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Some Mathematical Problems Concerning the Ecological Principle of Competitive Exclusion

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1. INTRODUCTION

The ecological principle of competitive exclusion asserts that two species cannot indefinitely occupy the same niche [5]. Attempts have been made to state this principle as a mathematical theorem. A standard example is due to Volterra [14]. (See Example 2.1 below.) He constructed a model of two species competing for a single resource and showed that one of the species must go extinct. Although the concept of niche is rather vague, it is generally agreed that Volterra's model is an example of two species competing for the same niche and is therefore an illustration of the principle of competitive exclusion.

The generalizations of Volterra's model have dealt largely with the introduction of more realistic assumptions about the interactions between species. These assumptions have led to some interesting mathematical problems, many of them unsolved. The purpose of this paper is to state these problems precisely, to give proofs of the known results, and to indicate the unanswered questions.

The basic object of study is an idealized ecological community consisting of a certain number of species living together in an isolated geographical area. We shall assume that the community interactions are independent of both space and time and that each species is distributed uniformly over the region. The basic variables are the population densities of each of the species. The

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state of the community is a vector whose components are these population densities. The dynamics of the community are given by a differential equation on the state space. We therefore must know the time rate of change of the population density of each species. This rate divided by the population density is called the *specific growth rate* of that species.

We are interested in whether some of the species must go extinct. Roughly speaking, we shall say that a community *persists* if all of the species remain indefinitely in some strongly stable way. This notion will be made precise in Section 3. We shall say that *exclusion* occurs if the community does not persist.

We shall place various assumptions on the structure of the community which can be interpreted ecologically to mean that the species are competing for certain resources. The principle of competitive exclusion would seem to predict that exclusion must occur if the number of resources is fewer than the number of species. We shall see that certain linearity assumptions on the specific growth rates make this prediction valid. However, we shall also see that the prediction is not necessarily valid if the linearity assumptions are relaxed.

2. Two Classical Examples

Before proceeding to the more general models, we present two standard examples due to Volterra [14] and Lotka [9]. These examples serve to illustrate some of the basic ideas in population ecology. They also serve to motivate the definitions given in the next section.

Example 2.1. Consider a community of two consumer species interacting only through competition for a single resource. For this example it is helpful to think of a resource such as an essential nutrient or living space. Let y_i be the population density of species i, and let z be the amount of available resource. We assume that the dynamics are given by

$$\begin{aligned} \dot{y}_1 &= y_1(-m_1 + c_1 z), \\ \dot{y}_2 &= y_2(-m_2 + c_2 z), \\ z &= z_0(1 - b_1 y_1 - b_2 y_2). \end{aligned} \tag{2.1}$$

The dot represents differentiation with respect to time, as it will throughout the paper. The constants m_i, c_i, b_i, and z_0 are all positive. The specific growth rate of species i is $-m_i + c_i z$. In the absence of any available resource ($z = 0$), species i dies off with mortality rate m_i. Availability of the resource increases the specific growth rate. The third equation gives the amount of available resource as a function of the population densities of the species. The total amount of the resource is z_0 and the amount available decreases as the population densities increase. We assume that $-m_i + c_i z_0 > 0$ so that both populations are able to grow at low densities. Substituting the third of Eqs. (2.1) into the first two, we obtain a differential equation in the plane.

The equilibrium points of Eqs. (2.1) have a special property which will occur analogously in other models. If $m_1 c_2 \neq m_2 c_1$, then there are no equilibrium points with both species present (Fig. 1.). If $m_1 c_2 = m_2 c_1$, then there is a line of equilibrium points given by

$$z_0(1 - b_1 y_1 - b_2 y_2) = m_1/c_1 = m_2/c_2$$

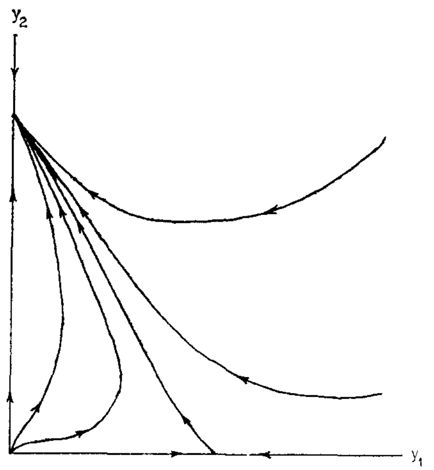

Fig. 1. Phase portrait for Eqs. (2.1) when $m_1 c_2 > m_2 c_1$.

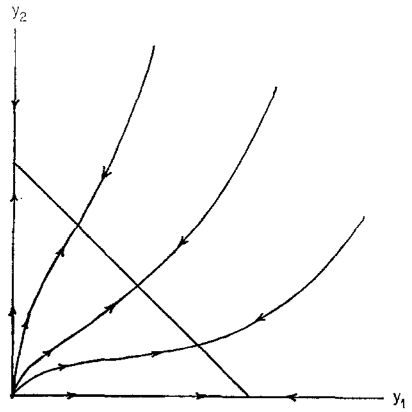

Fig. 2. Phase portrait for Eqs. (2.1) when $mc_2 = m_2 c_1$.

(Fig. 2.). If $m_1c_2 > m_2c_1$, then species 1 always goes extinct ($y_1 \to 0$ as $t \to \infty$), as shown in Fig. 1. If $m_1c_2 < m_2c_1$, then species 2 always goes extinct. These extinctions occur except in the trivial case when one species is absent.

We can argue in one of two ways that Example 2.1 illustrates the exclusion principle. For the first argument we note that, except in the unlikely case that $m_1c_2 = m_2c_1$, one or the other species must go extinct. Therefore the exclusion principle holds for almost all models of the form (2.1). The other argument looks at the question of persistence. Whether or not $m_1c_2 = m_2c_1$, there can be no asymptotically stable equilibrium point with both species present. Since no model of the form (2.1) exhibits persistence, we can say the exclusion principle holds.

The following justification is often given for the latter argument [10]. In case $m_1c_2 = m_2c_1$ the system will approach the line of equilibrium points. Since no equilibrium point is asymptotically stable, random fluctuations can move the system from one equilibrium point to another. Since the line of equilibrium points intersects both axes, these fluctuations will eventually move the system to a neighborhood of one of the axes, and one of the species can be considered extinct.

EXAMPLE 2.2. Now consider a community consisting of one predator species and one prey species. Let x be the prey density and y the predator density. We assume that the dynamics are given by

$$\begin{aligned} \dot{x} &= gx - pxy, \\ \dot{y} &= -my + cpxy, \end{aligned} \tag{2.2}$$

where g, p, m, and c are positive constants. The specific growth rate of the prey in the absence of the predator is g. The mortality rate of the predator in the absence of the prey is m. Note that without the predator the prey density grows without bound and that without the prey the predator goes extinct. The rate of predation per predator per prey is p. The rate of conversion of consumed prey to predator is c.

Equations (2.2) have two equilibrium points, $(0, 0)$ and (x_e, y_e), where

$$-m + cpx_e = g - py_e = 0.$$

The equations also admit an integral of motion,

$$V(x, y) = x_e v(x/x_e) + y_e v(y/y_e)/C, \tag{2.3}$$

where

$$v(\xi) = \xi - \log \xi.$$

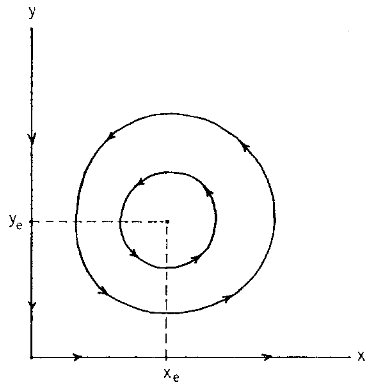

FIG. 3. Phase portrait for Eqs. (2.2).

Therefore all solutions are periodic orbits except the two critical points and the two axes (Fig. 3).

In a predator–prey system the prey can be considered as a resource for the predator. Note that there is an essential difference between the dynamics of the resources in the above two examples. In Example 2.1 the amount of available resource is a function of the consumer densities. In Example 2.2 the amount of resource is given by a differential equation which is a function of the consumer densities. We shall return to this distinction in Section 5.

3. Definitions and Notation

In this section we precisely define the notions of persistence and exclusion. We begin with some standard mathematical definitions.

The real numbers will be denoted by R. By a *flow* on a locally compact metric space X we mean a continuous map $\varphi: X \times R \to X$ such that $\varphi(x, 0) = x$ and $\varphi(\varphi(x, t_1), t_2) = \varphi(x, t_1 + t_2)$. For $K \subset X$ and $I \subset R$, we write

$$\varphi(K, I) = \{\varphi(x, t): x \in K, t \in I\}.$$

A point $x \in X$ will be called a *rest point* if $\varphi(x, R) = x$. For flows generated by vector fields, a rest point corresponds to a *critical point*, or *zero*, of the vector field. In such cases, the rest point x will be called *degenerate* if the Jacobian matrix of the vector field at x has a zero eigenvalue.

If $K \subset X$ satisfies $\varphi(K, R) = K$, then K will be called *invariant*. Note that a rest point is an invariant set. For $U \subset X$ we define the *ω-limit set* of U as

$$\omega(U) = \bigcap\{\text{cl}(\varphi(U, [t, \infty))): t \geqslant 0\}.$$

Here cl denotes topological closure.

A compact invariant set K will be called an *attractor* if there is an open $U \supset K$ such that $\omega(U) = K$. By an *attractor block* B we mean a compact set with nonempty interior such that, for each $x \in \partial B$, $\varphi(x, (0, \infty)) \subset \text{int}(B)$. Here ∂ denotes the boundary and int denotes the interior. It is a standard result that every attractor block contains an attractor and that every attractor is the maximal invariant set inside some attractor block [1, 2, 12]. For smooth flows an attractor block can be chosen with smooth boundary and with $\dot{\varphi}$ transverse to the boundary [2].

A *repeller* is an attractor for the time reverse flow $\varphi(x, -t)$. Similarly, a *repeller block* is an attractor block for the reverse flow.

The concept of an attractor block is particularly well suited for our purposes because it combines two different notions of stability. First, the attractor itself is "asymptotically stable" in the sense that orbits starting close to it approach it asymptotically. Second, the attractor block is "stable under perturbation" in the sense that nearby flows have nearby attractor blocks. Indeed, for smooth flows, an attractor block with $\dot{\varphi}$ transverse to its boundary remains an attractor block under C^1 perturbations. The attractor itself may change considerably after a perturbation, but the existence of an attractor remains.

We now turn to the general n-species model

$$\dot{y}_i = y_i g_i(y_1, \ldots, y_n), \qquad i = 1, \ldots, n. \tag{3.1}$$

Here $y_i \geqslant 0$ is the population density, and $g_i(y_1, \ldots, y_n)$ is the specific growth rate, of species i. The two examples of the previous section are models of this type. Equations (3.1) determine a vector field on the manifold

$$E^n = \{(y_1, \ldots, y_n) \in R^n : y_i \geqslant 0 \; \forall i\}.$$

All functions in this paper will be assumed to be infinitely differentiable. We write

$$\mathscr{E}^n = C^\infty(E^n, R^n).$$

A function $\mathbf{g} = (g_1, \ldots, g_n) \in \mathscr{E}^n$ can be thought of as the n-species ecological community whose dynamics are given by Eq. (3.1).

For $\mathbf{g} \in \mathscr{E}^n$ we denote by $\varphi_g(y, t)$ the solution of (3.1) starting at $y \in E^n$ at time $t = 0$. Standard theorems of differential equations imply that φ_g satisfies all the properties of a flow except possibly that solutions may not be defined for all time. This difficulty could be overcome in several ways. In order to streamline our presentation we choose the easiest way and simply assume that φ_g is a flow. This assumption places restrictions only on the behavior of $\mathbf{g}$ near infinity. Such assumptions are of no biological importance.

We are now ready to define "persistence" and "exclusion," at least in the context of Eq. (3.1). The following definition generalizes that of Levin [8], who restricts his attention to attractors which are either rest points or periodic orbits.

DEFINITION. An ecological community $\mathbf{g} \in \mathscr{E}^n$ will be called *persistent* if φ_g has an attractor in $\operatorname{int}(E^n)$. We shall say that $\mathbf{g}$ exhibits *exclusion* if it is not persistent. We shall say that a class of communities $\mathscr{C} \subset \mathscr{E}^n$ satisfies the *exclusion property* if $\mathbf{g}$ exhibits exclusion for all $\mathbf{g} \in \mathscr{C}$.

Clearly, $\mathscr{E}^n$ contains both persistent communities and communities which exhibit exclusion. Example 2.1 gives a class of communities satisfying the exclusion property. Whether the above definition of exclusion is ecologically justifiable is probably debatable. However, it seems a reasonable generalization of previous definitions.

4. Limiting Factors

Example 2.1 provides a prototype for a model proposed by Levin [8]. For this model we assume that the community is structured so that the specific growth rate of a species is only indirectly a function of the population densities of the other species. The growth rates are given as functions of certain "limiting factors," such as available space, available light, or available nutrients. These limiting factors are, in turn, functions of the population densities. The following equations give the dynamics of such a community with n species and k limiting factors [8].

$$\begin{aligned} \dot{y}_i &= y_i u_i(z_1, \ldots, z_k), \qquad & i &= 1, \ldots, n, \\ z_j &= r_j(y_1, \ldots, y_n), \qquad & j &= 1, \ldots, k. \end{aligned} \tag{4.1}$$

Here y_i is the population density of species i, z_j is the amount of limiting factor j and $u_i(z_1, \ldots, z_k)$ is the specific growth rate of species i. Note that Example 2.1 is a special case of this model with $n = 2$ and $k = 1$.

We define the class of n-species communities with k limiting factors:

$$\mathscr{F}_k^n = \{\mathbf{g} = \mathbf{u} \circ \mathbf{r} \colon \mathbf{r} \in C^\infty(E^n, R^k), \mathbf{u} \in C^\infty(R^k, R^n)\}.$$

Note that elements in $\mathscr{F}_k^n$ do not have unique representations in the form $\mathbf{u} \circ \mathbf{r}$. Clearly, $\mathscr{F}_k^n \subset \mathscr{E}^n$ for all k and n, and $\mathscr{F}_k^n = \mathscr{E}^n$ for $k \geqslant n$. Therefore $\mathscr{F}_k^n$ does not satisfy the exclusion property for $k \geqslant n$. The interesting question is whether $\mathscr{F}_k^n$ satisfies the exclusion property for $k < n$. In other words, can there exist persistent communities with fewer limiting factors than species? The naive application of the ecological principle of competitive exclusion predicts that the answer is no. However, we shall see that the answer is not so simple.

We first consider the nature of rest points for communities in $\mathscr{F}_k^n$ with $k < n$. Any rest point in $\text{int}(E^n)$ must be degenerate, since the Jacobian matrix can have rank at most k. In fact, the following theorem shows that rest points can be destroyed by arbitrarily small perturbations of the equations. The topology for these perturbations is not very important for the purposes of this paper. Probably the uniform C^∞ topology on $\mathscr{E}^n$, and the induced topology on $\mathscr{F}_k^n \subset \mathscr{E}^n$, are the most natural.

THEOREM 4.1. *Suppose $k < n$. For a dense set of $\mathbf{g} \in \mathscr{F}_k^n$, φ_g has no rest point in* $\text{int}(E^n)$.

Proof. We prove equivalently that $\mathbf{g}$ has no zero in $\text{int}(E^n)$. Let

$$\mathscr{U} = \{\mathbf{g} \in \mathscr{F}_k^n\colon \mathbf{g}(y) \neq 0 \; \forall y \in \text{int}(E^n)\}.$$

We shall show that $\mathscr{U}$ is dense in $\mathscr{F}_k^n$. Write $\mathbf{g} = \mathbf{u} \circ \mathbf{r} \in \mathscr{F}_k^n$, where u: $R^k \to R^n$. By Sard's theorem (see [11, p. 10]), $u(R^k) \subset R^n$ has Lebesgue measure zero. Therefore we can find an arbitrarily small $\epsilon \in R^n$ such that $0 \notin \mathbf{u}(R^k) + \epsilon$. Let $\mathbf{g}' = (\mathbf{u} + \epsilon) \circ \mathbf{r} = \mathbf{g} + \epsilon$. Then $\mathbf{g}'$ is arbitrarily close to $\mathbf{g}$ and $\mathbf{g}' \in \mathscr{U}$. Therefore $\mathscr{U}$ is dense in $\mathscr{F}_k^n$ and the proof is complete.

It follows from Theorem 4.1 that φ_g cannot have a point attractor in $\text{int}(E^n)$. Actually, one has a stronger condition on attractors:

THEOREM 4.2. *Let $\mathbf{g} \in \mathscr{F}_k^n$ with $k < n$. Suppose $K \subset \text{int}(E^n)$ is an attractor for φ_g. Then the Euler characteristic of K is zero.*

The attractor K need not be a manifold. However, it can always be surrounded by an attractor block which is a manifold. We define the Euler characteristic of K to be the Euler characteristic of B, where B is an attractor block containing K as the maximal invariant set in B. This number is well defined and reduces to the ordinary Euler characteristic of K if K is a manifold [2].

Proof of Theorem 4.2. Let $B \subset \text{int}(E^n)$ be an attractor block containing K as the maximal invariant set in B. Choose B so that the vector field is transverse to ∂B. For $\mathbf{g}'$ close to $\mathbf{g}$, B is an attractor block for $\varphi_{g'}$. By Theorem 4.1 we can choose $\mathbf{g}'$ with no critical points in B. Therefore the Euler characteristic of B is zero, by the Poincare–Hopf theorem. (See [11, p. 35].) The proof is complete.

Since the Euler characteristic of a point is 1, we have the following.

COROLLARY 4.3. *Let $k < n$ and $\mathbf{g} \in \mathscr{F}_k^n$. Then φ_g can have no point attractors in* $\text{int}(E^n)$.

Since the Euler characteristic of a circle is zero, Theorem 4.2 does not rule out attracting periodic orbits and so does not settle the exclusion question in general. However, it does settle the case $n = 2$. Since any connected attractor block in the plane must be contained in a disclike attractor block, we have the following generalization of Example 2.1.

COROLLARY 4.4. *$\mathscr{F}_1^2$ satisfies the exclusion property.*

Unfortunately, $\mathscr{F}_1^2$ is the only class among $\mathscr{F}_k^n$ which is known to satisfy the exclusion property. In Section 7 we shall construct an example of a persistent community in $\mathscr{F}_2^3$. In fact, we shall show that $\mathscr{F}_k^n$ does not satisfy the exclusion property for $3k \geqslant 2n$. The question of whether $\mathscr{F}_k^n$ satisfies the exclusion property for $3k < 2n$, $n > 2$, is open.

However, the exclusion question is settled for a certain subclass of $\mathscr{F}_k^n$, namely that for which the functions u_i in Eqs. (4.1) are linear. By a linear function we shall always mean a polynomial of degree 1, not necessarily homogeneous. We define the classes

$$\mathscr{L}\mathscr{F}_k^n = \{\mathbf{g} = \mathbf{u} \circ \mathbf{r} \in \mathscr{F}_k^n : u \text{ is linear}\}.$$

For these classes we have the following theorem.

THEOREM 4.5. *$\mathscr{L}\mathscr{F}_k^n$ satisfies the exclusion property for $k < n$.*

This theorem was known to Volterra [14] for $k = 1$. A slightly different result was proved by Rescigno and Richardson [13] with some additional hypotheses. Levin [8] proved that $\mathscr{L}\mathscr{F}_k^n$, $k < n$, can have no point attractors or attracting periodic orbits. The following proof was suggested to us by Floris Takens.

Proof of Theorem 4.5. It is more convenient to work with the logarithms of the population densities. We therefore introduce the following functions.

$$\log\colon \operatorname{int}(E^n) \to R^n\colon (y_1, \ldots, y_n) \mapsto (\log y_1, \ldots, \log y_n),$$
$$\exp\colon R^n \to \operatorname{int}(E^n)\colon (\eta_1, \ldots, \eta_n) \mapsto (e^{\eta_1}, \ldots, e^{\eta_n}).$$

These functions are diffeomorphisms and are inverses of each other. For $\mathbf{g} \in \mathscr{E}^n$, we define ψ_g to be the flow on R^n given by

$$\dot{\eta} = (\mathbf{g} \circ \exp)(\eta), \tag{4.2}$$

which is simply Eq. (3.1) transformed by the change of variable $y = \exp(\eta)$. Therefore, to prove Theorem 4.5, it is only necessary to show that ψ_g can have no attractor for $\mathbf{g} \in \mathscr{L}\mathscr{F}_k^n$, $k < n$.

Write $\mathbf{g} = \mathbf{u} \circ \mathbf{r} \in \mathscr{L}\mathscr{F}_k{}^n$, where $\mathbf{u}(z) = Az - m$, A is a homogeneous linear map from R^k to R^n, and $m \in R^n$. We rewrite Eq. (4.2) as

$$\dot{\eta} = (A \circ \mathbf{r} \circ \exp)(\eta) - m. \tag{4.3}$$

Now let L_1 = range (A) and L_2 = nullspace (A^T). Then $R^n = L_1 \oplus L_2$, and L_1 and L_2 are orthogonal. Write

$$\eta = (\eta_1, \eta_2) \in L_1 \oplus L_2 \qquad \text{and} \qquad m = (m_1, m_2) \in L_1 \oplus L_2 .$$

Then Eq. (4.3) becomes

$$\dot{\eta}_1 = (A \circ \mathbf{r} \circ \exp)(\eta_1, \eta_2) - m_1,$$
$$\dot{\eta}_2 = -m_2 .$$

Therefore, vector field (4.3) projects to a constant vector field on L_2. Since a constant vector field can have no attractors, ψ_g can have no attractors, and the proof is complete.

As pointed out by Haussmann [6], we can replace the hypothesis that $\mathbf{u}$ is linear with the hypothesis that $\mathbf{u}(R^k)$ is the translation of a proper linear subspace L_1 of R^n. The same proof shows that such communities exhibit exclusion.

5. Biotic Resources

As noted in Section 2, one can consider a predator as a consumer and its prey as a resource. We shall call a resource which is itself a living organism a *biotic resource*. For such resources the limiting factors model of the previous section is inappropriate. It is more appropriate to use a differential equation to describe the amount of available resource. One should contrast Example 2.1, which is a community of two consumers and one limiting factor, with Example 2.2, which is a community of one consumer and one biotic resource.

The dynamics of a community of n consumers (predators) and k biotic resources (prey) can be written

$$\begin{aligned} \dot{y}_i &= y_i u_i(x_1, \dots, x_k), && i = 1, \dots, n, \\ \dot{x}_j &= x_j s_j(y_1, \dots, y_n, x_1, \dots, x_k), && j = 1, \dots, k. \end{aligned} \tag{5.1}$$

Here y_i is the population density of consumer i, and x_j is the population density of resource j. As with the limiting factors model, the important assumption is that the specific growth rate of each consumer is a function only of the resources.

We define the class of communities with n consumers and k biotic resources:

$$\mathscr{B}_k{}^n = \{\mathbf{g}: E^n \times E^k \to R^n \times R^k: (y, x) \mapsto (\mathbf{u}(x), \mathbf{s}(y, x))\}.$$

Making the standard identifications $E^n \times E^k = E^{n+k}$ and $R^n \times R^k = R^{n+k}$, we see that $\mathscr{B}_k{}^n \subset \mathscr{E}^{n+k}$. That is, communities in $\mathscr{B}_k{}^n$ are $(n + k)$-species communities, where n of the species are consumers and k of the species are resources. The following lemma shows that these communities have only $2k$ limiting factors. The factors are the k population densities of the prey and the k specific growth rates of the prey.

LEMMA 5.1. $\mathscr{B}_k{}^n \subset \mathscr{F}_{2k}^{n+k}$.

Proof. Let $\mathbf{g} \in \mathscr{B}_k{}^n$ and write

$$\mathbf{g}(y, x) = (\mathbf{u}(x), \mathbf{s}(y, x)).$$

Define

$$\mathbf{u}^*: E^k \times R^k \to R^n \times R^k: (\eta, \xi) \mapsto (\mathbf{u}(\eta), \xi),$$

$$\mathbf{r}: E^n \times E^k \to E^k \times R^k: (y, x) \mapsto (x, \mathbf{s}(y, x)).$$

Then $\mathbf{g} = \mathbf{u}^* \circ \mathbf{r} \in \mathscr{F}_{2k}^{n+k}$, and the proof is complete.

The class $\mathscr{B}_1{}^1$ has been extensively studied and it is well-known that such communities can persist. The example given in Section 7 is a persistent community in $\mathscr{B}_1{}^2$. Since the cartesian product of persistent communities is a persistent community, one can construct examples of persistent communities in $\mathscr{B}_k{}^n$, whenever $2k \geqslant n$. However, it is unknown whether $\mathscr{B}_k{}^n$ satisfies the exclusion property for $2k < n$.

Lemma 5.1 implies that the example given in Section 7 is a persistent community in $\mathscr{F}_2{}^3$. The same lemma, together with the above comments, gives us the result stated in Section 4: $\mathscr{F}_k{}^n$ does not satisfy the exclusion property for $3k \geqslant 2n$.

As before, we can simplify Eqs. (5.1) by assuming that the specific growth rates of the consumers are linear functions of the resources. We define

$$\mathscr{L}\mathscr{B}_k{}^n = \{\mathbf{g} \in \mathscr{B}_k{}^n: \mathbf{g}(y, x) = (\mathbf{u}(x), \mathbf{s}(y, x)), \mathbf{u} \text{ linear}\}.$$

From the proof of Lemma 5.1 we see that $\mathbf{u}^*$ is linear if $\mathbf{u}$ is linear, so $\mathscr{L}\mathscr{B}_k{}^n \subset \mathscr{L}\mathscr{F}_{2k}^{n+k}$. Theorem 4.5 then implies:

COROLLARY 5.2. *$\mathscr{L}\mathscr{B}_k{}^n$ satisfies the exclusion property for $k < n$.*

In other words, if the specific growth rates of the predators are linear functions of the prey densities, then n predators cannot coexist on fewer than

n prey. Note that this case includes the so-called Lotka–Volterra systems in higher dimensions, where all the functions u_i and s_j in Eqs. (5.1) are assumed to be linear.

6. Systems of One Predator and One Prey

In this section we develop some properties of simple predator–prey systems. We shall use these properties in the construction of our example in the next section.

Recall the Lotka–Volterra predator–prey equations given in Example 2.2. Gause *et al.* [4] suggested that the predation constant p should be a function of the prey density. One can further assume that the specific growth rate g of the prey is also a function of the prey density. Making these assumptions, we write

$$\begin{aligned} \dot{x} &= xg(x) - y\rho(x), \\ \dot{y} &= -my + cy\rho(x). \end{aligned} \tag{6.1}$$

Here x is the prey density, y is the predator density, $g(x)$ is the specific growth rate of the prey in the absence of the predator, and $\rho(x)$ is the predation rate per predator. The positive constants m and c are the same as for Example 2.2.

Some authors assume a specific form for the predation function ρ (cf. [10, Chap. 4]). However, it is more convenient for our purposes to assume only that $\rho\colon [0, \infty) \to [0, \infty)$ is a smooth strictly increasing function with $\rho(0) = 0$. Eqs. (6.1) then define a two-species community in $\mathscr{B}_1^{\,1}$. The most significant assumption in Eqs. (6.1) is that the predator density y appears only linearly in the equations. The corresponding biological assumption is that each individual predator acts independently of all the others, interacting only through the prey.

We assume that there is an $x_e > 0$ so that $-m + c\rho(x_e) = 0$. Since ρ is strictly increasing, x_e is unique. In addition we assume that

$$y_e = x_e g(x_e)/\rho(x_e) > 0.$$

Then (x_e, y_e) is the unique critical point for Eqs. (6.1) in $\operatorname{int}(E^2)$.

By computing the Jacobian matrix at the critical point, one finds that the point is an attractor if $g(x_e) + x_e g'(x_e) - y_e\rho'(x_e) < 0$ and is a repeller if the same quantity is positive. The case of most interest to us occurs when $g'(x_e) = 0$, in which case a simple computation shows [3, 4]:

Lemma 6.1. *Consider Eqs.* (6.1) *and assume* $g'(x_e) = 0$. *Then* (x_e, y_e) *is an attractor if* $x_e\rho'(x_e) > \rho(x_e)$ *and a repeller if* $x_e\rho'(x_e) < \rho(x_e)$.

In Example 2.2 we showed that Eqs. (2.2) have an integral V given by Eq. (2.3). In some very special cases this integral becomes a Lyapunov function for Eqs. (6.1).

LEMMA 6.2. *Consider Eqs.* (6.1) *and let I be an interval containing x_e. Assume that g is decreasing on I and that $\rho(x) = \rho'(x_e)x$ for $x \in I$. Then $(dV/dt)(x, y) \leqslant 0$ for $x \in I$, with $(dV/dt)(x, y) = 0$ if and only if $g(x) = g(x_e)$.*

Proof. A straightforward computation shows that

$$(dV/dt)(x, y) = (x - x_e)(g(x) - g(x_e)).$$

Since g is decreasing, the conclusion follows.

7. A PERSISTENT SYSTEM OF TWO PREDATORS AND ONE PREY

In this section we shall show that the class $\mathscr{B}_1^2$ does not satisfy the exclusion property by constructing an example of a persistent community in $\mathscr{B}_1^2$. This result was indicated previously in some computer simulations by Koch [7].

Consider the system

$$\begin{aligned} \dot{x} &= xg(x) - y_1\rho_1(x) - y_2\rho_2(x), \\ \dot{y}_1 &= -m_1y_1 + c_1y_1\rho_1(x), \\ \dot{y}_2 &= -m_2y_2 + c_2y_2\rho_2(x). \end{aligned} \tag{7.1}$$

Here x is the density of the prey, and y_i is the density of predator i. The constants m_i and c_i are positive. The function g is the specific growth rate of the prey in the absence of both predators and is assumed to be decreasing. The predation function for predator i is ρ_i, assumed to be strictly increasing with $\rho_i(0) = 0$. Equations (7.1) with the preceding assumptions give an example of a community in $\mathscr{B}_1^2$. Note that these equations reduce to Eqs. (6.1) if we let $y_1 = y, y_2 = 0$, or $y_2 = y, y_1 = 0$.

Equations (7.1) have a property analogous to a property encountered in Example 2.1. They will have a critical point in $\operatorname{int}(E^3)$ only if

$$\begin{aligned} -m_1 + c_1\rho_1(x) &= 0, \\ -m_2 + c_2\rho_2(x) &= 0. \end{aligned} \tag{7.2}$$

Since it is unlikely that these two equalities will be met simultaneously, the existence of critical points in int(E^3) is rare. If x_e satisfies Eqs. (7.2), then there is a line of critical points given by

$$x = x_e ,$$
$$y_1\rho_1(x_e) + y_2\rho_2(x_e) = x_e g(x_e).$$

Therefore the critical points of Eqs. (7.1) in int(E^3) occur either along a line or not at all. Hence there can be no point attractors in int(E^3), a result we already knew by Corollary 4.3 and Lemma 5.1. In fact, Theorem 4.2 tells us that any attractor must have Euler characteristic zero.

We shall show that certain equations of the form (7.1) have an attractor in int(E^3). We shall find an attractor block homeomorphic to a solid torus. Note that the attractor block, and hence the attractor, has Euler characteristic zero. One expects that there is usually an attracting periodic orbit inside the block. However, whether equations of the form (7.1) can have an attracting periodic orbit is unknown.

We construct a sequence of six examples, all special cases of Eqs. (7.1), indexed by $\alpha = 1,..., 6$. They will all be of the form

$$\begin{aligned} \dot{x} &= xg^\alpha(x) - y_1\rho_1{}^\alpha(x) - y_2\rho_2{}^\alpha(x), \\ \dot{y}_1 &= -my_1 + cy_1\rho_1{}^\alpha(x), \\ \dot{y}_2 &= -my_2 + cy_2\rho_2{}^\alpha(x). \end{aligned} \tag{7.3}$$

We shall successively perturb each example to construct the next one, until we have arrived at an example with an attractor block in int(E^3) (Fig. 4). Throughout these examples we shall always require that the vector field be transverse to the boundary of an attractor or repeller block.

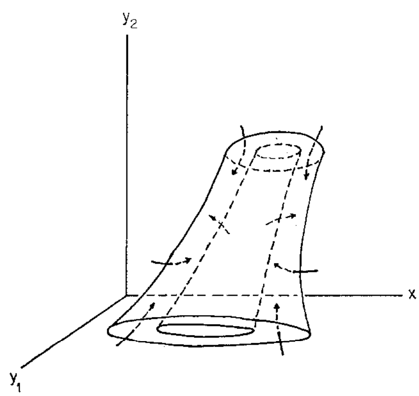

FIG. 4. The attractor block B^6.

EXAMPLE 7.1. We start with the assumptions

$$\rho_1{}^1(x) = \rho_2{}^1(x) = \beta_0 x \qquad \forall x,$$

$$g^1(x) = \gamma_0 \quad \text{if} \quad x \leqslant x_1\,,$$
$$g^1(x) < \gamma_0 \quad \text{if} \quad x > x_1\,.$$

Let x_e satisfy

$$-m + c\rho_1{}^1(x_e) = -m + c\rho_2{}^1(x_e) = 0,$$

and assume that $x_e < x_1$.

Since the two predators behave identically, the ratio y_2/y_1 remains constant and the system behaves as though there were a single predator with density $y = y_1 + y_2$:

$$\begin{aligned} \dot{x} &= xg^1(x) - y\beta_0 x, \\ \dot{y} &= -my + cy\beta_0 x. \end{aligned} \tag{7.4}$$

For $x \leqslant x_1$, Eqs. (7.4) are the Lotka–Volterra equations of Example 2.2. There is a distinguished periodic orbit Γ^1 which is tangent to the line $x = x_1$. Inside Γ^1 all orbits are periodic. Since Lemma 6.2 provides us with a Lyapunov function, we see that all orbits starting outside of Γ^1 wind down asymptotically to Γ^1 (Fig. 5). We can therefore construct a disc D^1, with Γ^1 in its interior, such that orbits of Eqs. (7.4) cross ∂D^1 transversely from outside to inside. Let

$$B^1 = \{(x, y_1, y_2) \in E^3 \colon (x, y_1 + y_2) \in D^1\}.$$

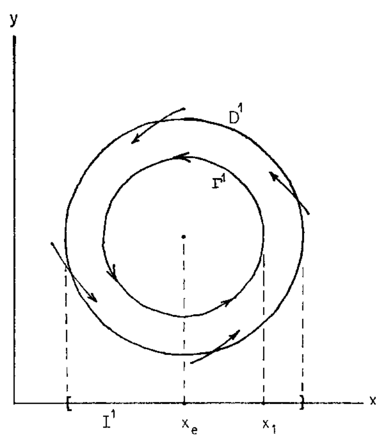

FIG. 5. The attractor block D^1.

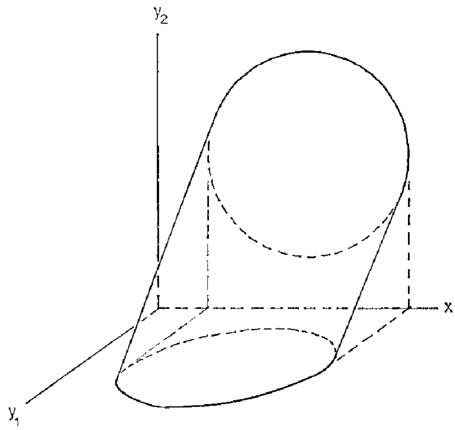

FIG. 6. The attractor block B^1.

Then B^1 is an attractor block for Example 7.1 (Fig. 6). Note that there is a line of critical points in int(E^3).

Let π_x denote the projection of E^3 onto the x-axis. Let $I^1 = \pi_x(B^1)$. Note that x_e , $x_1 \in I^1$.

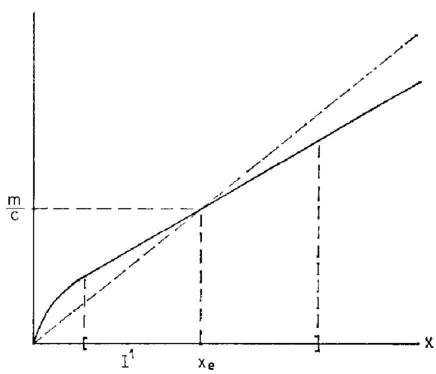

FIG. 7. The graphs of $\rho_1{}^2$ (solid) and $\rho_1{}^1$ (dashed).

EXAMPLE 7.2. Now let $g^2 = g^1$, $\rho_2{}^2 = \rho_2{}^1$, and let $\rho_1{}^2$ satisfy (Fig. 7)

$$(d\rho_1{}^2/dx)(x) = \beta_1 < \beta_0 \qquad \text{for} \quad x \in I^1,$$

$$\rho_1{}^2(x_e) = \rho_1{}^1(x_e) = m/c.$$

Also choose $\rho_1{}^2$ so close to $\rho_1{}^1$ that B^1 remains an attractor block.

Consider the flow restricted to the plane $\{y_2 = 0\}$. Lemma 6.1 tells us that the rest point is a repeller. Therefore we can find a disc D^2 which is a

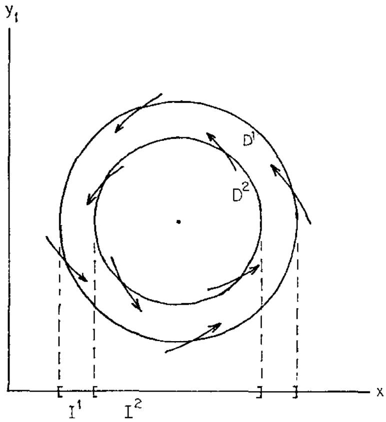

FIG. 8. The attractor block D^1 and the repeller block D^2.

repeller block containing the rest point as the maximal invariant set (Fig. 8). Let $I^2 = \pi_x(D^2)$.

For the next step we restrict our attention to the plane $\{y_1 = 0\}$. We consider the disc D^1 and the curve Γ^1 to be subsets of this plane. Recall that all orbits inside Γ^1 are periodic for Example 7.1 and hence for Example 7.2. Choose a nontrivial periodic orbit Γ^2 so that $\pi_x(\Gamma^2) \subset \text{int}(I^2)$ (Fig. 9). Let b^2 be the right-hand endpoint of $\pi_x(\Gamma^2)$.

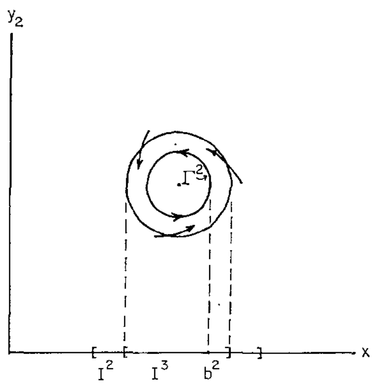

FIG. 9. The attractor block D^3.

EXAMPLE 7.3. Now let $\rho_1^3 = \rho_1^2$, $\rho_2^3 = \rho_2^2$, and let g^3 satisfy (Fig. 10)

$$g^3(x) = \gamma_0 \quad \text{if} \quad x \leqslant b^2,$$

$$g^3(x) < \gamma_0 \quad \text{if} \quad x > b^2.$$

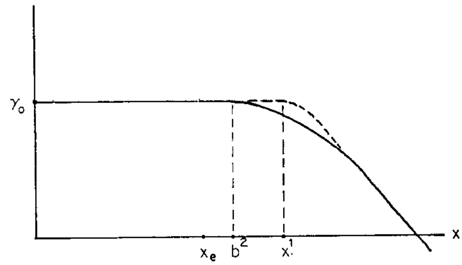

FIG. 10. The graphs of g^3 (solid) and $g^1 = g^2$ (dashed).

Also choose g^3 so close to g^2 that B^1 remains an attractor block for the flow in E^3 and D^2 remains a repeller block for the flow in the plane $\{y_2 = 0\}$.

Just as for Example 7.1, Lemma 6.2 allows us to construct an attractor disc D^3 such that $I^3 = \pi_x(D^3) \subset \text{int}(I^2)$ (Fig. 9). Now using standard techniques [1, 2, 12], we can shrink the block B^1 down to an attractor block B^3 with the following properties: (1) $B^3 \cap \{y_2 = 0\} = D^1$, (2) $B^3 \cap \{y_1 = 0\} = D^3$, and (3) ∂B is transverse to $\{y_1 = 0\}$ and $\{y_2 = 0\}$ (Fig. 11).

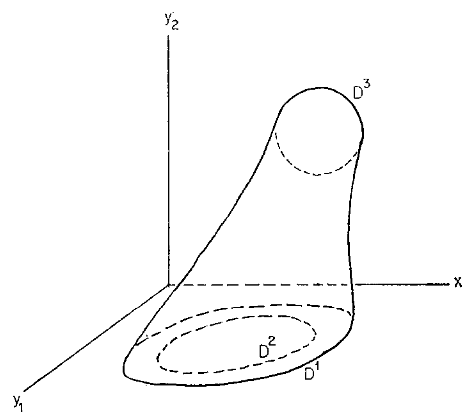

FIG. 11. The attractor block B^3.

EXAMPLE 7.4. Now let $g^4 = g^3$, $\rho_1{}^4 = \rho_1{}^3$, and let $\rho_2{}^4$ satisfy (Fig. 12)

$$(d\rho_2{}^4/dx)(x) = \beta_2 < \beta_0 \qquad \text{for} \quad x \in I^1,$$
$$\rho_2{}^4(x_e) = \rho_2{}^3(x_e) = m/c.$$

Also choose $\rho_2{}^4$ so close to $\rho_2{}^3$ that B^3 remains an attractor block in E^3 and D^2 remains a repeller block in the plane.

Since $\rho_1{}^4(x_e) = \rho_2{}^4(x_e)$, we have a line of critical points for Example 7.4. A computation of the Jacobian at these critical points shows that the line

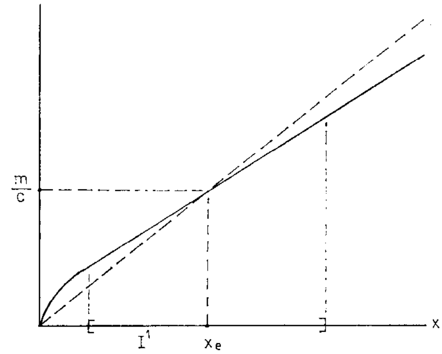

FIG. 12. The graphs of ρ_2^4 (solid) and $\rho_2^3 = \rho_2^2 = \rho_2^1$ (dashed).

repels, since $\beta_1 < \beta_0$ and $\beta_2 < \beta_0$. Therefore we can construct a repeller block C' around the line of critical points. Since D^2 is a repeller block in the plane $\{y_2 = 0\}$, we can extend the repeller block C' to a repeller block C so that $D^2 = C \cap \{y_2 = 0\}$ (Fig. 13). We can also choose C so that its boundary is tranverse to both $\{y_1 = 0\}$ and $\{y_2 = 0\}$.

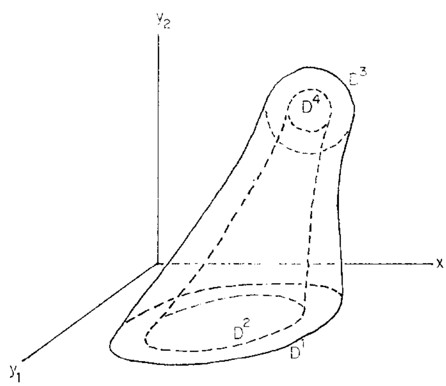

FIG. 13. The attractor block B^4.

Now let $B^4 = B^3 - \text{int}(C)$. Then B^4 is an attractor block. Also let $D^4 = C \cap \{y_1 = 0\}$.

EXAMPLE 7.5. Now let $g^5 = g^4$, $\rho_2^5 = \rho_2^4$, and let ρ_1^5 satisfy (Fig. 14):

$$\rho_1^5(x) = \rho_1^4(x) \quad \text{for} \quad x \in I^3,$$
$$\rho_1^5(x) < \rho_1^4(x) \quad \text{for} \quad x \in I^1 - \text{int}(I^2).$$

Also choose ρ_1^5 so close to ρ_1^4 that B^4 remains an attractor block.

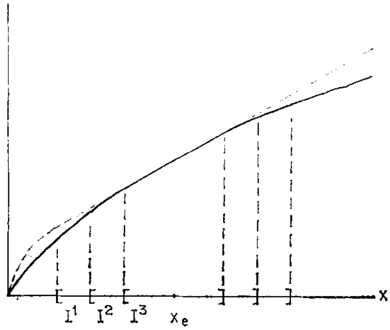

FIG. 14. The graphs of $\rho_1{}^5$ (solid) and $\rho_1{}^4 = \rho_1{}^3 = \rho_1{}^2$ (dashed).

Consider the function

$$L_2(x, y_1, y_2) = y_2^{c\beta_1}/y_1^{c\beta_2}.$$

Computing the time derivative of this function, we find, for $x \in I^1$,

$$(dL_2/dt)(x, y_1, y_2) = \beta_2 c^2 (y_2^{c\beta_1}/y_1^{c\beta_2})((m/c) + \beta_1(x - x_e) - \rho_1{}^5(x)).$$

But $\rho_1{}^5(x)$ is chosen so that

$$(m/c) + \beta_1(x - x_e) - \rho_1{}^5(x) \geqslant 0 \qquad \text{for} \quad x \in I^1,$$

with strict inequality for $x \in I^1 - \text{int}(I^2)$. Thus the entire annulus $D^1 - \text{int}(D^2)$ repels in the y_2-direction. Therefore we can shrink the attractor block B^4 away from the plane $\{y_2 = 0\}$ to obtain an attractor block B^5 whose only intersection with ∂E^3 is $D^3 - \text{int}(D^4)$ on the plane $\{y_1 = 0\}$. We have only left to shrink the block away from this plane.

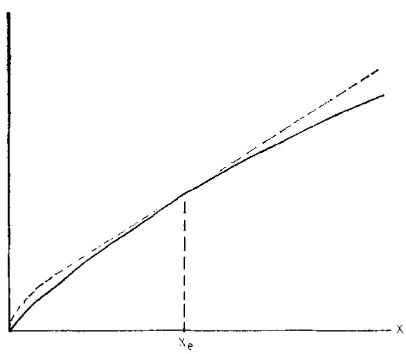

FIG. 15. The graphs of $\rho_2{}^6$ (solid) and $\rho_2{}^5 = \rho_2{}^4$ (dashed).

EXAMPLE 7.6. Finally let $g^6 = g^5$, $\rho_1{}^6 = \rho_1{}^5$, and let $\rho_2{}^6$ satisfy (Fig. 15)

$$\rho_2{}^6(x) < \rho_2{}^5(x) \qquad \text{for} \quad x \in I^3 - \{x_e\}.$$

Also choose $\rho_2{}^6$ so close to $\rho_2{}^5$ that B^5 remains an attractor block.

Now consider the function

$$L_1(x, y_1, y_2) = y_1^{c\beta_2}/y_2^{c\beta_1}.$$

Computing the time derivative, we have, for $x \in I^3$,

$$(dL_1/dt)(x, y_1, y_2) = \beta_1 c^2 (y_1^{c\beta_2}/y_2^{c\beta_1})((m/c) + \beta_2(x - x_e) - \rho_2{}^6(x)).$$

But $\rho_2{}^6$ is chosen to make this expression positive. Therefore we can shrink B^5 away from the plane $\{y_1 = 0\}$ to obtain an attractor block B^6 in $\text{int}(E^3)$ (Fig. 4).

Note that in this last step we can choose either $\rho_2{}^6(x_e) < \rho_2{}^5(x_e)$ or $\rho_2{}^6(x_e) = \rho_2{}^5(x_e)$. With inequality we have no interior rest points. With equality the line of rest points remains.

8. SUMMARY OF RESULTS AND OPEN QUESTIONS

We first considered the class $\mathscr{F}_k{}^n$ of n-species communities with k limiting factors. We showed that $\mathscr{F}_k{}^n$ does not satisfy the exclusion property for $3k \geqslant 2n$. The exclusion question is open for $3k < 2n$ except for one case: $\mathscr{F}_1{}^2$ is known to satisfy the exclusion property.

We also considered the class $\mathscr{B}_k{}^n$ of communities with n consumers and k biotic resources. We showed that $\mathscr{B}_k{}^n$ does not satisfy the exclusion property for $2k \geqslant n$. It is unknown whether $\mathscr{B}_k{}^n$ satisfies this property for $2k < n$.

We also considered special subclasses $\mathscr{L}\mathscr{F}_k{}^n$ and $\mathscr{L}\mathscr{B}_k{}^n$, where the specific growth rates of the consumers are assumed to be linear functions. These subclasses have the exclusion property for $k < n$ and do not have this property for $k \geqslant n$.

From the biological viewpoint one can argue that the classes $\mathscr{F}_k{}^n$ and $\mathscr{B}_k{}^n$ are too large, while the classes $\mathscr{L}\mathscr{F}_k{}^n$ and $\mathscr{L}\mathscr{B}_k{}^n$ are too small. It is unreasonable to assume that specific growth rates of consumers are linear functions of resources. On the other hand, they are not arbitrary. One should place some restrictions on these functions.

Let us reconsider the limiting factors model given by Eqs. (4.1) and think of the factors as resources. One could reasonably assume that the specific growth rate of each species increases as the available amount of each resource increases. One could also assume that the available amount of each resource decreases as the population density of each species increases. Note that Example 2.1 satisfies both of these assumptions. For Eqs. (4.1) these assumptions can be written

$$\begin{aligned}(\partial u_i/\partial z_j)(z_1, \ldots, z_k) &> 0 \qquad \forall i, j, z,\\ (\partial r_j/\partial y_i)(y_1, \ldots, y_n) &< 0 \qquad \forall i, j, y.\end{aligned} \tag{8.1}$$

We denote the class of communities satisfying these monotonicity requirements by

$$\mathscr{M}\mathscr{F}_k^n = \{\mathbf{g} \in \mathscr{F}_k^n \colon (8.1) \text{ is satisfied}\}.$$

This class may model the utilization of resources in a community more appropriately than either $\mathscr{F}_k^n$ or $\mathscr{L}\mathscr{F}_k^n$. Unfortunately, nothing is known about $\mathscr{M}\mathscr{F}_k^n$, $k < n$, except that $\mathscr{M}\mathscr{F}_1^2$ satisfies the exclusion property. From the ecological viewpoint it would be very interesting to settle the exclusion question for these classes.

Similar comments hold for $\mathscr{B}_k^n$. Although the linearity assumptions for $\mathscr{L}\mathscr{B}_k^n$ seem too strong, one might reasonably assume some monotonicity. For Eqs. (5.1) the following assumptions might be appropriate:

$$\begin{aligned}&(\partial u_i/\partial x_j)(x_1, \ldots, x_k) > 0 \qquad \forall i, j, x,\\ &\mathbf{s} \text{ is linear in } y.\end{aligned} \tag{8.2}$$

The first assumption states that the specific growth rate of each consumer increases as the density of each resource increases. The second assumption can be interpreted to mean that each individual consumer acts independently from all the others. The only interaction among consumers is competition for the resources.

We denote the class of communities satisfying the preceeding assumptions by

$$\mathscr{M}\mathscr{B}_k^n = \{\mathbf{g} \in \mathscr{B}_k^n \colon (8.2) \text{ is satisfied}\}.$$

Note that the predator–prey models discussed in Sections 6 and 7 are in these classes. We therefore know that $\mathscr{M}\mathscr{B}_k^n$ does not satisfy the exclusion property for $2k \geqslant n$. For $2k < n$, the exclusion question is open.

Acknowledgments

We are indebted to Floris Takens for his many suggestions during our research for this paper. Many of the ideas in Section 4 came from discussions with him. In particular, the proof of Theorem 4.5 is his. This paper has also benefited from our discussions with Charles Conley and Hans Weinberger.

Note added in proof. Much progress has been made since this paper was written. Zicarelli has shown that $\mathcal{MB}_k^n$, $\forall k, n$, does not satisfy the exclusion property [19]. Hence $\mathcal{B}_k^n$, $\forall k, n$, does not satisfy this property.

A corollary of Zicarelli's work is that $\mathcal{F}_k^n$ does not satisfy the exclusion property for $k \geqslant 2$. Working independently, Kaplan and Yorke showed that $\mathcal{F}_k^n$, $k \geqslant 3$, does not satisfy this property [17]. Nitecki has recently constructed an example which shows that $\mathcal{F}_1^n$, $n \geqslant 3$, does not satisfy this property [18]. Thus, $\mathcal{F}_k^n$ satisfies the exclusion property only for $n = 2$, $k = 1$.

The class $\mathcal{MF}_k^n$ is probably the most ecologically interesting. Armstrong and McGehee have shown that $\mathcal{MF}_k^n$ does not satisfy the exclusion property for $k \geqslant 4$ [15], but does satisfy this property for $n > k = 1$ [16]. The cases with $k = 2$ or 3 remain unsettled.

REFERENCES

1. R. Churchill, Isolated invariant sets in compact metric spaces, *J. Differential Equations* **12** (1972), 330–352.
2. C. Conley and R. Easton, Isolated invariant sets and isolating blocks, *Trans. Amer. Math. Soc.* **158** (1971), 35–61.
3. H. Freedman, Two graphical methods for determining the stability of a two-species predator–prey interaction, preprint.
4. G. Gause, N. Smaragdova, and A. Witt, Further studies of interactions between predators and prey, *J. Animal Écology* **5**, (1936), 1–18.
5. G. Hardin, The competitive exclusion principle, *Science* **131** (1960), 1292–1298.
6. U. Haussman, On the principle of competitive exclusion, *Theoret. Population Biology* **4** (1973), 31–41.
7. A. Koch, Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. *J. Theoret. Biology* **44** (1974), 387–395.
8. S. Levin, Community equilibria and stability, and an extension of the competitive exclusion principle, *Amer. Naturalist* **104**, No. 939 (1970), 413–423.
9. A. Lotka, "Elements of Mathematical Biology," Dover, New York, 1956.
10. R. May, "Stability and Complexity in Model Ecosystems," Princeton Univ. Press, Princeton, N.J., 1973.
11. J. Milnor, "Topology from the Differentiable Viewpoint," Univ. Press of Virginia, Charlottesville, 1965.
12. J. Montgomery, Cohomology of isolated invariant sets under perturbation, *J. Differential Equations* **13** (1973), 257–299.
13. A. Rescigno and I. Richardson, On the competitive exclusion principle, *Bull. Math. Biophys.* **27**, special issue (1965), 85–89.
14. V. Volterra, Variations and fluctuations of the number of individuals in animal species living together, *J. Cons. Internat. Explor. Mer* **3**, (1928), 3–51.
15. R. Armstrong and R. McGehee, Coexistence of species competing for shared resources, *Theoret. Population Biology* **9** (1976), 317–328.
16. R. Armstrong and R. McGehee, in preparation.
17. J. Kaplan and J. Yorke, Competitive exclusion and nonequilibrium coexistence, preprint.
18. Z. Nitecki, A periodic attractor determined by one function, preprint.
19. J. Zicarelli, Mathematical analysis of a population model with several predators on a single prey, PhD Thesis, Univ. of Minnesota (1975).