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Coexistence of Species Competing for Shared Resources

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In this paper we develop a mathematical model in which any number of competing species can coexist on four resources which regenerate according to an algebraic relationship. We show that previous attempts to prove that n species cannot coexist on fewer that n resources (the "competitive exclusion principle") all make use of the very restrictive assumption that the specific growth rates of all competing species are linear functions of resource densities. When this restriction is relaxed, it becomes possible to find situations in which n species can coexist on fewer than n resources. On the basis of this and other observations we conclude that the competitive exclusion principle should be considered to apply only to coexistence at fixed densities.

1. INTRODUCTION

Volterra (1928) was apparently the first to use a mathematical model to suggest that the indefinite coexistence of two or more species limited by the same resource is impossible. This theme has been expanded by several authors into the statements that n species cannot coexist on fewer than n resources (MacArthur and Levins, 1964; Levins, 1968) or in fewer than n "niches" (Rescigno and Richardson, 1965), or most recently, on fewer than n "factors" (Levin, 1970).

Within the context of his model, Volterra proved a very strong result: that as time goes to infinity, all species except one will approach extinction. Rescigno and Richardson (1965) and Levin (1970) have attempted to provide equally strong statements in the case of multiple resources: they have attempted to show that

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whenever n species compete for fewer than n resources (factors), at least one species must approach extinction.

Unfortunately, these attempts to prove that n species cannot coexist on fewer than n resources (factors) all make use of the very restrictive assumption that the specific growth rates of all competing species are linear functions of resource (factor) densities. In this paper we show that when this linearity restriction is relaxed, it becomes possible to find situations in which n species can indeed coexist on fewer than n resources.

We begin with a derivation of Volterra's original model. Postulate the existence of m species N_i, $i = 1, \ldots, m$, competing for the same resource R. Assume that the specific growth rate of each species increases linearly with the amount of resource present so that

$$(1/N_i)(dN_i/dt) = \gamma_i R - \sigma_i, \qquad i = 1, \ldots, m. \tag{1}$$

Next assume that the amount of resource available to any competitor at time t is diminished by the presence of the competitors so that at any instant

$$R = R_{\max} - F(N_1, \ldots, N_m), \tag{2}$$

where $F(N_1, \ldots, N_m)$ is an unbounded increasing function of the population densities N_i. Substituting (2) into (1) and replacing $\gamma_i R_{\max} - \sigma_i$ by ϵ_i yields Volterra's original equations

$$dN_i/dt = N_i[\epsilon_i - \gamma_i F(N_1, \ldots, N_m)]. \tag{3}$$

Volterra showed that as $t \to \infty$ the species with the largest value of ϵ_i/γ_i will approach a finite nonzero density and the remaining species will all approach extinction.

Several simplifying assumptions are implicit in the above model. (i) The competitors are totally resource-limited: Their specific growth rates are functions of R alone, not of the N_i. (ii) There is no age structure or spatial patterning of competitor populations. (iii) The resource is uniform in quality. For example, if the resource consists of particles of food, these are uniform in size and nutritional value. (iv) There is no explicit time dependence to the interaction either in terms of time-dependent interaction parameters or external forcing, and there are no time lags. Coexistence has been shown to be possible in many cases where one or more of these assumptions are violated (Hutchinson, 1961; Haigh and Maynard Smith, 1972; Stewart and Levin, 1973; Koch, 1974a).

Two other assumptions have received less attention. These assumptions are (v) that the resource available at time t is a function of the population densities of the competitors at time t (cf. Eq. 2), and (vi) that the specific growth rate of each competitor is a linear function of resource density. Previous work (Koch, 1974b; McGehee and Armstrong, 1976) has shown that if both restrictions (v) and (vi) are relaxed simultaneously, so that the resource regenerates according to a differential equation (relaxing condition [v]) and the growth rates of the competitors are not linear functions of resource density (relaxing condition [vi]), then the coexistence of two competitors on one resource is indeed possible. Zicarelli (1975) has extended this result to the case of any number of species on one resource.

In the above studies, both conditions (v) and (vi) have been relaxed simultaneously. It is therefore of considerable interest to note that the coexistence of n species on fewer than n resources can be obtained even if condition (v), which requires the resource to regenerate according to an algebraic relationship, remains intact. The proof of this assertion is the subject of the following section.

It therefore appears that the linearity restriction (vi) on competitor growth rates is by itself of critical importance to any proof of the competitive exclusion principle.

2. Coexistence of Any Number of Species on Four Conservative Resources

2.1. *Definitions of Coexistence, Persistence. and Competitive Exclusion*

Our basic assumption is that the population dynamics of a community consisting of n species is modeled by a system of differential equations of the form

$$\dot{x}_i = x_i f_i(x_1, \ldots, x_n), \qquad i = 1, \ldots, n. \tag{4}$$

Here x_i is the density of species i and $f_i(x_1, \ldots, x_n)$ is its specific growth rate. In terms of this model we can give two definitions of "coexistence" and "persistence." We shall make the somewhat arbitrary distinction that persistence is a property of communities while coexistence is a property of species.

Definition 1. System (4) is said to exhibit *persistence at fixed densities* if it has an asymptotically stable equilibrium point $(\bar{x}_1, \ldots, \bar{x}_n)$ with $\bar{x}_i > 0$, $i = 1, \ldots, n$.

If each species starts near its equilibrium density $\bar{x}_i$, then all species in a system satisfying the above definition will tend asymptotically to their equilibrium densities. Since all species are present at the equilibrium we say that they are coexisting at fixed densities.

Definition 1 is far too restrictive to serve as a general definition of persistence. A predator–prey system can exhibit oscillations with neither species ever approaching either extinction or constant density. Such a system should be considered persistent. To include possibilities other than coexistence at fixed densities we use a notion common in the mathematical theory of dynamical systems, namely, the notion of an "attractor." Roughly speaking, we define an *attractor block* to be a region in the state space $\{(x_1, ..., x_n)\}$ such that solutions starting on the boundary of the region pass into its interior. (A precise definition of "attractor block" can be found in a previous paper [McGehee and Armstrong, 1976].) If the species start initially with densities in the attractor block, their densities will remain in the block for all future time. If $x_i > 0$, $i = 1, ..., n$, at all points within the block, then no species will ever approach extinction for any solution in the block, and the system is considered persistent.

DEFINITION 2. The system (4) is said to exhibit *persistence* if it has an attractor block bounded away from the n faces $\{x_i = 0\}$, $i = 1, ..., n$.

If a community is persistent and if the population densities lie within the attractor block, then we shall say that all species are coexisting. Note that persistence at fixed densities (Definition 1) is a special case of persistence (Definition 2). In the first case, the densities are either constant or are approaching constant values. In the second case, the densities may be fluctuating in a seemingly unpredictable way.

In Section 2.3 we shall consider communities in a periodically changing environment, so that each f_i is a function also of time. In such cases we add the time axis to the state space and Definition 2 still applies. It is possible that the attractor block as seen in $(x_1, ..., x_n)$-space may be different at different times t.

We are interested in imposing certain structures on the system (4) and in determining whether those structures imply the impossibility of persistence. These structures can be interpreted to model the situation where the species in the community are competing for resources. We are interested in the case where there are fewer resources than species.

DEFINITION 3. A given structure will be said to exhibit *competitive exclusion* if no system with that structure is persistent.

The Volterra model described in Section 1 is an example of such a structure. The parameters of the model are the constants m, γ_i, σ_i, and $R_{\max}$ and the function F. For different parameters, we get different systems, but they all have the same structure. Volterra proved that no system with this structure can be persistent and hence that this structure exhibits competitive exclusion.

Our major objection to Volterra's model is the assumption of linearity in Eq. (1). It is conceivable that the function F in Eq. (2) is linear, but it is entirely unreasonable biologically to assume that the specific growth rates are linear functions of the resources. A species will always have a maximum growth rate, even when resources are unlimited.

In the following sections we relax Volterra's linearity assumption and show that the resulting structure does not exhibit competitive exclusion. To accomplish this task, we need produce only one system with this structure which exhibits persistence. In the sections which follow we develop such a system.

2.2. *Conservative Resources*

A resource which satisfies assumption (v), that the resource available at time t is a function of the densities of the competing species at time t, will be called a resource regenerating according to an algebraic relationship. A special subclass of resources regenerating to algebraic relationships is the class of "conservative resources," in which the function F of Eq. 2 is a linear function at species densities. Examples of conservative resources are space and nutrients. In such cases the total amount of resource is fixed, and the amount available for exploitation at any given time is simply the difference between the total amount and the sum of the amounts in use by the competitors at that time.

More precisely, we consider a system of n species and k conservative resources. Let x_i be the density of species i and let z_j be the available amount of resource j. We then write

$$\begin{aligned} \dot{x}_i &= x_i u_i(z_1, \ldots, z_k), \qquad & i &= 1, \ldots, n, \\ z_j &= z_{j\max} - \sum_{i=1}^{n} s_{ji} x_i, \qquad & j &= 1, \ldots, k, \end{aligned} \tag{5a}$$

where we also demand that

$$s_{ji} \geqslant 0 \qquad \text{and} \qquad \partial u_i/\partial z_j \geqslant 0 \qquad \text{for all } i, j. \tag{5b}$$

In other words, the amount of resource j in use by species i increases linearly with the density of species i and the specific growth rate of species i is a nondecreasing function of the available amount of resource j. We do not demand strict inequality since species i may not use resource j. However, it is reasonable to assume that

$$s_{ji} > 0 \qquad \text{if and only if} \quad \partial u_i/\partial z_j > 0; \tag{5c}$$

that is, if species i uses resource j, we demand strict inequalities in (5b).

In the following sections we shall construct a system of the form (5a), satisfying assumptions (5b) and (5c), with $k = 4$ and n arbitrary. In this system none of the n competing species can ever approach extinction, so that this example will constitute a proof that n species can coexist indefinitely on four conservative resources. Since the class of conservative resources is contained in the more general class of resources which regenerate algebraically (i.e., by a function such as [2]), this example will also show that any number of species can coexist on four resources which regenerate algebraically.

We shall proceed in three steps. First we shall show that any number of species can coexist on one conservative resource in a periodically changing environment. Next we shall interpret a result of Smale to show that a system of three species and three conservative resources can have an attracting periodic orbit. Finally, we shall combine these two results to construct the desired system.

2.3. *Coexistence of n Species on One Conservative Resource Plus Time*

Consider a set of n species x_i which inhabit an environment periodic in time and whose growth is described by the equations

$$\dot{x}_i = x_i u_i(z, t), \qquad i = 1,\dots, n, \tag{6a}$$

where

$$z = z_{\max} - \sum_{i=1}^{n} s_i x_i . \tag{6b}$$

We shall show that all species will coexist for appropriate growth functions u_i.

The basic idea is very simple. Each species has a growing season disjoint from all others. When a species starts its growing season, the densities of all other species are always low enough (hence the available resource abundant enough) that this species is able to increase to near its carrying capacity. After its growing season each species dies off sufficiently rapidly that it interferes only slightly with the growth of the other species.

Assume that the environment is periodic with period 1. Suppose that the growing season for species i begins at time α_i and ends at time β_i. For simplicity we assume that the growth functions in (6a) are given by

$$u_i(z, t) = \gamma_i z g_i(t) - \sigma_i . \tag{7a}$$

The $g_i(t)$ are "gating functions" which are defined to be

$$\begin{aligned} g_i(t) &= 1 \qquad \text{for} \quad \alpha_i \leqslant t \leqslant \beta_i . \\ &= 0 \qquad \text{for} \quad 0 \leqslant t < \alpha_i \quad \text{or} \quad \beta_i < t \leqslant 1. \end{aligned} \tag{7b}$$

Thus species i grows at a rate $\gamma_i z - \sigma_i$ during its growing season and dies off at a rate σ_i outside this season. The exact form of these gating functions is unimportant; the "square pulse" form (7b) is used only because it will make later computations easier.

We assume the growing seasons to be sequential and disjoint so that

$$0 < \alpha_i < \beta_i < \alpha_{i+1} < \beta_{i+1} < 1, \qquad i = 1,\dots, n-1. \tag{8}$$

For each species we define a time interval δ_i and a small amount of resource ζ_i such that

$$\delta_i = \alpha_{i+1} - \beta_i , \qquad i = 1,\dots, n-1; \quad \delta_n = \alpha_1 + 1 - \beta_n , \tag{9a}$$

and

$$\zeta_i = z_{\max} \exp(-\sigma_i \delta_i). \tag{9b}$$

We can interpret (9b) as follows. We require that the amount of resource in use by species i be small (less than ζ_i) during the growing seasons of the other species. Species i cannot be using more than $z_{\max}$ of the resource at the end of its growing season. Since the mortality rate of species i outside its growing season is σ_i, it can be using no more than $z_{\max} \exp(-\sigma_i \delta_i)$ of the resource at time $\beta_i + \delta_i$, which by (9a) is the start of the growing season of species $i + 1$.

Since the total amount of resource available is finite, it is obvious that no species can increase indefinitely. To prove coexistence, however, we must also show that when a species is near extinction its average growth rate over one cycle is positive. The argument proceeds as follows.

During the growing season of species i, the amount of resource in use by species j ($j \neq i$) is not more than ζ_j. Therefore the amount in use by all species $j \neq i$ is not more than $\sum_{j \neq i} \zeta_j$, which is less than $\zeta = \sum_{j=1}^{n} \zeta_j$. If $\zeta < z_{\max}$, the amount of resource available to species i at the beginning of its growth season is at least $z_{\max} - \zeta$. When species i is so rare that it possesses an amount of resource less than ζ_i even at the end of its growth season, an event which must occur whenever $x_i < (\zeta_i/s_i) \exp[-(\gamma_i z_{\max} - \sigma_i)(\beta_i - \alpha_i)]$ at the beginning of its growth season, then the growth rate of species i during its growing season will be at least $\gamma_i(z_{\max} - \zeta) - \sigma_i$. A sufficient condition that the average growth rate over the cycle be positive is then

$$[\gamma_i(z_{\max} - \zeta) - \sigma_i](\beta_i - \alpha_i) - \sigma_i(1 - \beta_i + \alpha_i) > 0. \tag{10}$$

This condition assures that each species increases when rare and hence that none can approach extinction.

We have only left to show that all the above assumptions can be satisfied simultaneously. We first take any positive numbers $z_{\max}$ and s_i. We then choose positive ζ_i whose sum is less than $z_{\max}$. Next we choose α_i, β_i, and δ_i satisfying (8) and (9a). We can then choose σ_i so large that (9b) is satisfied. Finally, we choose the γ_i such that (10) holds.

2.4. *Periodic Orbits in Competition Communities*

Consider the system of equations

$$\dot{x}_i = x_i f_i(x_1, x_2, x_3), \qquad i = 1, 2, 3, \tag{11a}$$

where

$$\partial f_i / \partial x_j < 0 \qquad \text{for all } i, j. \tag{11b}$$

Smale (1976) has shown that a system of form (11) can be constructed such that almost all solution trajectories tend asymptotically to a single hyperbolic attracting periodic orbit.

System (11) can be decomposed into a three-competitor three-conservative resource system by use of the change of variables

$$\begin{aligned} \dot{x}_i &= x_i h_i(z_1, z_2, z_3), \\ z_i &= z_{i\,\mathrm{max}} - x_i, \\ h_i(z_1, z_2, z_3) &\equiv f_i(z_{1\,\mathrm{max}} - z_1, z_{2\,\mathrm{max}} - z_2, z_{3\,\mathrm{max}} - z_3), \end{aligned} \tag{12}$$

for $i = 1, 2, 3$. System (12) has the form (5a) and satisfies assumption (5b). With an arbitrarily small perturbation we can ensure that (5c) also holds. If we choose a system of form (11) which exhibits a stable periodic orbit and decompose it as in (12), taking care that the $z_{i\mathrm{max}}$ are chosen large enough with respect to both the size of the periodic orbit and the initial conditions that the z_i never become negative, we have in fact constructed a three-competitor three-conservative resource system which possesses an attracting periodic orbit.

2.5. *Coexistence of any Number of Species on Four Conservative Resources*

The results of the previous two sections can be combined to allow the coexistence of any number of species on four conservative resources. To achieve this result, we let the gating functions of (7) be functions of the two resources z_1 and z_2 instead of functions of time. We are led to the set of equations

$$\begin{aligned} \dot{x}_i &= x_i h_i(z_1, z_2, z_3), && i = 1, 2, 3, \\ \dot{x}_i &= x_i[\gamma_i z_4 g_i(z_1, z_2) - \sigma_i], && i = 4, \dots, n, \\ z_i &= z_{i\,\mathrm{max}} - x_i, && i = 1, 2, 3, \\ z_4 &= z_{4\,\mathrm{max}} - \sum_{i=4}^{n} s_{4i} x_i . \end{aligned} \tag{13}$$

Species x_1, x_2, and x_3 are assumed to approach a periodic orbit. It is seen that x_1, x_2 and x_3 affect the growth of the other species (through the gating functions g_i) but that there is no reverse effect.

We choose the gating function $g_i(z_1, z_2)$ to be the product of two functions $g_{i1}(z_1)$ and $g_{i2}(z_2)$ which are nondecreasing functions of their arguments. We let $g_{i1} = 0$ for $z_1 < z'_{i1}$ and $g_{i1} = 1$ for $z_i \geqslant z'_{i1}$, and similarly for g_{i2}. If we then choose pairs of values (z'_{i1}, z'_{i2}) such that the species $x_4, \dots, x_n$ grow along disjoint segments of the periodic orbit of the first three species (Fig. 1), the "gating" effect will be identical to that produced by the explicit time dependence of Section 2.3, and the coexistence of all species will be assured. The system (13) has the form (5a) and satisfies assumption (5b). With an arbitrarily small perturbation we can assure that (5c) also holds.

Intuitively, we see that the system first tends to adjust so that species 1, 2, and 3 cycle on a periodic orbit. Their cycling then provides a time-dependent environment in which any number of additional species are able to coexist.

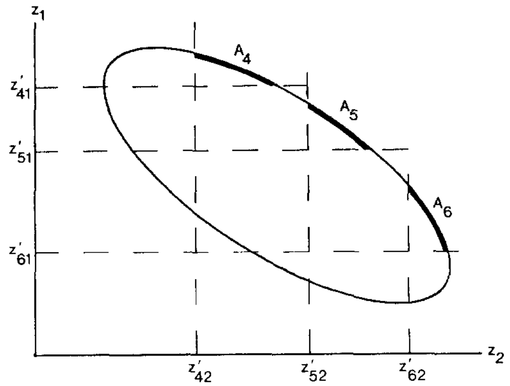

FIG. 1. Division of the periodic orbit of species x_1, x_2, x_3, into segments (A_4, A_5, A_6) along which the gating functions of three other species (x_4, x_5, x_6) are nonzero. In principle the periodic orbit can be divided as finely as desired, with the result that any number of species can be made to coexist on four conservative resources.

2.6. *Biological Rationalization*

In this section we hope to make more plausible a certain feature of model (13) which is perhaps biologically a bit strained. In the decomposition of Eqs. (11) into Eqs. (12) we have in effect stated that the growth rate of each species is affected by the concentration of all resources but that the concentration of each resource is affected by the density of only one species. A similar feature is present when models (6) and (12) are combined to yield model (13).

This unpleasant aspect of (13) is made more palatable by the perturbation described at the end of the preceding section. However, the perturbation is small and we have still not overcome the objection (to model [12] and, by extension, to [13]) that while the growth rate of the *i*th species ($i = 1, 2, 3$) is affected strongly by all resource densities, still the density of the *i*th species affects only the density of the *i*th resource strongly, affecting the other resource densities only weakly. This difficulty is easily rationalized if we regard the *i*th resource as a resource consumed by the *i*th competitor in great quantities, while the other resources act in the manner of catalysts to the *i*th species; that is, they are needed by the *i*th species for growth but their concentrations are little affected by the density of species i. Similar arguments can be extended to all the species in the full model (13).

This interpretation is offered only in the interest of making the mathematical form of the model (13) biologically more palatable. Mathematically, once the perturbation has been performed so that assumption (5c) holds, the system (13) satisfies all the mathematical requirements for a competitive community limited by conservative resources.

It should be stressed that the particular functional forms used in our model system were chosen for convenience in obtaining the mathematical proof, and not for biological realism. We needed to construct only one system in which n species could coexist on fewer than n resources to prove that the class of models obeying only assumptions (i)–(v) does not exhibit competitive exclusion, and the particular model chosen made our task relatively easy. We emphasize, however, that similar results should be obtainable in models of greater biological realism.

3. Mathematical Discussion

We have shown, in this paper and elsewhere (Armstrong and McGehee, 1976; McGehee and Armstrong, 1976), that the assumption that the specific growth rate of a population is a linear function of resource density, an assumption which was implicit in the work of Volterra (1928) and explicit in various later extensions of this work (MacArthur and Levins, 1964; Rescigno and Richardson, 1965; Levin, 1970), is crucial for any "proof" of the so-called competitive exclusion principle (Hardin, 1960). Without this assumption little of a general nature can be proved regarding the number of resources (or factors) necessary for the maintenance of stable coexistence.

The following facts have been established, however. First, if n species are to coexist on fewer than n of Levin's (1970) factors, the attractor must have Euler characteristic 0 (McGehee and Armstrong, 1975). Since the Euler characteristic of a point is 1, point attractors are not possible. Therefore the statement that n species cannot coexist at fixed densities when limited by fewer than n factors is true. This statement is also true if "factors" is replaced by "conservative resources."

Second, any number of predator species can coexist on a single prey species if the prey is allowed to regenerate according to a differential equation (Zicarelli, 1975). By the use of an appropriate change of variables (see Armstrong and McGehee, 1976), it can be shown that Zicarelli's proof also implies that any number of species can coexist on as few as two of Levin's "factors" (Levin, 1970).

Third, any number of competing species can coexist on as few as four conservative resources. We conjecture that coexistence should be possible with three conservative resources but find this question to be more of mathematical than of ecological interest. Since each conservative resource can be identified as a factor in the sense of Levin (1970), the present work also provides an alternative proof that any number of species can coexist on a fixed number of factors.

Fourth, the question of how many species can coexist on one factor is still in doubt. It is certain that two species cannot coexist on one factor (McGehee and Armstrong, 1976), but whether more than two can coexist is an open question.

4. Biological Discussion

In his classic paper "The Paradox of the Plankton," Hutchinson (1961) argued that the competitive exclusion principle is useful to ecologists because it "can be used to examine a situation where its main conclusions seem to be empirically false. Just because the theory is analytically true and in a certain sense tautological, we can trust it in the work of finding out what has happened to cause its empirical falsification." Hutchinson's view is that the competitive exclusion principle is an idealized case, and that when coexistence is observed it is because one or more of the biological assumptions necessary for the proof of this principle have been violated.

We would argue, however, that it is difficult to rationalize as "biological" the assumption that species growth rates must be linear functions of resource densities. It is possible, at least in an experimental system such as a chemostat and using simple organisms such as bacteria (cf. Jost *et al.*, 1973), to approximate the biological assumptions of environmental homogeneity and constancy, lack of age structure, and so on. But no example can be found where growth increases linearly with food density; in all real cases there must be some upper limit on growth rate no matter how much resource is present. The assumption of linearity was undoubtedly included by previous authors only for the purpose of mathematical simplicity. However, because we have shown that this assumption is necessary for any proof of the competitive exclusion principle which does not require biological assumptions in addition to assumptions (i)–(v), we are left with a dilemma: Do we somehow try to rationalize the assumption of linearity as "biological," a course which is plainly undesirable, or do we reject entirely the proposition that the competitive exclusion principle can be proved using only "biological" assumptions?

We suggest a third course. As noted in Section 3, it can be shown (McGehee and Armstrong, 1976) that n species cannot coexist *at fixed densities* on fewer than n resources (or when limited by fewer than n factors). We would therefore suggest that the principle of competitive exclusion, as a biological principle, should be recognized as applying only to coexistence at fixed densities. The principle does not apply to cases in which species coexist at fluctuating densities, even when these fluctuations occur in a constant environment.

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