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COMPETITIVE EXCLUSION

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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, which 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 when limited by fewer than n "limiting factors" (Levin 1970), has become known as the "competitive exclusion principle" (Hardin 1960).

The "principle" has been the center of much heated debate. Slobodkin (1961) has argued that it is not really a principle at all, but rather a tautology, and can serve only as a "rule of ecological procedure" to be followed in examining cases of species coexistence. Hutchinson (1961, p. 143) has phrased essentially the same thought in a more positive manner: "Just because the theory is analytically true and in a certain sense tautological, we can trust it in the work of trying to find out what has happened" to allow coexistence. In Hutchinson's view the principle is useful precisely because it is believed to be a tautology, a statement which is logically true and therefore not subject to empirical falsification.

It is therefore not surprising, given Hutchinson's influential view on the utility of the competitive exclusion principle, that a number of authors have attempted to extend the range of the tautology by generalizing Volterra's model to cases of more than one resource or limiting factor (MacArthur and Levins 1964; Rescigno and Richardson 1965; Levins 1968; Levin 1970; Haigh and Maynard Smith 1972; Haussman 1973; Armstrong and McGehee 1976a, 1976b; Kaplan and Yorke 1977; McGehee and Armstrong 1977). Our purpose in this paper to review these attempts, to examine the basis for recent results, and to provide a general framework for examining theoretical problems of competitive exclusion.

In Section 1 we examine Volterra's original proof of competitive exclusion, paying particular attention to the biological assumptions underlying Volterra's model. In this section we also introduce the various models which have been used in attempts to extend Volterra's model to cases of more than one resource, and discuss the results of previous authors. Section 2 contains a detailed discussion of

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the work of Koch (1974*b*) and ourselves (Armstrong and McGehee 1976*a*; McGehee and Armstrong 1977), which proves that two species can indeed coexist on one resource in a time-invariant and spatially homogeneous environment.

In Section 3 we discuss the mathematical notion of an attractor and restate the general question of competitive exclusion. Section 4 summarizes current knowledge on all aspects of this general question. In Section 5 we explore the special problem of coexistence at fixed densities. We conclude that, in this special case, n species cannot coexist on fewer than n resources.

1. THE BASIC MODELS

We begin with a close examination of Volterra's (1928) original model. Volterra first assumed that the dynamics of competing species can be described by the use of differential equations. This assumption is very important, and has been almost universally adopted by those who have studied competitive exclusion from a mathematical point of view. We shall discuss this most basic assumption more fully in Section 3.

For the moment, postulate the existence of n species $x_i, i = 1, \dots, n$, competing for the same resource R . Let the specific (or per capita) growth rate of each species increase linearly with the amount of resource present, so that

$$\frac{1}{x_i} \frac{dx_i}{dt} = \gamma_i R - \sigma_i, \quad i = 1, \dots, n, \quad (1)$$

where $\sigma_i > 0$ is the rate at which the population would decline in the absence of resource and $\gamma_i > 0$ relates increased resource abundance to increased growth. Next assume that the amount of resource available to any competitor at time t is diminished by the presence of the competitors such that at any time t ,

$$R = R_{\max} - F(x_1, \dots, x_n). \quad (2)$$

Here $F(x_1, \dots, x_n)$ is an unbounded increasing function of the population densities x_i , with $F(0, \dots, 0) = 0$. Substituting (2) into (1) and replacing $\gamma_i R_{\max} - \sigma_i$ by ϵ_i yields Volterra's original equations:

$$\frac{dx_i}{dt} = x_i[\epsilon_i - \gamma_i F(x_1, \dots, x_n)], \quad i = 1, \dots, n. \quad (3)$$

Volterra showed that, as $t \rightarrow \infty$, 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, provided that $\epsilon_i > 0$ and $x_i(0) \neq 0$ for the winning species.

Several simplifying assumptions are implicit in the above model. (i) The organisms under consideration are "simple" in the sense that the dynamics of the system can be adequately described by the species densities x_i . Complications arising from age structure or physiological state are assumed unimportant. (ii) The species interact only through the resource, so that their specific growth rates are functions of R alone, not of the x_i . (iii) The system under consideration is spatially homogeneous. (iv) The resource is uniform in quality. For example, if the resource consists of particles of food, these are uniform in size and nutritional value.

(v) There is no explicit time dependence to the interactions, either in terms of time-dependent interaction parameters or external forcing. There are no time lags.

Coexistence has been shown to be possible in many cases where one or more of these assumptions are violated. For example, Haigh and Maynard Smith (1972) showed that two predators could coexist on one prey species if they utilized different life stages of the prey (contra assumption [i]); and Stewart and Levin (1973) and Koch (1974a), following the suggestion of Hutchinson (1961), demonstrated that two species can coexist on a single resource in a time-varying environment (contra [v]).

The Volterra model (1)–(3) is an example of a “linear abiotic resource” model: “linear” because the specific growth rates of the competitors are linear functions of resource densities, and “abiotic resource” because the resource regenerates according to an algebraic relationship. At any given time a parcel of abiotic resource exists either in a “free” state or in a “bound” state. In the free state it is available for use by any individual, while in the bound state it is in use by some individual. For example, if the resource were a chemical nutrient, that part of the nutrient pool which is currently in use by living individuals is in a bound state; the remainder is in a free state. A second example of an abiotic resource is space, a parcel of which is in the bound state if it is occupied by some individual and in the free state if it is not occupied. A parcel of abiotic resource is regenerated from the bound state to the free state through the death of the individual by which it was bound. Such regeneration is assumed to occur instantaneously.

The Volterra model (1)–(3) is easily generalized to include k resources (Rescigno and Richardson 1965). It can be further generalized by relaxing the assumption of linearity in equation (1), yielding the class of “abiotic resource” models:

$$\frac{dx_i}{dt} = x_i u_i(R_1, \dots, R_k), \quad i = 1, \dots, n, \quad (4)$$

$$R_j = R_{j \max} - F_j(x_1, \dots, x_n) \quad (5a)$$

$$= s_j(x_1, \dots, x_n), \quad j = 1, \dots, k. \quad (5b)$$

Since the R_j are to be considered resources, it is assumed that species growth rates will increase with resource availability, and that resource densities will decrease with species densities. These conditions are specified by

$$\frac{\partial u_i}{\partial R_j} \geq 0 \quad \text{and} \quad \frac{\partial s_j}{\partial x_i} \leq 0, \quad (6)$$

where the equalities hold if and only if a particular species i does not use a particular resource j . A large class of chemostat models can be reduced to the abiotic resources model (Canale 1970; Waldon 1975; see also Appendix A). The “limiting factor” equations of Levin (1970) are exactly (4) and (5b) without the monotonicity restrictions (6).

Another important class of models concerns “biotic” resources, resources which regenerate according to their own differential equations, as would prey species (MacArthur and Levins 1964; Koch 1974b; Armstrong and McGehee 1976a; McGehee and Armstrong 1977). The defining equations for this class of

models are

$$\begin{aligned}\frac{dx_i}{dt} &= x_i u_i(R_1, \dots, R_k), & i &= 1, \dots, n, \\ \frac{dR_j}{dt} &= R_j g_j(R_1, \dots, R_k, x_1, \dots, x_n), & j &= 1, \dots, k.\end{aligned}\tag{7}$$

The monotonicity conditions

$$\frac{\partial u_i}{\partial R_j} \geq 0 \quad \text{and} \quad \frac{\partial g_j}{\partial x_i} \leq 0,\tag{8}$$

analogous to equations (6), are expected to apply to this model.

Various authors have used these models in attempting to prove that n species cannot indefinitely coexist on $k < n$ resources or limiting factors (Volterra 1928; MacArthur and Levins 1964; Rescigno and Richardson 1965; Levins 1968; Levin 1970). All such early attempts contained the assumption that the specific growth rates u_i of the competing species are linear functions of resource or factor densities. In addition, these authors (with the exception of Levin 1970) restricted their attention to coexistence at fixed densities.

More recently, several authors (Koch 1974*b*; Zicarelli 1975; Armstrong and McGehee 1976*a*, 1976*b*; Kaplan and Yorke 1977; McGehee and Armstrong 1977) have shown that when these two restraints are simultaneously relaxed the coexistence of n species on $k < n$ resources becomes possible. In the following sections we detail the conditions under which this coexistence is possible and provide a coherent framework for viewing problems of competitive exclusion.

2. COEXISTENCE OF TWO SPECIES ON ONE BIOTIC RESOURCE

Koch (1974*b*) was the first to point out via computer simulation that two species could coexist on one biotic resource. This coexistence occurred along what appeared to be a periodic orbit, not at an equilibrium point. The coexistence of two species on one biotic resource was later confirmed analytically (McGehee and Armstrong 1977) and expanded to the case of n species coexisting on one biotic resource (Zicarelli 1975).

In this section we provide insight into the mechanism behind this coexistence. We will present an intuitive look at why the coexistence depends both on the nonlinearity of the growth functions u_i and on the lack of system equilibrium. Those who desire complete proofs should consult the papers of McGehee and Armstrong (1977) and Zicarelli (1975).

Consider a system composed of two species x_1 and x_2 competing for the same biotic resource R . Let the defining equations for this system be:

$$\frac{dx_1}{dt} = x_1 \left(-m_1 + \frac{c_1 \eta_1 R}{R + \Gamma} \right),\tag{9a}$$

$$\frac{dx_2}{dt} = x_2 (-m_2 + c_2 \eta_2 R),\tag{9b}$$

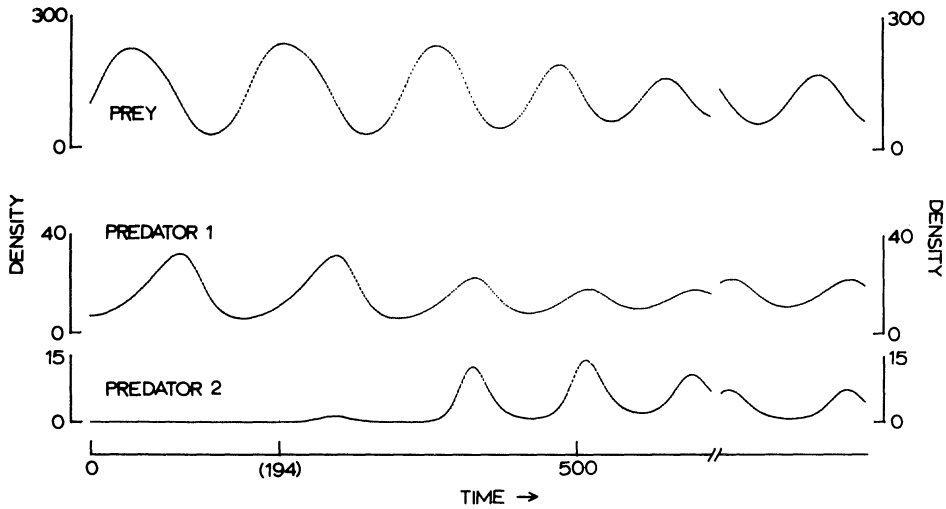


FIG. 1.—Computer simulation of two predators coexisting on a single prey (biotic resource). The model is that of eqq. (9) with $m_1 = .1$, $c_1 = .3$, $\eta_1 = .5$, $\Gamma = 50$, $r = .1$, $K = 300$, $m_2 = .11$, $c_2 = .33$, $\eta_2 = .003$. The system was started at $x_1 = 1$, $R = 400$, $x_2 = 0$, a point very near the two-species periodic orbit of x_1 and R . At $t = 194$, a small amount (.01) of predator x_2 is added; it readily invades the limit cycle. To the right of the break in the axis the apparent periodic behavior of the three-species system is shown. This limiting configuration is also reached if a small amount of x_1 is added to the two-species system (x_2 , R) near its stable equilibrium.

$$\frac{dR}{dt} = R \left[r \left(1 - \frac{R}{K} \right) - \frac{\eta_1 x_1}{R + \Gamma} - \eta_2 x_2 \right]. \quad (9c)$$

In these equations m_1 and m_2 are the death rates of the competitors in the absence of resource; η_1 and η_2 are rate constants for resource consumption (per unit competitor and per unit resource); c_1 and c_2 are conversion efficiencies of resource biomass into competitor biomass; r and K are, respectively, the maximum growth rate and carrying capacity of the prey; and Γ is a half-saturation constant in the functional response of competitor 1. Note that competitor 2 is of the Lotka-Volterra type.

Computer simulation of the above system (fig. 1) suggests that the three species coexist along a periodic orbit for appropriate parameter values. How is this coexistence effected?

Consider first the species pair (x_1 , R) in the absence of species 2. This pair has an equilibrium point (x_1^* , R^*) defined by

$$-m_1 + \frac{c_1 \eta_1 R^*}{R^* + \Gamma} = 0, \quad r \frac{1 + R^*}{K} - \frac{\eta_1 x_1^*}{R^* + \Gamma} = 0.$$

The equilibrium point (x_1^* , R^*) may be stable or unstable, depending on parameter values.

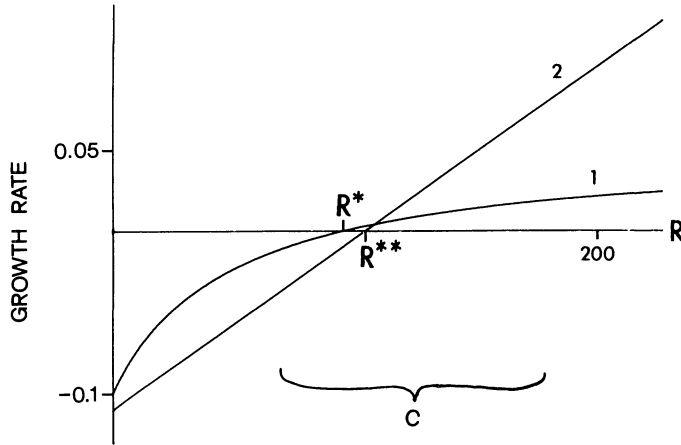


FIG. 2.—Growth rates of the predators of fig. 1 as functions of prey density R . The region C represents the approximate range of variation of R over one cycle in the three-species system.

Consider next the species pair (x_2, R) in the absence of species 1. This pair has an equilibrium point (x_2^{**}, R^{**}) defined by

$$-m_2 + c_2\eta_2 R^{**} = 0, \quad r \frac{1 - R^{**}}{K} - \eta_2 x_2^{**} = 0.$$

The equilibrium point (x_2^{**}, R^{**}) will be globally stable for all parameter values (McGehee and Armstrong 1977).

Now think of a small amount of species 1 introduced into the system (x_2, R) near its equilibrium point. Species 1 can successfully invade if and only if $dx_1/dt > 0$ when x_1 is small and (x_2, R) is near (x_2^{**}, R^{**}) . From equation (9a) we see that invasion can occur if and only if $-m_1 + c_1\eta_1 R^{**}/(R^{**} + \Gamma) > 0$. Since the specific growth rate of species 1 is an increasing function of R , this inequality holds if and only if $R^{**} > R^*$. In the simulation (fig. 1) the parameters were chosen such that $R^* = 100$ and $R^{**} = 110$ (fig. 2), insuring that species 1 can indeed invade the two-species equilibrium point (x_2^{**}, R^{**}) .

Why, then, does competitor 1 not exclude competitor 2? By reasoning similar to that given above, we know that $dx_2/dt < 0$ near the two-species equilibrium point (x_1^*, R^*) if $R^{**} > R^*$. However, we also know that this equilibrium point may not be stable. In fact, for certain parameter values the two-species system (x_1, R) approaches a periodic orbit. Furthermore, around this orbit the average prey density $\bar{R}$ will be greater than R^* (Appendix B). Species 2 will be able to invade the system (x_1, R) along this periodic orbit if and only if its average rate of increase along the orbit is positive. That is, invasion is possible if and only if

$$\frac{1}{\tau} \int_0^\tau \frac{1}{x_2} \frac{dx_2}{dt} dt = \frac{1}{\tau} \int_0^\tau [-m_2 + \eta_2 c_2 R(t)] dt > 0, \quad (10)$$

where τ is the period of the two-species limit cycle of x_1 and R . The right-hand side of (10) reduces to $-m_2 + \eta_2 c_2 \bar{R} > 0$, where $\bar{R} \equiv (1/\tau) \int_0^\tau R(t) dt$, so that invasion is

possible if and only if $\bar{R} > R^{**}$. Therefore, if parameters in the model (9) are chosen such that $R^* < R^{**} < \bar{R}$, mutual invasibility is insured. Such is the case in the example of figure 1.

Although the foregoing argument shows that each species is able to invade the other near its equilibrium configuration, it does not constitute a proof of coexistence (see Appendix C). Such a proof requires consideration of the global properties of the three-species system, as in McGehee and Armstrong (1977). The above argument does expose two crucial points, however. (1) We could not have obtained mutual invasibility or stable coexistence if both competitors had obeyed Lotka-Volterra dynamics, since for Lotka-Volterra predators $R^* = \bar{R}$ (Appendix B). (2) The cycling of the two-species system (x_1, R) is necessary for coexistence for exactly the same reason: Without such cycling $R^* = \bar{R}$.

Although the properties of nonlinearity and lack of equilibrium are crucial for the coexistence of n species on $k < n$ resources, these properties are in no sense pathological. First, the assumption of nonlinear, saturating functional response curves is much more realistic than the assumption of Lotka-Volterra functional response, since the latter implies that the specific growth rate of a species increases indefinitely with increased resource density (Armstrong and McGehee 1976b). (We specified a Lotka-Volterra functional response for x_2 in system [9] for purely expository purposes; in Koch's (1974b) original computer simulation, both competitors had saturating functional response curves.)

Second, we follow Levin (1970) in feeling that coexistence which is not at fixed densities still deserves to be considered coexistence. For example, if a system composed of a predator species and a prey species persists indefinitely, even if this persistence is along a cycle, we would assert that the two species are indeed coexisting.

3. REPHRASING THE PROBLEM

With the realization that two species could be made to coexist on a single biotic resource, we were led to rephrase the problem of competitive exclusion in more fundamental terms (McGehee and Armstrong 1977).

Our basic assumption is that the population dynamics of a community consisting of m species is adequately described by a set of ordinary differential equations of the form

$$\frac{dx_i}{dt} = x_i f_i(x_1, \dots, x_m), \quad i = 1, \dots, m. \quad (11)$$

Here x_i is the density of species i and $f_i(x_1, \dots, x_m)$ is its per capita growth rate. For the purposes of this section, the k resource equations of the biotic resource model (7) are not explicitly distinguished from the n competitor equations of the same model. Thus, for biotic resources, $m = n + k$.

The decision to use differential equations is not totally innocuous. Cole (1960) has objected to the competitive exclusion principle on the basis that all species with finite population sizes (i.e., all real species) are doomed to eventual extinction because of statistical fluctuations in population size. We must recognize,

therefore, that we cannot use differential equation models to prove indefinite coexistence. Rather, we seek from differential equation models indications of strong tendencies towards coexistence.

In terms of the model (11) we can now define the term *persistence*.

Definition 1.—The system (11) is said to exhibit “persistence at fixed densities” if it possesses an asymptotically stable equilibrium point $x^* = (x_1^*, \dots, x_m^*)$ with $x_i^* > 0$ for all $i = 1, \dots, m$.

If the system is started near its equilibrium point x^* , then each species in a system satisfying definition 1 will tend asymptotically to its equilibrium density x_i^* ; that is, the distance between the state vector x and the equilibrium position x^* will tend to zero as $t \rightarrow \infty$. Since all species are present at the final equilibrium, we say they are coexisting at fixed densities.

Definition 1 is far too restrictive to serve as a general definition of persistence. For example, a predator and prey can coexist 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, that of an “attractor.” Roughly speaking, we define an “attractor block” to be a region in the state space $\{(x_1, \dots, x_m)\}$ 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 1977].)

Definition 2.—The system (4) is said to exhibit “persistence” if it has an attractor block bounded away from the m faces $\{x_i = 0\}$, $i = 1, \dots, m$.

If the species start initially with densities in the attractor block, their densities will remain in the block for all future time. If $x_i > 0$, $i = 1, \dots, m$, 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 (fig. 3).

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.

We are interested in imposing certain structures on the system (11) and in determining whether those structures imply the impossibility of persistence.

Definition 3.—A given structure will be said to exhibit “competitive exclusion” if no system with such a structure is persistent.

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

More concretely, consider a two-species Volterra model (3) with $F(x_1, x_2) = \alpha x_1 + \beta x_2$. If $\epsilon_1/\gamma_1 \neq \epsilon_2/\gamma_2$, then there are no equilibrium points with both species present (fig. 4a). If $\epsilon_1/\gamma_1 = \epsilon_2/\gamma_2$, then there is a whole line of equilibrium points (fig. 4b). If $\epsilon_1/\gamma_1 < \epsilon_2/\gamma_2$, species 1 will go extinct (i.e., $x_1 \rightarrow 0$ as $t \rightarrow \infty$), as shown

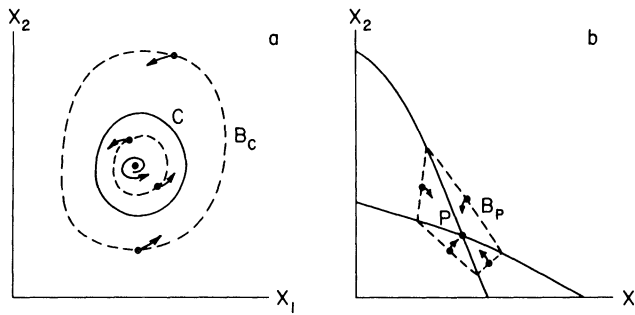


FIG. 3.—Two examples of attractor blocks bounded away from the faces $x_1 = 0$, $x_2 = 0$. *a*, A predator-prey cycle C surrounded by an attractor block B_C . *b*, Isocline diagram and stable equilibrium point P of a two-competitor system. The attractor block B_P has been drawn around the equilibrium point.

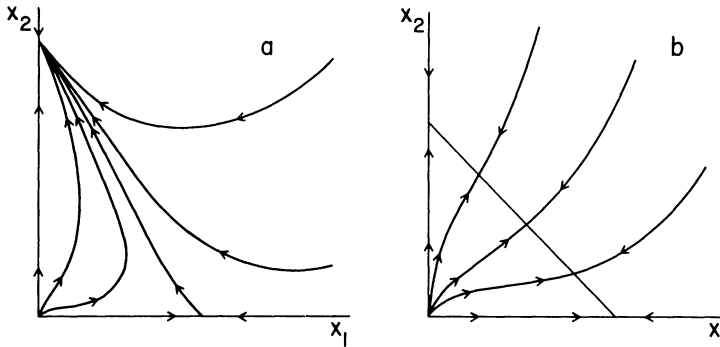


FIG. 4.—*a*, Exclusion of species 1 (x_1) in the Volterra model when $\epsilon_1/\gamma_1 < \epsilon_2/\gamma_2$. *b*, Phase portrait of the case $\epsilon_1/\gamma_1 = \epsilon_2/\gamma_2$. Note the line of critical points, none of which is asymptotically stable. In neither case can an attractor block bounded away from the faces $x_1 = 0$, $x_2 = 0$ be constructed.

in figure 4*a*. If $\epsilon_1/\gamma_1 > \epsilon_2/\gamma_2$, species 2 will go extinct. These extinctions will occur except in the trivial case where one species is initially absent.

This example illustrates the exclusion principle. Note first that, except in the case that $\epsilon_1/\gamma_1 = \epsilon_2/\gamma_2$, one or the other species exhibits a strong deterministic tendency towards extinction. In the exceptional case $\epsilon_1/\gamma_1 = \epsilon_2/\gamma_2$, the system will approach the line of equilibrium points. Since the line of equilibrium points intersects both axes, no attractor block bounded away from the axes can be constructed. Since no model of the Volterra type exhibits a deterministic tendency toward persistence, models of the Volterra type are said to exhibit competitive exclusion.

We should emphasize that our criterion for competitive exclusion is essentially a negative one: a system which does not exhibit a deterministic tendency toward coexistence is considered to exhibit exclusion. An alternative approach would have

been to define competitive exclusion by the extinction of "excess" species. An example follows.

Definition 4.—A system of n species and $k < n$ resources or limiting factors is said to exhibit "strict competitive exclusion" if at least $n - k$ species become asymptotically extinct.

We feel that the weaker definition 3 is superior because "excess" species may not go extinct asymptotically. For example, consider the Volterra model described above. Except when $\epsilon_1/\gamma_1 = \epsilon_2/\gamma_2$, all models with this structure exhibit strict competitive exclusion. When $\epsilon_1/\gamma_1 = \epsilon_2/\gamma_2$, all trajectories approach a line of fixed points (fig. 4b) and hence the system does not exhibit strict competitive exclusion. However, no single fixed point is asymptotically stable, and it can be argued that small external forces may move the system from one fixed point to another. Eventually, such disturbances will move the system close to the boundary, and one or the other species may be considered extinct.

This example shows that there exist systems which exhibit no strong deterministic tendencies toward coexistence, but also in which no species becomes asymptotically extinct. Our criterion for competitive exclusion (definition 3) categorizes such systems as nonpersistent.

4. RESULTS OF MORE RECENT INVESTIGATIONS

The attractor block formulation of the competitive exclusion problem was first applied to the coexistence of two competitors on one biotic resource. McGehee and Armstrong (1977) constructed an attractor block for this three-species system, proving that a strong deterministic tendency towards coexistence could exist in such a system (fig. 5).

Since that time, several further results have been proved.

4.1. *Coexistence of Any Number of Species on One Biotic Resource*

Zicarelli (1975) has extended the proof of McGehee and Armstrong (1977) to show that any number of species can be made to stably coexist on one biotic resource. Therefore, the set of abiotic resource models (eqq. [7] and [8]) does not exhibit competitive exclusion.

4.2. *Coexistence of Species on "Limiting Factors"*

Zicarelli's (1975) proof implies that any number of species can coexist on as few as two of Levin's (1970) limiting factors. To see this, note that Zicarelli's model is a special case of equations (7) and (8) with one resource; i.e., $dx_i/dt = x_i u_i(R)$, $i = 1, \dots, n$, and $dR/dt = Rg(R, x_1, \dots, x_n)$. The two limiting factors are the density of resource R and the function $g(R, x_1, \dots, x_n)$. (See Levin 1970; Armstrong and McGehee 1976a.) Zicarelli's result thus implies that the set of limiting factors models does not obey the competitive exclusion principle for $k > 2$ limiting factors. Kaplan and Yorke (1977) have provided an independent proof of this fact for $k > 3$ limiting factors.

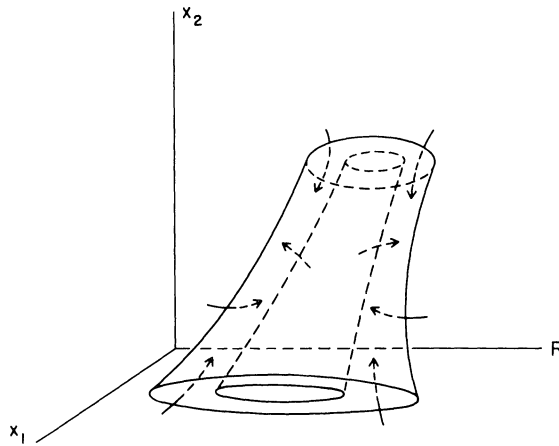


FIG. 5.—Attractor block for a two-predator, one-prey model. Once inside the solid torus the trajectory never leaves, implying a strong deterministic tendency toward indefinite coexistence.

The case of one limiting factor has also been solved. McGehee and Armstrong (1977) showed that two species cannot coexist on one limiting factor. More recently, Nitecki (1978) has shown that persistent systems with $n \geq 3$ species and one limiting factor can be constructed. Therefore, the only case in which a limiting factors model exhibits competitive exclusion is the case of two species on one limiting factor.

4.3. Coexistence of Species on Abiotic Resources

N species on four abiotic resources.—Armstrong and McGehee (1976b) have shown that it is possible to construct persistent systems of $n > 4$ species on four abiotic resources. To prove this point, we first constructed a system in which any number of species could coexist on a single resource in a time-varying environment. Next we asserted that it is possible to construct three-species, three-abiotic resource competition systems whose solutions tend to asymptotically stable periodic orbits. Smale (1976) has proved that such systems exist; Strobeck (1973, p. 652) has constructed a three-species competition system, unstable near its three-species equilibrium point, which in computer simulations appears to approach a periodic orbit.

We then combined these two subsystems, making the three-species–three-resource subsystem provide a periodic environment for the n -species–one-resource subsystem. The resulting system has $n > 4$ species coexisting on $k = 4$ conservative resources.

N species on one abiotic resource: Volterra revisited.—Volterra (1928) showed that n species could not coexist on one abiotic resource. Volterra's proof, however, is plagued by the same drawback as many of the succeeding models: the assumption that the $u_i(R)$ in equations (4) are linear. It is somewhat surprising,

then, that in the one-abiotic resource case the linearity assumption is unnecessary. The monotonicity conditions on the u_i (eqq. 6) are sufficient to insure that all species except one will become extinct. When n species compete for a single limiting resource, the species which can exist at the lowest level of available resource will prevail. A proof is given in Appendix D.

An open question.—The behavior of models of n species on two or three abiotic resources remains unknown. It seems clear to us that the methods used by Zicarelli (1975) could be used to show the existence of persistent systems of n species on three abiotic resources. The case of two abiotic resources seems much more delicate. However, the work of Nitecki (1978) leads us to conjecture that there exist persistent systems of n species on two abiotic resources.

5. COEXISTENCE AT FIXED DENSITIES

McGehee and Armstrong (1977) have shown that coexistence at fixed densities of n species on $k < n$ resources or limiting factors is impossible. Assertions to this effect have been made before. MacArthur and Levins (1964) noted that it is "infinitely unlikely" that n planes drawn in a k -dimensional space will intersect at a point. They interpreted this fact to mean that the coexistence at fixed densities of n species on $k < n$ resources is "infinitely unlikely." Kaplan and Yorke (1977) have added mathematical precision to these statements.

Whittaker and Levin (1976) have taken issue with MacArthur and Levins, stating that convergent evolutionary pressures may indeed result in point coexistence of n species on $k < n$ resources with probability greater than zero. They assert, however, that although such coexistence is deterministically possible, the fact that the community matrix at the equilibrium point is singular (has at least one eigenvalue equal to zero) means that the system will be extremely vulnerable to stochastic perturbations. Hence they too conclude that the point coexistence of n species on the $k < n$ resources or limiting factors is impossible.

We would argue, however, that a dominant eigenvalue of zero does not necessarily imply vulnerability to perturbation. Consider, for example, the model $dx/dt = x(k - x)^3$. This model has a dominant eigenvalue of zero, and yet is asymptotically stable near $x^* = k$. Furthermore, the system is rather insensitive to perturbation, in the sense that small environmental variations will not move the system far from its deterministic equilibrium. For example, consider any sort of environmental change which causes the carrying capacity k to vary in time. Let this variation be bounded, so that at any time t , $0 < k_1 < k(t) < k_2 < \infty$, where k_1 and k_2 are, respectively, the minimum and maximum values of the carrying capacity $k(t)$. It is evident that if the population density x lies in the interval (k_1, k_2) at time $t = 0$, then $x(t)$ will remain in that interval for all time. Furthermore, any trajectory which starts outside the interval (k_1, k_2) at $t = 0$ will eventually enter the interval, provided $x(0) \neq 0$. Thus the Whittaker-Levin argument does not always apply.

We have been able to show that n species cannot coexist on $k < n$ resources, in the sense of definition 1. That is, we have been able to show that attracting point equilibria cannot exist for $k < n$. The first key word in this statement is *attracting*. Point equilibria may exist, even for $k < n$. However, attracting point equilibria,

which we consider the proper criterion for coexistence at fixed densities, cannot exist for $k < n$.

The second key part of this statement is *cannot exist*. Attracting point equilibria are literally impossible, not just “very unlikely,” when $k < n$.

Our proof rests on some rather technical mathematical points. The basic scenario is outlined below. Those readers wishing a more precise statement of the proof should consult McGehee and Armstrong (1977).

Recall that Levin’s limiting factors model is defined by

$$\begin{aligned} \frac{dx_i}{dt} &= x_i u_i(R_1, \dots, R_k), & i &= 1, \dots, n, \\ R_j &= s_j(x_1, \dots, x_n), & j &= 1, \dots, k. \end{aligned} \quad (12)$$

Note further that the class of limiting factors models contains both the class of abiotic resource models and the class of biotic resource models (McGehee and Armstrong 1977). Therefore, if we can prove that coexistence at fixed densities of n species on $k < n$ limiting factors is impossible, we will automatically have proved the same result for both abiotic resource and biotic resource models.

We first note that the set of systems of the form (12), and with no equilibrium points, is “dense” (McGehee and Armstrong 1977). In other words, if we are given a system of n species and $k < n$ limiting factors, and if this system has an equilibrium point, we can always find a “nearby” system with no equilibrium points.

We next note that a fundamental property of an attractor block is that it shares certain topological properties with the attractor within it. In particular, the Euler characteristic is shared. The Euler characteristic is an integer associated with every geometric object. The Euler characteristic of a point is 1, that of a circle is 0, that of a solid sphere is 1, and that of a solid torus is 0. An attractor block which surrounds a point attractor will be topologically equivalent to a solid sphere (fig. 3b). Both the block and the attractor have Euler characteristic 1. An attractor block which surrounds a periodic attractor will be topologically equivalent to a solid torus (figs. 3a, 5). Both have Euler characteristic 0.

A second fundamental property of attractor blocks is that they remain attractor blocks under slight perturbation, even though the attractor itself may change. Therefore, the Euler characteristic of the attractor cannot change under small perturbations. For example, imagine a system having a point attractor. Surround this point with an attractor block constructed so that the vector field is everywhere transverse to its boundary. Now perturb the system slightly, perhaps by altering one of the parameters in the original set of equations. The attractor block for the unperturbed system is still an attractor block for the perturbed system. Therefore, even though the new attractor may no longer be a point, it must have the same Euler characteristic as a point, namely 1.

Given any system of n species and $k < n$ limiting factors, we know that we can find a system arbitrarily nearby which has no equilibrium points. Therefore all attractor blocks for systems of n species and $k < n$ resources must be topologically compatible with the fact that the attractor inside the attractor block may have no equilibrium points. Mathematically, all attractor blocks for such systems must

have Euler characteristic 0. (The torus of fig. 5 is an example of such a block.) Since point attractors have Euler characteristic 1, point attractors cannot exist.

DISCUSSION

We have shown that it is possible to construct systems in which n species can coexist on $k < n$ resources or limiting factors. Why, then, have many authors (MacArthur and Levins 1964; Rescigno and Richardson 1965; Levins 1968; Levin 1970) been led to assert that such coexistence is impossible? Three observations are germane.

First, in all these earlier models, species' per capita growth rates (the functions u_i in eqq. [4] and [7]) were assumed to be linear functions of resource densities. It is indeed true that if the functions u_i are linear in resource densities or in limiting factors, persistence (Sec. 3, definition 2) is impossible (Levin 1970; McGehee and Armstrong 1977). This result may apply directly to species with Holling type I functional response curves (Holling 1965) if resource densities always remain below the levels needed to saturate the functional responses of the competitors and if the competitors' growth rates are directly proportional to resource consumption rates. However, this result will not in general apply to species with other types of functional response curves, except in the case $k = 1$ (sec. 4.3 and Appendix D).

The second point is that some authors (MacArthur and Levins 1964; Levins 1968) have considered only coexistence at fixed densities. Indeed, it can be proved that in a large class of biologically reasonable models, n species cannot coexist at fixed densities on $k < n$ resources (Sec. 5). Because this last result does not require the assumption of linearity, Armstrong and McGehee (1976b) have suggested that the competitive exclusion principle will in general apply only to cases of coexistence at fixed densities.

Third, note that if the assumption of linearity and the assumption of coexistence at fixed densities are simultaneously relaxed, it becomes possible to construct examples of n species coexisting on $k < n$ resources or limiting factors. The species coexist because of internally generated cyclic behavior.

These observations allow us to clarify the relationship of Volterra's work to that of his successors. In the case of only one resource, the system must eventually approach a point equilibrium (Appendix D). Since the requirement of equilibrium is sufficient to assure that competitive exclusion will hold (Sec. 5), Volterra's linearity assumption can be relaxed without affecting his results. When more than one resource or limiting factor is involved, however, equilibrium is not assured, and the assumption of linearity becomes critical. Therefore, the assumption that species' per capita growth rates are linear in resource densities, an assumption that occurs only as a mathematical convenience in Volterra's proof, becomes critical in cases where more than one resource is involved.

SUMMARY

Recent developments in the mathematical theory of competitive exclusion are discussed and placed in historical perspective. The models which have been used

in theoretical investigations of competitive exclusion are classified into two groups: those in which the resources regenerate according to an algebraic relationship (abiotic resource models), and those in which resource regeneration is governed by differential equations (biotic resource models). We then propose a mathematical framework for considering problems of competitive exclusion, and provide examples in which n competitors can coexist on $k < n$ resources (both biotic and abiotic). These systems persist because of internally generated cyclic behavior. We conclude that the competitive exclusion principle applies in general only to coexistence at fixed densities.

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APPENDIX A

Consider the following chemostat model of n species competing for k nutrients:

$$\begin{aligned}\frac{dx_i}{dt} &= x_i[u_i(R_1, \dots, R_k) - D], \quad i = 1, \dots, n, \\ \frac{dR_j}{dt} &= -\sum_{i=1}^n c_{ji}x_i u_i(R_1, \dots, R_k) + D(C_j - R_j), \quad j = 1, \dots, k.\end{aligned}$$

Here x_i is the concentration of species i , R_j is the concentration of nutrient j , and $u_i(R_1, \dots, R_k)$ is the specific growth rate of species i (cf. eqq. (4), (5), the abiotic resource model). The constant D is the dilution rate of the growth medium, the constant C_j is the concentration of nutrient j in the incoming medium, and the constant c_{ji} relates the uptake of nutrient j to the production of species i .

Following Canale (1970) and Waldon (1975), we introduce the variables ϕ_j which measure the total concentration of nutrient j in the chemostat: $\phi_j = R_j + \sum_{i=1}^n c_{ji}x_i$. One easily computes that $d\phi_j/dt = D(C_j - \phi_j)$, from which it follows that ϕ_j exponentially approaches C_j , regardless of the concentrations of any of the species.

Therefore, when considering any sort of ultimate behavior of the model (such as steady-state behavior), one may assume that $\phi_j = C_j$. The model then reduces to

$$\begin{aligned}\frac{dx_i}{dt} &= x_i[u_i(R_1, \dots, R_k) - D], \quad i = 1, \dots, n, \\ R_j &= C_j - \sum_{i=1}^n c_{ji}x_i, \quad j = 1, \dots, k,\end{aligned}$$

which has the form of equations (4) and (5a) with $u_i - D$ replacing u_i and $F_j(x_1, \dots, x_n) = \sum_{i=1}^n c_{ji}x_i$.

The results discussed in Sections 4 and 5 for abiotic resource models now can be applied directly to this class of chemostat models. For example, if $k < n$, then any attractor for the above model must have Euler characteristic zero. In particular, there can be no point attractors. Also, if $4 \leq k < n$, then there exist chemostat models of the above form with periodic attractors; therefore the chemostat structure does not imply competitive exclusion. Finally, if $k = 1$, then the model does exhibit competitive exclusion. Indeed, as shown in Appendix D, most models of this form exhibit strict competitive exclusion. This last result generalizes theorems of Hsu et al. (1976) and Hsu (1978).

APPENDIX B

We first show that a species whose growth rate increases linearly with resource density requires the same average resource density to maintain itself in an environment where the resource density varies as it does to maintain itself in an environment where the resource level is constant in time. Second, we show that if the growth response curve saturates with increasing prey density, the average prey density required for maintenance in a time-varying environment is higher than that required in a constant environment.

Consider a species x whose growth rate is determined by the density of some limiting resource R . Assume that the growth of species x is determined by the equation $dx/dt = xf(R)$, where $f(R)$ is the specific growth rate of species x as a function of resource density R . The response of the resource to utilization will be determined by a separate equation. However, the dynamics of resource regeneration are unimportant for the present argument.

We first consider a constant environment and determine the resource level R which will allow the population to maintain a constant size. Assuming that $f(0) < 0$, $f(\infty) > 0$, and that f is strictly increasing, we see that there is a unique value R^* such that $f(R^*) = 0$; R^* is the resource density required for x to maintain itself in a constant environment.

We next consider a time-varying environment and assume that the resource density is given by $R(t)$. Assume that, after some time τ , the population $x(t)$ returns to its initial value. (For example, $R(t)$ and $x(t)$ might both be periodic with period τ .) Now define $\bar{R} = (1/\tau) \int_0^\tau R(t) dt$, the average value of the resource density over the interval $0 \rightarrow \tau$. Also define $\bar{f}(\bar{R}) = (1/\tau) \int_0^\tau f[R(t)] dt$, the average value of the specific growth rate of x . Since x returns to its initial value after time τ , we have

$$\int_0^\tau \frac{1}{x} \frac{dx}{dt} dt = \log x(\tau) - \log x(0) = 0.$$

Therefore,

$$\bar{f}(\bar{R}) = \frac{1}{\tau} \int_0^\tau \frac{1}{x} \frac{dx}{dt} dt = 0.$$

We now ask: What is the relation between $\bar{R}$, the average value of resource density required by x to maintain itself in a time-varying environment, and R^* , the value of resource density required by x to maintain itself in a constant environment?

The answer is immediate if f is linear, since if $f(R) = aR + b$ then $f(\bar{R}) = \bar{f}(\bar{R}) = 0$. Therefore $\bar{R} = R^*$. This result was first noted by Volterra (1928) in the special case of Lotka-Volterra population oscillations.

Consider now the case in which the growth response $f(R)$ saturates with increasing R ; i.e., assume that f is concave downward. Draw the tangent line $L(R)$ to the curve $f(R)$ at $R = R^*$ (fig. 6). Since $L(R) > f(R)$ for $R \neq R^*$, we have that $\bar{L}(\bar{R}) > \bar{f}(\bar{R}) = 0$ in a time-varying environment. Since L is linear, $\bar{L}(\bar{R}) = L(\bar{R}) > 0$. Therefore, since $L(R^*) = 0$, $\bar{R} > R^*$. Therefore, a species possessing a growth curve which is concave downward requires a higher average resource supply to persist when the resource level varies in time than it does when the resource level is maintained at $R = R^*$.

APPENDIX C

Does mutual invasibility imply coexistence? For a simple two-species Lotka-Volterra competition model, mutual invasibility does imply coexistence, since coexistence will occur if each species is able to invade the equilibrium of the other. However, in higher dimensions the situation is more complicated.

Consider a competition model of three species. Suppose that, in the absence of any one species, the remaining two come to an equilibrium. Suppose further that in each case the third species is able to invade the equilibrium of the other two. Do these conditions imply that the system is persistent?

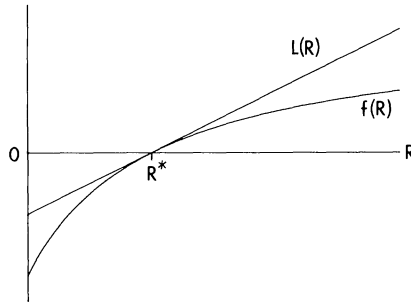


FIG. 6.—Graphs of the functions $f(R)$ and $L(R)$ discussed in Appendix B. The function $f(R)$ is concave downward; $L(R)$ is the tangent line to $f(R)$ at $R = R^*$.

The answer is not simple, as is illustrated in the example of three competing species discussed by May and Leonard (1975). For any given species pair, one species excludes the other so that each pairwise equilibrium point has one species absent. The third species can always invade this pairwise equilibrium. Therefore this example satisfies the conditions stated in the previous paragraph. However, the system oscillates wildly, with each species infinitely often coming arbitrarily close to extinction, followed by a recovery to a large population density. Thus the system is not persistent and illustrates the subtlety of the original question.

Now consider the system of two predators and one prey discussed in Section 2. One can imagine that the following behavior might occur. The system starts with x_1 and R near their periodic orbit and with x_2 small. Species 2 first invades, but then declines in such a way that the system approaches the equilibrium point (x_1^*, R^*) . Then, with x_2 small, the system approaches the periodic orbit in the (x_1, R) plane, and the process starts anew. With each successive occurrence the minimum value of x_2 becomes smaller, so that species 2 comes arbitrarily close to extinction infinitely often. However, each near-extinction of species 2 is followed by a successful invasion. If one could construct a system whose only attractor contains such an orbit, this system would not be persistent.

Although the above argument is not precise, it does illustrate the danger of supposing that mutual invasibility always implies coexistence.

APPENDIX D

Consider equations (4) and (5a) with $k = 1$:

$$\frac{dx_i}{dt} = x_i u_i(R), \quad i = 1, \dots, n,$$

$$R = R_{\max} - F(x_1, \dots, x_n).$$

We wish to state conditions which imply that this system exhibits strict competitive exclusion. Nitecki (1978) showed that if no assumptions are made on the partial derivatives of the functions u_i and F , then there are persistent systems with this form. Volterra (1928) showed that if the u_i are linear functions, then the system exhibits strict competitive exclusion for most values of the parameters. The following assumptions are more general than Volterra's but restrictive enough to exclude Nitecki's example.

Assume a slightly stronger version of (6): $\partial u_i / \partial R > 0$ and $\partial F / \partial x_i > 0$. Assume that each species has a positive value of R for which it is just able to maintain its density, i.e., for each i there is an $R_i^* > 0$ such that

$$u_i(R) < 0 \quad \text{for } R < R_i^*,$$

$$\begin{aligned} u_i(R) &= 0 & \text{for } R &= R_i^*, \\ u_i(R) &> 0 & \text{for } R &> R_i^*. \end{aligned}$$

Assume that only one of the species has the smallest value of R_i^* . If necessary, relabel the species so that R_1^* is the smallest, i.e. $R_1^* < R_i^*, i = 2, \dots, n$. Let K_1 be the carrying capacity of species 1 in the absence of all other species, i.e. K_1 is the unique density such that $F(K_1, 0, \dots, 0) = R_{\max} - R_1^*$. Given the above assumptions, we prove the following theorem.

THEOREM D1. If $x_1(0) > 0$, then, as $t \rightarrow \infty$, $x_1(t) \rightarrow K_1$ and $x_i(t) \rightarrow 0$ for $i = 2, \dots, n$.

The intuitive idea behind the proof is the following. If the available resource R is below the critical level R_1^* , then all the species will decline until R exceeds this critical level. At that point species 1 will start to increase while the others continue to decline. Species 1 will then asymptotically reach its carrying capacity while the others asymptotically approach extinction.

We prove the theorem by constructing two Liapunov functions. For the basic definitions and examples of Liapunov functions, see LaSalle and Lefschetz (1961).

Write $\mathbf{x} = (x_1, \dots, x_n)$, $\mathbf{x}_e = (K_1, 0, \dots, 0)$. Define the three sets

$$\begin{aligned} \mathcal{B} &= \{\mathbf{x}: x_i \geq 0 \ \forall_i \text{ and } F(\mathbf{x}) < R_{\max} - R_1^*\}, \\ \mathcal{C} &= \{\mathbf{x}: x_i \geq 0 \ \forall_i \text{ and } F(\mathbf{x}) > R_{\max} - R_1^*\}, \\ \Delta &= \{\mathbf{x}: x_i \geq 0 \ \forall_i \text{ and } F(\mathbf{x}) = R_{\max} - R_1^*\}. \end{aligned}$$

The set $\mathcal{B}$ consists of all points in the state space for which the concentration of available resource R is greater than the critical concentration R_1^* , $\mathcal{C}$ is the set where $R < R_1^*$, and Δ is the set where $R = R_1^*$. The union of these three sets is the entire positive orthant, and Δ forms the common boundary between the two regions $\mathcal{B}$ and $\mathcal{C}$.

On Δ , we have $dx_1/dt = 0$. Therefore

$$\frac{dF}{dt} = \sum_{i=2}^n \frac{\partial F}{\partial x_i} \frac{dx_i}{dt} = \sum_{i=2}^n \frac{\partial F}{\partial x_i} x_i u_i(R_1^*).$$

Since $u_i(R_1^*) < 0, i = 2, \dots, n$, we know that $dF/dt < 0$ on Δ unless $\mathbf{x} = \mathbf{x}_e$. We have therefore proved the following:

LEMMA D2. If $\mathbf{x}(t_1) \in \Delta - \{\mathbf{x}_e\}$, then $dF/dt < 0$ when $t = t_1$.

In other words, we have shown that, except for the equilibrium point $\mathbf{x}_e$, any solution which at some time hits Δ passes immediately into $\mathcal{B}$. Note that D2 also implies that $\mathcal{B}$ is positively invariant, i.e. any solution which gets into $\mathcal{B}$ stays in $\mathcal{B}$ for all future time. More precisely,

LEMMA D3. If $\mathbf{x}(t_1) \in \mathcal{B}$, then $\mathbf{x}(t) \in \mathcal{B}$ for $t \geq t_1$.

Now consider the function on $\mathcal{B}$: $V(x_1, \dots, x_n) = -x_1$. This is a Liapunov function on $\mathcal{B}$, since

$$\frac{dV}{dt} = -\frac{dx_1}{dt} = -x_1 u_1(R) < 0, \quad \text{if } x_1 \neq 0.$$

Therefore D2 and D3 imply

LEMMA D4. If $\mathbf{x}(t_1) \in \mathcal{B}$ and if $x_1(t_1) \neq 0$, then $\mathbf{x}(t) \rightarrow \mathbf{x}_e$ as $t \rightarrow \infty$.

That is, any solution which gets into $\mathcal{B}$ must approach the equilibrium point $\mathbf{x}_e$. We have therefore proved the conclusion of theorem D1 for any solution which starts in $\mathcal{B}$ or Δ . We have only left to prove the result for a solution starting in $\mathcal{C}$.

Consider the function F on $\mathcal{C}$, which is a Liapunov function since

$$\frac{dF}{dt} = \sum_{i=1}^n \frac{\partial F}{\partial x_i} x_i u_i(R) < 0 \quad \text{in } \mathcal{C}.$$

Therefore the following is true:

LEMMA D5. If $\mathbf{x}(t_1) \in \mathcal{C}$, then either (a) there exists a $t_2 > t_1$ such that $\mathbf{x}(t_2) \in \Delta - \{\mathbf{x}_e\}$, or (b) $\mathbf{x}(t) \rightarrow \mathbf{x}_e$ as $t \rightarrow \infty$.

In other words, any solution which starts in $\mathcal{C}$ either approaches the equilibrium point $\mathbf{x}_e$ or hits Δ . If it approaches $\mathbf{x}_e$, then the conclusion holds; if it hits Δ , then we have shown above that it passes into $\mathcal{B}$ and then approaches $\mathbf{x}_e$. In either case the conclusion of theorem D1 holds, and the proof is complete.

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