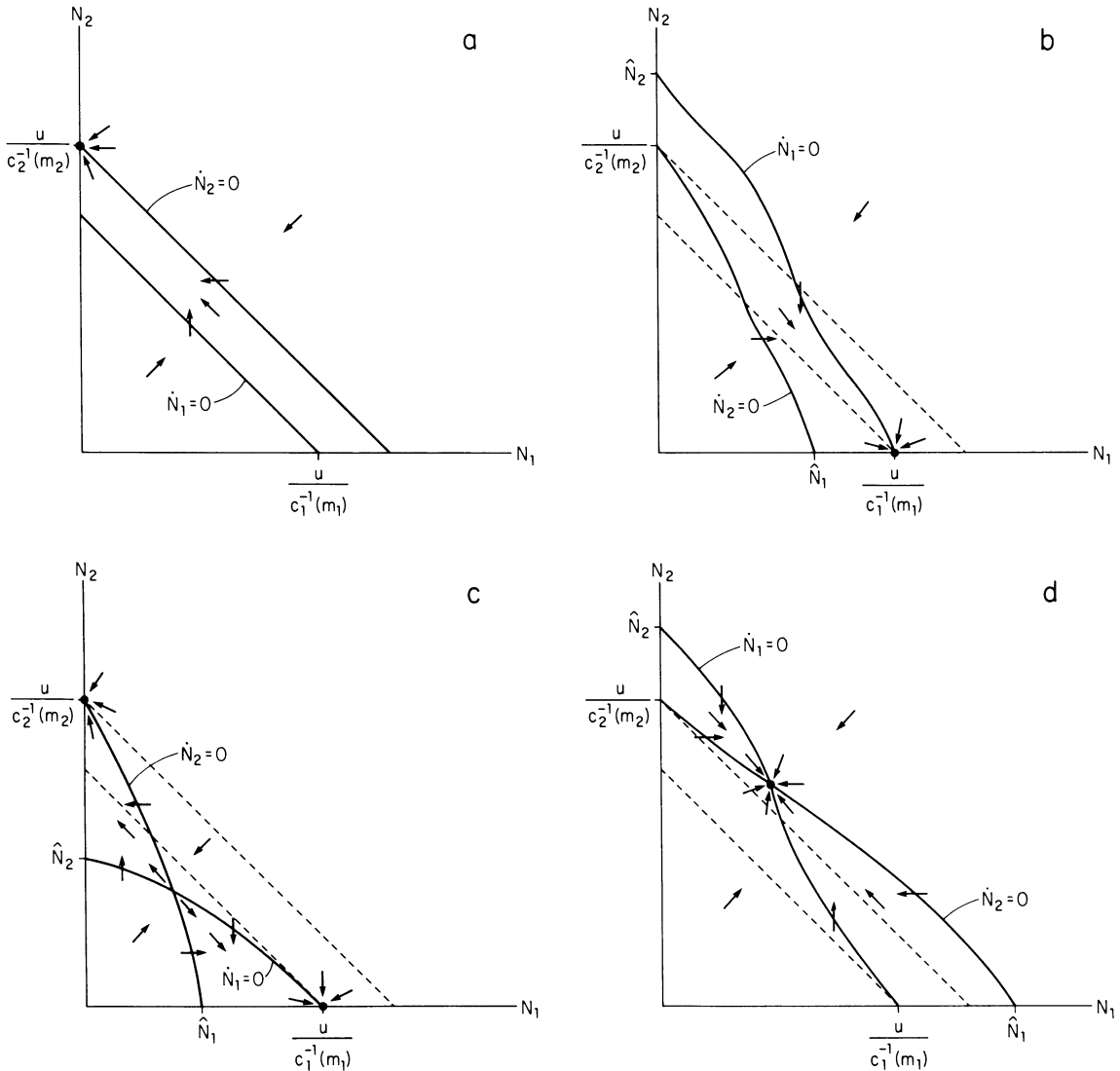The various equilibrium points emerge upon setting

Fig. 2. Isocline analysis of Model 3 (part a) and Model 1 (parts b, c, and d). (a) When competition is purely exploitative, species 2 wins because it exploits the resource more efficiently than species 1. These interference-free isoclines appear as dashed lines in the remaining parts of the figure. (b) In Model 1, case 1, species 1 wins because it is more aggressive than species 2. (c) In Model 1, case 3, there are two alternative locally stable, one-species equilibrium points because each species inhibits the other's relative resource encounter rate much more strongly than it inhibits its own. (d) In Model 1, case 4, globally stable two-species coexistence occurs because each species' relative resource encounter rate is much less inhibited by members of the other species than by members of its own species. The fact that the equilibrium point lies outside both dashed lines implies that the two species together reduce per capita resource abundance below the level that either species could by itself.

the $\dot{N}_i = 0$. One such point is the origin, but as in the one-species case this point is unstable. The values and the stability of the remaining equilibrium points are determined most easily by standard isocline analysis. Species i's isocline must satisfy $g_i\{c_i[u/(N_1 + N_2)]\} = 0$. By the monotonicity of g_i and c_i, this condition requires that $c_i[u/(N_1 + N_2)] = g_i^{-1}(0) = m_i$, or $u/(N_1 + N_2) = c_i^{-1}(m_i)$. That is, the species 1 and species 2 isoclines are given by, respectively,

$$N_1 + N_2 = u/c_1^{-1}(m_1)$$
$$N_1 + N_2 = u/c_2^{-1}(m_2).$$

By inspection, there are no values of N_1 and N_2 that satisfy both equations unless $c_1^{-1}(m_1) = c_2^{-1}(m_2)$ in which case the isoclines coincide. Otherwise, the two purely exploitative competitors of Model 3 can never coexist.

In general these two equations specify parallel straight

lines in the N_1-N_2 phase plane with the isocline of the species with the smaller value of $c_i^{-1}(m_i)$ farther from the origin. Qualitative behavor of system trajectories is determined exactly as in the well-known analysis of the Lotka-Volterra equations. As in the one-species case, species i increases if $N_1 + N_2 < u/c_i^{-1}(m_i)$ and decreases if this inequality is reversed. It follows that the winner of the competitive interaction is the species whose isocline lies farther from the origin (Fig. 2a).

The winner therefore has the smaller value of $c_i^{-1}(m_i)$. Inspection of Fig. 1 reveals that properties conducive to the competitive success of a species are a low maintenance energy requirement m_i and a steep resource consumption curve $c_i(R_i)$, which in turn requires high resource capture efficiency. These conclusions confirm biological intuition. A small value of $c_i^{-1}(m_i)$ guarantees a large population N_i^* and a small value of per capita resource abundance u/N_i^*. Hence the winner is the species that can reduce per capita resource abundance to the lowest level, a conclusion that also confirms the assertions of Hsu et al. (1977), Tilman (1977), and Waltman et al. (1980), who studied more complicated competition models.

The principal message of this section is that if competitive coexistence is possible in the full Model 1, then it must arise from the added effects of interference, since it is not possible without them.

INTERFERENCE COMPETITION

Analysis of Model 1 proceeds along lines similar to the foregoing but is complicated by the fact that the isocline equations define the isoclines implicitly rather than explicitly. Arguing as before, the species 1 and species 2 isoclines, respectively, are given by:

$$e_1(N_1,N_2)N_1 + e_2(N_1,N_2)N_2 = e_1(N_1,N_2)u/c_1^{-1}(m_1)$$
$$e_1(N_1,N_2)N_1 + e_2(N_1,N_2)N_2 = e_2(N_1,N_2)u/c_2^{-1}(m_2), \quad (4)$$

which this time do not describe straight lines.

What Eqs. 4 do describe are unique, continuous, strictly decreasing functions in the first quadrant of the phase plane. These conclusions can be proved using the implicit function theorem (Apostol 1974:Chap. 13). Alternatively, they can be established by the following direct argument. Continuity arises from the continuity of the functions $e_i(N_1,N_2)$ implied by their differentiability. For the remaining assertions, consider the species 1 isocline, which can be rewritten as:

$$e_2(N_1,N_2)N_2 = e_1(N_1,N_2)[u/c_1^{-1}(m_1) - N_1]. \quad (5)$$

Eq. 5 reveals that the isocline lies in the closed first quadrant only for N_1 in the interval $[0, u/c_1^{-1}(m_1)]$, since only then can both sides of the equation have the same sign. For any N_1 in this interval, Eq. 5 specifies a unique value of N_2 since the left-hand side (LHS) is a continuous function that strictly increases with N_2 from zero, and the right-hand side (RHS) is a continuous function that strictly decreases with N_2 toward

zero. The N_1-intercept of the isocline occurs at $N_1 = u/c_1^{-1}(m_1)$, and the N_2-intercept occurs at $N_2 = \hat{N}_2$, where $\hat{N}_2$ is the (unique) solution of Eq. 5, with $N_1 = 0$. For any N_2 in the interval $[0,\hat{N}_2]$, the associated value of N_1 is unique, because in the original species 1 isocline equation of Expression 4, the LHS is a strictly increasing continuous function of N_1, and the RHS is a strictly decreasing continuous function of N_1. It follows that the isocline equation specifies a one-to-one function. This function is necessarily monotonic and, because of its endpoints, strictly decreasing. Similar reasoning applies to the species 2 isocline.

The positions and detailed shapes of the isoclines, of course, depend on parameter values and on the functions $e_i(N_1,N_2)$. The new feature that arises from interference is the possibility that the isoclines may intersect. Consequently, all four of the qualitative outcomes well known from the Lotka-Volterra equations can occur in this system as well.

As they are stated, the four assumptions of this model fail to exclude the possibility of multiple intersections of the isoclines. Because this event violates my biological intuition, I shall henceforth cling to a fifth, rather vague assumption that the functions $e_i(N_1,N_2)$ are sufficiently "well behaved" that multiple intersections do not occur. Making this assumption explicit and understanding system behavior when it fails will require further study.

I shall now discuss the four "simple" possibilities in turn. The first possible outcome is that species 1 outcompetes species 2. As shown in Fig. 2b, this case arises if species 1's isocline lies outside species 2's isocline, which itself can arise from either (or both) of two sets of causes. Species 1 may be "more efficient" at exploiting the resource in the sense discussed in the last section, and interference effects may not be strong enough to change this relative advantage. Alternatively, interference effects may be so strong as to overwhelm any efficiency differences, and species 1 may be the "more aggressive" competitor.

Competitive aggressiveness of species 1 can arise in two ways. First, species 1 may inhibit the relative resource encounter rate of species 2 more than it inhibits its own. Since, from Eq. 4, the N_1-intercept of the species 2 isocline satisfies

$$\hat{N}_1 = \left[\frac{e_2(\hat{N}_1,0)}{e_1(\hat{N}_1,0)}\right] \cdot \frac{u}{c_2^{-1}(m_2)}, \quad (6)$$

such a pattern of inhibition would move this intercept toward the origin, inasmuch as the bracketed quantity would be <1. Second, species 1's relative resource encounter rate may be less inhibited by species 2 than is species 2's own rate. Since the N_2-intercept of the species 1 isocline satisfies

$$\hat{N}_2 = \left[\frac{e_1(0,\hat{N}_2)}{e_2(0,\hat{N}_2)}\right] \cdot \frac{u}{c_1^{-1}(m_1)}, \quad (7)$$

this pattern of inhibition would move the intercept

away from the origin by virtue of the bracketed quantity exceeding 1. If both of these effects occur at the same time, strong interference can reverse which species wins the competition. This is the situation depicted in Fig. 2b.

The second possible outcome of competition is that species 2 may win. This result is symmetrical to the previous case.

The third possible outcome (Fig. 2c) is that the isoclines may cross in such a way that the two-species equilibrium point is unstable. In this case, the system always converges to one or the other of the two locally stable one-species equilibrium points. This pattern results if the bracketed quantities in Eqs. 6 and 7 are both small, i.e., if each species inhibits the relative resource encounter rate of the other much more strongly than it inhibits its own. I do not know whether such situations occur in nature. Earlier theoretical models (Case and Gilpin 1974, Hsu 1981) have associated this outcome with interference, but these models lack a mechanistic description of how interference actually occurs biologically.

The fourth possible outcome (Fig. 2d) is stable coexistence. Competition produces this result if both of the bracketed quantities in Eqs. 6 and 7 are large enough. Biologically, this effect arises if each species inhibits the relative resource encounter rate of the other species less than it inhibits its own, and if this effect is strong enough to overwhelm the advantage of the more efficient exploitation competitor.

The dashed lines in Fig. 2d represent the species isoclines if there were no interference competition. As drawn, the two-species equilibrium point lies outside both dashed lines. Interference can cause this effect if intraspecific interference substantially exceeds interspecific interference. In this case, the combined equilibrium population size $N_1^* + N_2^*$ becomes large enough that the equilibrium per capita resource abundance $u/(N_1^* + N_1^*)$ is less than would occur if the more efficient exploitation competitor occupied the system alone. That is, the two species together exploit the resource more efficiently than either species can by itself.

Whether this kind of interference occurs in nature awaits appropriate empirical study. I suspect that such a pattern might characterize two sessile species that have different growth forms. Two tree species with different leaf placement patterns might each intercept some of the sunlight that is not as easily intercepted by the other. Similarly, two filter-feeding marine invertebrate species with different growth forms might each encounter planktonic material that sometimes escapes the other. In either of these cases, the relative resource encounter rate of an individual surrounded by heterospecifics would be less inhibited than one surrounded by an equal number of conspecifics, and stable coexistence would be expected even though both species exploit the same limited energy source.

Because the component functions appear in rather general form in Model 1, this model implicitly includes a variety of factors not mentioned so far; two of these are competition for space and physical environmental disturbances. I shall discuss these in the next two sections and then point out in the following section a useful connection between this model and the classical competition model of Lotka and Volterra.

COMPETITION FOR SPACE

Space itself is often viewed as the major limiting resource for sessile organisms like terrestrial plants and benthic marine invertebrates (Connell 1961, Paine 1966, Yodzis 1978). Because space is so important for these organisms, many have evolved elaborate mechanisms for securing it, protecting it, and usurping it from competitors. Ultimately, of course, the most indispensable resource for any organism, sessile or free living, is its energy supply. The significance of the attachment site of an organism adapted to a sessile way of life is that it makes possible the organism's acquisition of this energy. Space competition appears in Model 1, not explicitly, but rather in the form of interference (by shading, overgrowth, or otherwise) between organisms that arises during their competition for access to a common energy supply. When one organism takes away another's space, it eliminates its ability to acquire food.

Space competition between organisms that depend on different energy sources would, of course, require reformulation.

ENVIRONMENTAL DISTURBANCE

In recent years considerable attention has focused on the fact that environmental mortality-inducing disturbances can alter the outcome of competition (Connell 1978, Sousa 1979a, b). Sporadic disturbances like storms can prevent communities from ever reaching equilibrium. These nonequilibrium communities often support an increased number of species since repeated disturbances allow the persistence of colonizing species poorly adapted to survival under crowded conditions.

It has been argued independently by several authors that species composition in simple models of these nonequilibrium situations exactly corresponds to species composition in related equilibrium models provided that the latter include a constant mortality term of appropriate magnitude (Armstrong and Gilpin 1977, Cushing 1980, de Mottoni and Schiaffino 1981, Gopalsamy 1981). The nonequilibrium case then turns out to be simply an elaboration of the equilibrium model. Invoking this principle, I shall now discuss potential consequences of environmental disturbance in the relatively mechanistic Model 1 by examining the effects of constant density-independent mortality.

Again I shall proceed in three stages beginning with the single-species Model 2. Suppose that environmentally induced deaths occur at constant per capita rate

d. Then the growth function consists of two components, $g(c) = \tilde{g}(c) - d$, where $\tilde{g}(c)$ would be the growth function in the absence of such mortality. It is the same as $g(c)$ in Fig. 1, but $g(c)$ lies d growth rate units below $\tilde{g}(c)$. Now, $\tilde{g}(c)$ must obey assumption 1, and therefore there exists a fixed $\tilde{m}$ such that $\tilde{g}(\tilde{m}) = 0$. Since $\tilde{g}$, and hence $\tilde{g}^{-1}$, are strictly increasing functions, we have that m, the resource consumption rate at which g vanishes, must exceed $\tilde{m}$. That is, $g(m) = \tilde{g}(m) - d = 0$, or $\tilde{g}(m) = d$. Hence, $m = \tilde{g}^{-1}(d) > \tilde{g}^{-1}(0) = \tilde{m}$. Since c, and hence c^{-1}, are increasing functions, the fact that m exceeds $\tilde{m}$ implies that equilibrium population size $N^* = u/c^{-1}(m)$ declines, and per capita resource availability $R^* = u/N^*$ increases, as environmental harshness d increases. Of course, if d becomes too large, then even the maximum energy consumption rate M cannot produce sufficient growth to balance deaths, and the population becomes extinct.

Moving to the two-species exploitation competition Model 3, suppose that d_i is the per capita death rate of species i caused by physical disturbances. Then species i's growth function can be written as $g_i(c_i) = \tilde{g}_i(c_i) - d_i$, where $\tilde{g}_i(c_i)$ is its growth function in a disturbance-free environment. Since $\tilde{g}_i(c_i)$ must obey assumption 1, there exists a fixed $\tilde{m}_i$ at which $\tilde{g}_i$ vanishes. Disturbances guarantee that m_i exceeds $\tilde{m}_i$ by an amount that increases with d_i. As m_i increases, species i's isocline moves toward the origin, but its slope does not change. That is, disturbance-induced mortality affects the positions of the isoclines but cannot alter the fact that they are parallel. Since they never cross, stable two-species coexistence is never possible.

It remains true that a low maintenance energy requirement m_i increases a species' likelihood of winning in competition. In a disturbed environment, a low m_i arises from some combination of a low sensitivity to disturbances (i.e., a low d_i) and a steep growth curve $g_i(c_i)$, which amounts to a well-developed ability to convert consumed energy into growth. These conclusions confirm biological intuition.

Finally, consider the effect of density-independent mortality when competition involves interference as well as exploitation, Model 1. As shown in Fig. 2, interference can potentially affect several aspects of species isocline shapes, most notably their slopes. The one feature of each species isocline not affected by interference is the point at which it intersects its own axis, $u/c_i^{-1}(m_i)$. This point is, however, partly determined by the species' environment which includes mortality-inducing physical disturbances. Consider two competitors whose interference pattern alters isocline slopes in a way conducive to stable coexistence. Actual coexistence will occur only if the isoclines' fixed endpoints are such that the isoclines cross. Such crossing may occur if the physical environment experiences disturbances but fail to occur without these disturbances.

In this case, disturbance can be said to "cause" the coexistence of two competitors on a single limiting resource. The preceding argument establishes, however, at least for Model 1, that this effect can arise only in species with appropriate patterns of inter- and intraspecific interference.

CLASSICAL COMPETITION THEORY

The basic question I have addressed with Model 1 was first posed in mathematical form in the original works of Volterra (1928) and Lotka (1932). Standard analysis of their model has long been interpreted as proving the impossibility of two competitors coexisting stably on a single limiting resource (e.g., MacArthur and Levins 1967). The fact that this conclusion is wrong arises less from the simplified form of the Lotka-Volterra equations than from overinterpretation of the parameters r, K, and α in which this model is usually expressed.

Following a similar exposition by Tilman (1982), I shall show how the dynamics of the mechanistic Model 1 can be approximated by the phenomenological Lotka-Volterra system:

$$\begin{aligned}
\dot{N}_1 &= N_1[\beta_1 - \gamma_{11}N_1 - \gamma_{12}N_2] \\
\dot{N}_2 &= N_2[\beta_2 - \gamma_{21}N_1 - \gamma_{22}N_2],
\end{aligned} \tag{8}$$

where the β's and γ's are positive constants. To make the connection, it is necessary to interpret these constants in terms of appropriate quantities in Model 1.

Consider the equation for species 1. The per capita growth rate reaches its maximum value in both models as both $N_i \to 0$. This growth rate is $g_1(M_1)$ in Model 1 and β_1 in Model 8. Let $\beta_1 = g_1(M_1)$. The endpoints of the species 1 isocline for Model 1 are $N_1 = u/c_1^{-1}(m_1)$ and $N_2 = \hat{N}_2$. These endpoints for Model 8 are $N_1 = \beta_1/\gamma_{11}$ and $N_2 = \beta_1/\gamma_{12}$. Equating corresponding quantities yields $\gamma_{11} = \beta_1 c_1^{-1}(m_1)/u$ and $\gamma_{12} = \beta_1/\hat{N}_2$. When these same parameter interpretations are applied to the equation for species 2, there results a Lotka-Volterra system whose isoclines have the same endpoints as those of Model 1.

Unfortunately, the magnitude of the internal equilibrium point differs in the two models. The more important observation is that the existence and stability of the two-species equilibrium is preserved in the approximation. That is, if the isoclines cross in Model 1 then they also cross, and in the same direction, in the Lotka-Volterra approximation.

The foregoing argument supports two general claims. First, if parameters are interpreted appropriately, the Lotka-Volterra equations can provide qualitatively accurate information on a wide range of interspecies interactions. Second, since the competitive exclusion principle (Hardin 1960) can be derived explicitly from the Lotka-Volterra equations, which in turn reflect the qualitative behavior of Model 1, the conclusion that two competitors can coexist stably on a single limiting resource if their interaction involves interference as well as exploitation can be considered as a special case of the competitive exclusion principle.

DISCUSSION

The model of this paper advances understanding of competition in two ways. First, it describes competition mechanistically in terms of mathematical functions that depend upon the morphological, physiological, and behavioral properties of the organisms involved. This description reveals how organisms' various traits can work in tandem to produce the overall competitive vigor of species and the species composition of guilds. The main strength of this mechanistic description is that it brings competition theory closer to being empirically testable.

The second advance is the demonstration that two competing species can, in principle, coexist in stable equilibrium while exploiting a single limiting resource. The model provides a statement of conditions under which coexistence is possible, and it reveals the crucial role of interference between the competitors.

Previous mechanistic models have produced coexistence of several competitors on few resources, but by different means. Armstrong and McGehee (1980) and Butler and Waltman (1981) and coworkers have argued that n competitors can coexist while exploiting fewer than n resources provided that inherent nonlinearities produce a certain sort of perpetual system oscillations. Tilman (1980, 1982) and others have suggested that regional competitive coexistence is possible without oscillations provided the physical habitat exhibits sufficient spatial variation in resource abundance. Actually, the conceptual content (if not the formal mathematics) of my model relates to Tilman's view. Interference can take the form of one plant shading another. There results spatial heterogeneity in resource availability to the two plants. My model differs from Tilman's in that this heterogeneity is produced by the plants themselves.

This model invites empirical testing. As with any mathematical model, I envision this effort as proceeding in two stages. The first is qualitative, and its goal is simply to determine whether the model's basic idea content fits the particular natural system being studied. If it does not, some reformulation may be necessary. The second stage is quantitative, and its goal is to determine explicit forms for the general functions g_i, c_i, and e_i, complete with numerical estimates of all constants involved. The required measurements may not be easy. With these explicit functions, the model can be examined analytically or numerically to determine how various features of the species' biology influence their relative abundances and their coexistence.

There remain mathematical and ecological problems with the model that may require further analytical study to make empirical testing practical. First, some of the conclusions depend on the fifth assumption that the species' isoclines cross at most once. This requirement places some restriction on the relative resource encounter rate function e_i, whose nature is not clear.

Dropping this assumption opens the possibility of multiple stable points and a variety of limit cycles (Hirsch and Smale 1974:Chap. 12) which can give way to strange dynamical behavior when more than two species are involved (Hirsch 1982). Even without this assumption, however, it remains true that if isocline endpoints occur as in Fig. 2d, then the species can always coexist, though possibly not at uniquely determined stable population sizes.

Second, the realism of assumption 3, in which resource availability depends on resource encounter rates, is open to question. I chose this formulation because it insures that no system instabilities result from the dynamics of the resource itself. This feature seems realistic for the kind of resource considered. However, a reversal of functional dependence may be more natural. That is, it seems that resource encounter rates should depend in some way on the ambient resource level in the environment. It turns out that such formulations produce the same conclusions as this model but at the cost of a less complete understanding of resource dynamics. I shall explain this assertion in a future report. Which formulation will ultimately turn out to be more realistic and useful will be decided by empirical study.

The most serious flaw of this model is that it ignores the ages and sizes of individual organisms. This problem is shared by virtually all currently available competition models. Until this general issue receives appropriate mathematical treatment, field tests of these models must necessarily employ some ad hoc method of extracting "average" species properties from samples of individuals of all ages. For this model, a pragmatic procedure would be to consider the organisms' feeding organs, i.e., the leaves of trees or the feeding zooids of marine invertebrates, as the individuals comprising the population, and to simply ignore the fact that some of these share with others common support structures.

I view the present model as merely a step toward a truly realistic mathematical description of interspecies competition. I suspect that its conclusion that one limiting resource can support a stable assemblage of multiple consumer species when competition involves interference as well as exploitation will prove generic to a wide range of situations, both theoretical and natural.

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