

## On the stabilizing effect of predators and competitors on ecological communities

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**Abstract.** Ecological communities can lose their permanence if a predator or a competitor is removed: the remaining species no longer coexist. This well-known phenomenon is analysed for some low dimensional examples of Lotka–Volterra type, with special attention paid to the occurrence of heteroclinic cycles.

**Key words:** Permanence—Heteroclinic cycles—Lotka–Volterra equations

### 1. Introduction

A favourite theme in theoretical ecology is the relationship between complexity and stability (May 1973; Svirezhev and Logofet 1983). An interesting aspect of this is the role of a top predator in an ecosystem. Paine (1966) has shown that after removal of the top predator from an intertidal community consisting of 16 species, the number of surviving species dropped to 8 within a couple of years. Thus the occurrence of parasites may increase the diversity of a community. (This seems to have a parallel in human societies.)

Mathematical analyses have to stick to lower dimensional models of such phenomena. Their prototype was introduced by Parish and Sella (1970). These authors showed by computer simulation that in a two-prey, one-predator model of Lotka–Volterra type, the absence of the predator may shorten the time of coexistence of the two-prey species. A local stability analysis of the two-prey, one-predator equilibrium was performed by Cramer and May (1972) and, in a more general setup, by Fujii (1977), Vance (1978) and Hsu (1981). This showed that the three species may coexist in stable equilibrium while the two-prey subsystem admits no equilibrium. But the stable coexistence of species is not necessarily related to the existence of an asymptotically stable equilibrium. This was pointed out in Hutson and Vickers (1983) where the two-prey, one-predator

model was fully analysed from the point of view of permanence (see Sect. 2). We shall adopt this approach and investigate some four-dimensional ecological equations in the same spirit. In particular, we shall study the joint effect of *two* supplementary competing species (or one competing and one predating species) upon a bistable community, thus complementing Kurlingers (1986) work on two-prey, two-predator systems. We shall also investigate the effect of a predator (or a competitor) upon an ecological community consisting of three cyclically competing species which was originally studied by May and Leonard (1975). This yields examples where the removal of the top predator turns a four-species system into a one-species system, and where it is completely impossible to predict which species will be the survivor. Before turning to these examples, we shall briefly sketch some recent results on permanence for Lotka–Volterra equations. One point of this note is to show how these results facilitate the analysis of three- and four-dimensional systems considerably.

## 2. Permanence for Lotka–Volterra models

Like the authors mentioned above, we shall describe the ecological models by Lotka–Volterra equations, being more interested in general properties of the interaction networks than in specific biological situations. If  $x_1, \dots, x_n$  describe the species densities, their evolution is described by

$$\dot{x}_i = x_i \left( r_i - \sum_{j=1}^n a_{ij} x_j \right). \quad (1)$$

This is a dynamical system on the positive orthant leaving the boundary faces invariant. Such a system is said to be *permanent* if there exists a compact set  $K$  in the interior of  $R_+^n$  such that if  $x_i(0) > 0$  for all  $i$ , then  $\underline{x}(t) \in K$  for all  $t$  sufficiently large. Thus no species will tend to extinction. If (1) is permanent, there exists a unique fixed point in the interior of the orthant, but this equilibrium need not be stable. We refer to Hofbauer and Sigmund (1988) for a survey on permanence. Here, we shall only use two results, both related to the notion of a *saturated* rest point.

A fixed point  $\underline{z}$  of (1) is said to be saturated if  $r_i \leq (A\underline{z})_i$  for all  $i$  for which  $z_i = 0$ . (If  $z_i > 0$ , then the fixed point  $\underline{z}$  must satisfy  $r_i = (A\underline{z})_i$ .) The expression  $r_i - (A\underline{z})_i$ , which we shall sloppily denote by  $\dot{x}_i/x_i$ , is a *transversal* eigenvalue of the Jacobian of (1) at  $\underline{z}$ , in the sense that the corresponding (left) eigenvector is  $e_i$  and hence transversal to the boundary face  $\{\underline{x} \in R_+^n : x_j = 0 \text{ whenever } z_j = 0\}$  containing  $\underline{z}$ . If  $\underline{z}$  were not saturated, there would exist a missing species whose rate of increase  $\dot{x}_i/x_i$  is positive if it is introduced in a small amount. A fixed point in  $\text{int } R_+^n$  is trivially saturated.

Let us examine transversal eigenvalues in some low dimensional cases. For two competing species, (1) reduces without restriction of generality to

$$\begin{aligned} \dot{x}_1 &= x_1 r_1 (1 - x_1 - c_{12} x_2), \\ \dot{x}_2 &= x_2 r_2 (1 - c_{21} x_1 - x_2), \end{aligned} \quad (2)$$

with  $r_i, c_{ij} > 0$ . There are three rest points on  $\text{bd } R_+^2$ , namely  $\underline{0}$ ,  $\underline{e}_1$  and  $\underline{e}_2$ . The origin  $\underline{0}$  has two positive transversal eigenvalues, namely  $r_1$  and  $r_2$ , and is never saturated. The rest point  $\underline{e}_1$  has the transversal eigenvalue  $r_2(1 - c_{21})$  ( $= \dot{x}_2/x_2$ ) and  $\underline{e}_2$  has the transversal eigenvalue  $r_1(1 - c_{12})$ . We may distinguish three generic cases:

(a) if both transversal eigenvalues are positive, (2) has a globally stable equilibrium in  $\text{int } R_+^2$ . This is the case of *coexistence*.

(b) if both eigenvalues are negative, i.e. both  $\underline{e}_1$  and  $\underline{e}_2$  are saturated, then there exists a saddle equilibrium in  $\text{int } R_+^2$  whose stable manifold separates the basins of attraction of  $\underline{e}_1$  and  $\underline{e}_2$ . This is the case of *bistability*.

(c) if one eigenvalue is positive and the other negative, then all orbits in  $\text{int } R_+^2$  converge to the saturated fixed point. This is the case of *dominance*.

In the same way, the predator-prey model is completely specified by the transversal eigenvalue of the equilibrium consisting of prey alone, without predator.

But with three-species systems, the signs of the transversal eigenvalues of the boundary fixed points are no longer sufficient to classify the behaviour in the interior of the state space. This is best seen with the model of three cyclically competing species (May and Leonard 1975):

$$\begin{aligned} \dot{x}_1 &= x_1 r_1 (1 - x_1 - \alpha_2 x_2 - \beta_3 x_3), \\ \dot{x}_2 &= x_2 r_2 (1 - \beta_1 x_1 - x_2 - \alpha_3 x_3), \\ \dot{x}_3 &= x_3 r_3 (1 - \alpha_1 x_1 - \beta_2 x_2 - x_3), \end{aligned} \tag{3}$$

with  $r_i > 0$  and  $0 < \beta_i < 1 < \alpha_i$ . The fixed points on the boundary are  $\underline{0}$  (with eigenvalues  $r_1, r_2, r_3 > 0$ ) and the unit vectors. The transversal eigenvalues of  $\underline{e}_i$  are  $r_{i+1}(1 - \beta_i) > 0$  and  $r_{i-1}(1 - \alpha_i) < 0$  (indices counted mod 3). In the face  $x_i = 0$ , the  $(x_{i+1}, x_{i-1})$ -subsystem describes competition with dominance of  $\underline{e}_{i-1}$ . Thus 1 is dominated by 2, 2 by 3 and 3 by 1. The three saddles  $\underline{e}_i$  are connected by orbits  $\underline{q}_i$  lying in the face  $x_i = 0$  and with  $\omega$ -limit  $\underline{e}_{i-1}$  and  $\alpha$ -limit  $\underline{e}_{i+1}$  (see Fig. 1). As shown in Hofbauer and Sigmund (1988), there are two generic cases:

(a) if  $\prod (\alpha_i - 1) > \prod (1 - \beta_i)$ , then (3) is permanent;

(b) if the reverse inequality holds, (3) is not permanent.

In this case, the heteroclinic cycle consisting of the saddles  $\underline{e}_i$  and the connecting orbits  $\underline{q}_i$  is an attractor for the neighbouring orbits. In the former case, it is a repeller.

We shall use two main results in the sequel:

(a) the index theorem of Hofbauer (Hofbauer and Sigmund 1987), or more precisely, its corollary stating that in the generic case when all boundary fixed points are hyperbolic, the number of saturated fixed points is odd;

(b) the permanence condition of Jansen (1986): if the orbits of (1) are uniformly bounded (in the sense that for some  $K > 0$ , all orbits satisfy  $x_i(t) < K$  for all  $i$

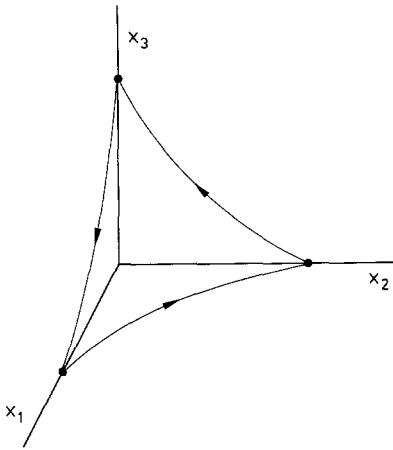


Fig. 1. The heteroclinic cycle for (3)

and for all  $t$  sufficiently large), then (1) is permanent provided there exists a solution  $\underline{p} \in \text{int } R_+^n$  of the system of inequalities

$$\sum p_i(r_i - (A\underline{z})_i) > 0, \tag{4}$$

where  $\underline{z}$  runs through all fixed points on  $\text{bd } R_+^n$ . The boundedness condition will be trivially satisfied for the following examples.

We shall always make the genericity assumption that no eigenvalues are zero.

### 3. Stabilizing bistable communities

The general Lotka–Volterra equation for one predator and two competing prey is of the form

$$\begin{aligned} \dot{x}_1 &= x_1 r_1 (1 - x_1 - c_{12} x_2 - k_1 y), \\ \dot{x}_2 &= x_2 r_2 (1 - c_{21} x_1 - x_2 - k_2 y), \\ \dot{y} &= y r (-1 + l_1 x_1 + l_2 x_2 - g y), \end{aligned} \tag{5}$$

with nonnegative parameters. Hutson and Vickers (1983) have shown that if the  $(x_1, x_2)$ -subsystem describes competition with dominance, the three-species system is permanent for some values of  $k_i, l_i$  and  $g$ . In this sense, a predator may ‘stabilize’ a system of two competing prey. Hutson and Vickers (1983) have also shown that if the  $(x_1, x_2)$ -subsystem is bistable, then (5) is never permanent. Kirlinger (1986) has shown, however, that the introduction of *two* suitable predator species can lead to a permanent four-species model.

A similar situation holds if supplementary competing species are added to a system of three competing species. The general Lotka–Volterra model for three

competing species is

$$\begin{aligned} \dot{x}_1 &= x_1 r_1 (1 - x_1 - c_{12} x_2 - c_{13} x_3), \\ \dot{x}_2 &= x_2 r_2 (1 - c_{21} x_1 - x_2 - c_{23} x_3), \\ \dot{x}_3 &= x_3 r_3 (1 - c_{31} x_1 - c_{32} x_2 - x_3). \end{aligned} \tag{6}$$

Let us assume first that the  $(x_1, x_2)$ -system describes competition with dominance: say  $c_{21} > 1$  and  $c_{12} < 1$ . Then species 1 dominates 2. It is easy to choose  $c_{23}, c_{31} \in (0, 1)$  and  $c_{13}, c_{32} > 1$  such that

$$(1 - c_{12})(1 - c_{23})(1 - c_{31}) \leq (c_{21} - 1)(c_{32} - 1)(c_{13} - 1).$$

This is a system of type (3) which is permanent.

On the other hand, (6) can never be permanent if the  $(x_1, x_2)$ -subsystem is bistable. In this case,  $c_{12} > 1$  and  $c_{21} > 1$ . In order to be permanent, the system can admit no saturated fixed point on the boundary. The two transversal eigenvalues of  $e_3$  are  $1 - c_{23}$  and  $1 - c_{13}$ . Without restricting generality, we may assume  $c_{23} > c_{13}$ . Since  $e_3$  is not saturated, at least its larger eigenvalue  $1 - c_{13}$  must be positive. Since  $e_1$  cannot be saturated, but  $(\dot{x}_2/x_2)(e_1) < 0$ , we must have  $(\dot{x}_3/x_3)(e_1) = 1 - c_{31} > 0$ . Now  $c_{31} < 1$  and  $c_{13} < 1$  imply the existence of an equilibrium  $F_{13} = (\hat{x}_1, 0, \hat{x}_3)$  in the face  $x_2 = 0$ . Its transversal eigenvalue is

$$\frac{\dot{x}_2}{x_2}(F_{13}) = 1 - c_{21} \hat{x}_1 - c_{23} \hat{x}_3.$$

This expression is smaller than  $1 - \hat{x}_1 - c_{13} \hat{x}_3$ . But this last expression is 0, since  $F_{13}$  is a fixed point. Hence  $F_{13}$  is a saturated boundary fixed point, a contradiction to permanence.

**Theorem 1.** *A bistable competition can be stabilized by the introduction of two suitable competitors.*

*Proof.* If  $x_3$  and  $x_4$  denote the frequencies of the two supplementary competitors, then the system is of the form

$$\begin{aligned} \dot{x}_1 &= x_1 r_1 (1 - x_1 - c_{12} x_2 - c_{13} x_3 - c_{14} x_4), \\ \dot{x}_2 &= x_2 r_2 (1 - c_{21} x_1 - x_2 - c_{23} x_3 - c_{24} x_4), \\ \dot{x}_3 &= x_3 r_3 (1 - c_{31} x_1 - c_{32} x_2 - x_3 - c_{34} x_4), \\ \dot{x}_4 &= x_4 r_4 (1 - c_{41} x_1 - c_{42} x_2 - c_{43} x_3 - x_4). \end{aligned} \tag{7}$$

The positive parameters  $r_1, r_2, c_{12}$  and  $c_{21}$  are given (with  $1 \leq c_{12}, c_{21}$  since they describe bistable competition). The other (nonnegative) parameters will be chosen in such a way that the species 1 and 4 can coexist, as well as the species 2 and 3, while 4 is dominated by 2 and 3, and 3 is dominated by 1. There will be a heteroclinic cycle  $F_1 \rightarrow F_{14} \rightarrow F_2 \rightarrow F_{23} \rightarrow F_1$ ; species 1 will be invaded by 4, the resulting equilibrium  $F_{14}$  superseded by species 2, which in turn is invaded by 3, leading to an equilibrium  $F_{23}$  which is superseded by 1. For suitable parameter values, this cycle will be repelling and the full system permanent.

**Table 1.** Transversal eigenvalues for (7)

	$\frac{\dot{x}_1}{r_1 x_1}$	$\frac{\dot{x}_2}{r_2 x_2}$	$\frac{\dot{x}_3}{r_3 x_3}$	$\frac{\dot{x}_4}{r_4 x_4}$
0	1	1	1	1
$F_1$	0	$1 - c_{21} < 0$	$1 - c_{31} < 0$	1
$F_2$	$1 - c_{12} < 0$	0	1	$1 - c_{42} < 0$
$F_3$	1	$1 - c_{23} > 0$	0	-1
$F_4$	$1 - c_{14} > 0$	1	$1 - c_{34} > 0$	0
$F_{12}$	0	0	$1 - c_{31} \bar{x}_1 > 0$	$1 - c_{42} \bar{x}_2 > 0$
$F_{23}$	$1 - c_{12}(1 - c_{23}) > 0$	0	0	$-1 - c_{42}(1 - c_{23}) < 0$
$F_{14}$	0	$1 - c_{21}(1 - c_{14}) > 0$	$1 - c_{31}(1 - c_{14}) - c_{34} < 0$	0

We shall choose  $c_{13} = c_{24} = c_{32} = c_{41} = 0$  and  $c_{43} = 2$ . The equilibria of (7) are then  $0, F_1, F_2, F_3, F_4, F_{12} = (\bar{x}_1, \bar{x}_2, 0, 0), F_{23} = (0, 1 - c_{23}, 1, 0)$  and  $F_{14} = (1 - c_{14}, 0, 0, 1)$ . We shall check later that these are the only fixed points on  $\text{bd } R_+^4$ . The transversal eigenvalues are given by Table 1.

Since  $1 - \bar{x}_1 = c_{12} \bar{x}_2 > 0$ , we obtain  $1 - c_{31} \bar{x}_1 > 0$  if  $c_{31}$  is only slightly larger than 1. Similarly, we have  $1 - c_{42} \bar{x}_2 > 0$  if  $c_{42}$  is only slightly larger than 1. Then the Jansen inequalities for  $F_{12}$  will be trivially satisfied. Furthermore, we choose  $c_{34} < 1, c_{14} < 1$  and  $c_{23} < 1$  such that  $0 < 1 - c_{23} < c_{12}^{-1}$  and  $0 < 1 - c_{14} < c_{21}^{-1}$ . Then all the signs of the transversal eigenvalues are as in Table 1, except for the sign of  $\dot{x}_3/x_3$  at  $F_{14}$  which will be specified later.

We shall now satisfy the Jansen inequalities by setting  $p_1 = 2, p_2 = \frac{1}{2}(c_{21} - 1), p_3 = 3(c_{12} - 1)$  and  $p_4 = (c_{21} - 1)^2$ . The inequalities for  $0, F_3$  and  $F_4$  are obviously satisfied. For  $F_2$ , the inequality is satisfied if  $c_{42} > 1$  is sufficiently close to 1, and for  $F_1$  if  $c_{31} > 1$  is sufficiently close to 1. The inequality corresponding to  $F_{23}$  is satisfied if  $c_{23} < 1$  is sufficiently close to 1. There remains the inequality for  $F_{14}$ . We choose  $c_{31} > 1$  so close to 1 that  $1 - c_{31}(1 - c_{14}) > 0$ , and then  $c_{34} < 1$  slightly larger than this number, so that  $\dot{x}_3/x_3$  is a small negative number and

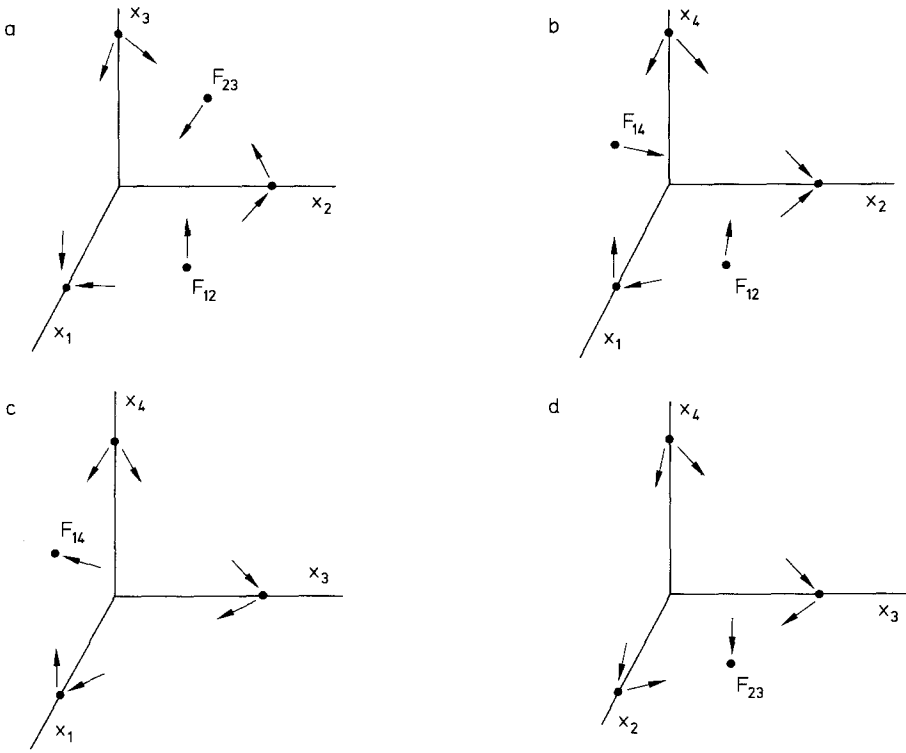
$$p_2 \frac{\dot{x}_2}{x_2} + p_3 \frac{\dot{x}_3}{x_3} > 0.$$

There remains to check that there are no other fixed points. The only possible candidates are interior fixed points of three species systems. But as Fig. 2 shows, each three-system has exactly one saturated fixed point on the boundary and hence no fixed point in the interior. For  $x_4 = 0$  it is  $F_1$ , for  $x_3 = 0$  it is  $F_2$ , for  $x_2 = 0$  it is  $F_{14}$  and for  $x_1 = 0$  it is  $F_{23}$ .

**Theorem 2.** *A bistable competition can be stabilized by the introduction of a suitable pair of a predator and a competitor.*

*Proof.* Let  $x_3$  denote the supplementary competitor and  $y$  the predator. We shall show that for any  $c_{12}, c_{21} > 1$ , the system

$$\begin{aligned} \dot{x}_1 &= x_1 r_1 (1 - x_1 - c_{12} x_2 - y), \\ \dot{x}_2 &= x_2 r_2 (1 - c_{21} x_1 - x_2 - c_{23} x_3), \\ \dot{x}_3 &= x_3 r_3 (1 - c_{31} x_1 - x_3 - l_3 y), \\ \dot{y} &= yr (-1 + d_1 x_1 + \frac{1}{2} x_2) \end{aligned} \tag{8}$$



**Fig. 2.** The three-dimensional boundary face for (7). **a**  $x_4 = 0$ ; **b**  $x_3 = 0$ ; **c**  $x_2 = 0$ ; **d**  $x_1 = 0$

is permanent, if the positive constants  $c_{31}$ ,  $c_{23}$ ,  $l_3$  and  $d_1$  are suitably chosen. We shall produce again a repelling heteroclinic cycle  $F_1 \rightarrow F_{1y} \rightarrow F_2 \rightarrow F_{23} \rightarrow F_1$ , where  $F_{23} = (0, 1 - c_{23}, 1, 0)$  is the equilibrium of species 2 and 3 and  $F_{1y} = (d_1^{-1}, 0, 0, 1 - d_1^{-1})$  the equilibrium of species 1 and the predator. The other fixed points will be  $Q$ ,  $F_1$ ,  $F_2$ ,  $F_3$  and  $F_{12} = (\bar{x}_1, \bar{x}_2, 0, 0)$ . The transversal eigenvalues are given by Table 2.

If  $c_{31}$  is chosen slightly larger than 1, then  $1 - c_{31}\bar{x}_1 > 0$ . Parameter  $d_1$  will be chosen larger than  $c_{21}$  and  $c_{31}$  and so that  $d_1\bar{x}_1 + \frac{1}{2}\bar{x}_2 > 1$ . Furthermore, one can

**Table 2.** Transversal eigenvalues for (9)

	$\frac{\dot{x}_1}{r_1 x_1}$	$\frac{\dot{x}_2}{r_2 x_2}$	$\frac{\dot{x}_3}{r_3 x_3}$	$\frac{\dot{y}}{ry}$
0	1	1	1	-1
$F_1$	0	$1 - c_{21} < 0$	$1 - c_{31} < 0$	$d_1 - 1 > 0$
$F_2$	$1 - c_{12} < 0$	0	1	$-\frac{1}{2}$
$F_3$	1	$1 - c_{23} > 0$	0	-1
$F_{12}$	0	0	$1 - c_{31}\bar{x}_1 > 0$	$d_1\bar{x}_1 + \frac{\bar{x}_2}{2} - 1 < 0$
$F_{1y}$	0	$1 - d_1^{-1}c_{21} > 0$	$1 - d_1^{-1}c_{31} - l_3(1 - d_1^{-1}) < 0$	0
$F_{23}$	$1 - c_{12}(1 - c_{23}) > 0$	0	0	$-2^{-1}(1 + c_{23}) < 0$

choose  $c_{23}$  so that  $1 - c_{12}^{-1} < c_{23} < 1$ . Then the signs of the transversal eigenvalues are as in Table 2, except that  $\dot{x}_3/x_3$  for  $F_{1y}$  is not yet specified.

With  $p_1 = 2$ ,  $p_2 = (d_1 - 1)/2(c_{21} - 1)$ ,  $p_3 = 2c_{12} - 1$  and  $p_4 = 1$ , the Jansen inequalities can be satisfied. For  $Q$ ,  $F_{12}$ ,  $F_2$  and  $F_3$  this is obvious. The inequality for  $F_{23}$  is satisfied if  $c_{23} < 1$  is sufficiently close to 1. For  $F_1$  it is satisfied if  $c_{31} > 1$  is sufficiently close to 1. Finally, we note that  $1 - (c_{31}/d_1) > 0$ , so that we can choose  $l_3$  such that  $1 - (c_{31}/d_1) - l_3(1 - 1/d_1)$  is a negative number which is so small that the Jansen inequality for  $F_{1y}$  is satisfied.

It remains to check that there are no other fixed points on the boundary. This can be done just as in the previous proof.

**4. Stabilizing heteroclinic repellers**

**Theorem 3.** *A three competitors system with a heteroclinic attractor can be stabilized by the introduction of a suitable predator.*

*Proof.* We may assume that the three cyclically dominating competitors are described by (3). Including the predator, whose density is given by  $y$ , yields

$$\begin{aligned} \dot{x}_1 &= x_1 r_1 (1 - x_1 - \alpha_2 x_2 - \beta_3 x_3 - k_1 y), \\ \dot{x}_2 &= x_2 r_2 (1 - \beta_1 x_1 - x_2 - \alpha_3 x_3 - k_2 y), \\ \dot{x}_3 &= x_3 r_3 (1 - \alpha_1 x_1 - \beta_2 x_2 - x_3 - k_3 y), \\ \dot{y} &= yr(-1 + l_1 x_1 + l_2 x_2 + l_3 x_3 - gy). \end{aligned} \tag{9}$$

The nonnegative parameters  $k_i$ ,  $l_i$  and  $g$  can be suitably chosen. We shall use  $k_2 = k_3 = 1$ ,  $g = 0$ , and specify  $k_1$  and the  $l_i$  in such a way that the only fixed points on the boundary are  $F_1$ ,  $F_2$ ,  $F_3$ , the three-species equilibrium  $F_{123} = (\bar{x}_1, \bar{x}_2, \bar{x}_3, 0)$  and the equilibrium  $F_{1y}$  between the predator and the prey 1. Thus we have to take  $l_1 > 1$  and  $l_2, l_3 < 1$ .

$F_{1y}$  has the coordinates  $(l_1^{-1}, 0, 0, (k_1 l_1)^{-1}(l_1 - 1))$ . The transversal eigenvalues are given by Table 3, where  $B_i = 1 - \beta_i$  and  $A_i = \alpha_i - 1$ . Since we have a heteroclinic attractor, we may assume (without restricting generality) that all  $A_i$  and  $B_i$  are positive and that  $A_1 A_2 A_3 > B_1 B_2 B_3$ . Since  $\alpha_1 \bar{x}_1 + \beta_2 \bar{x}_2 + \bar{x}_3 = 1$ , we

**Table 3.** Transversal eigenvalues for (11)

	$\frac{\dot{x}_1}{r_1 x_1}$	$\frac{\dot{x}_2}{r_2 x_2}$	$\frac{\dot{x}_3}{r_3 x_3}$	$\frac{\dot{y}}{ry}$
0	1	1	1	-1
$F_1$	0	$B_1$	$-A_1$	$l_1 - 1 > 0$
$F_2$	$-A_2$	0	$B_2$	$l_2 - 1 < 0$
$F_3$	$B_3$	$-A_3$	0	$l_3 - 1 < 0$
$F_{1y}$	0	$(l_1 - 1)(k_1 - 1) + k_1 B_1 > 0$	$(l_1 - 1)(k_1 - 1) - k_1 A_1 < 0$	0
$F_{123}$	0	0	0	$l_1 \bar{x}_1 + l_2 \bar{x}_2 + l_3 \bar{x}_3 - 1$
	> 0			



have  $\alpha_1 \bar{x}_1 + \bar{x}_2 + \bar{x}_3 > 1$  and hence

$$l_1 \bar{x}_1 + l_2 \bar{x}_2 + l_3 \bar{x}_3 > 1, \tag{10}$$

if  $\alpha_1 - l_1$ ,  $1 - l_2$  and  $1 - l_3$  are in  $(0, \epsilon)$  for some suitable  $\epsilon$ . We choose furthermore  $l_1$  such that

$$\frac{A_1 A_2 A_3 - B_1 B_2 B_3}{A_2 A_3 + B_2 B_3} < l_1 - 1 < A_1, \tag{11}$$

and  $k_1 > 1$  so large that

$$\frac{A_1 A_2 A_3 - B_1 B_2 B_3}{A_2 A_3 + B_2 B_3} < k_1^{-1} (l_1 - 1) (k_1 - 1). \tag{12}$$

With  $p'_2 = A_3^{-1} B_3$ ,  $p'_3 = B_2^{-1} A_2$  and  $p'_4 = 1 + p'_2 + p'_3$  we obtain

$$p'_2 B_1 - p'_3 A_1 + (l_1 - 1) p'_4 > 0 \tag{13}$$

(this follows from the left-hand side of (11)) and

$$p'_2 [(l_1 - 1)(k_1 - 1) + k_1 B_1] + p'_3 [(l_1 - 1)(k_1 - 1) - k_1 A_1] > 0 \tag{14}$$

(this is just (12)).

In (14), the coefficient of  $p'_2$  is positive and that of  $p'_3$  negative (this last fact is a consequence of the rightmost inequality in (11)). We now set  $p_2 = p'_2 - \eta$ ,  $p_3 = p'_3 + \eta$  and  $p_4 = p'_4 - \eta$ . For  $\eta > 0$  small enough, the inequalities (13) and (14) are still valid with  $p_i$  instead of  $p'_i$ . They correspond to the Jansen inequalities for  $F_1$  and  $F_{1y}$  (see Table 3). Furthermore

$$1 + p_2 + p_3 - p_4 > 0, \tag{15}$$

which is (with  $p_1 = 1$ ) the Jansen inequality for  $\underline{0}$ . By the definition of  $p'_3$ , we have  $-A_2 + p'_3 B_2 = 0$ , hence  $-A_2 + p_3 B_2 > 0$  and thus

$$-A_2 + p_3 B_2 + p_4 (l_2 - 1) > 0, \tag{16}$$

if  $l_2 < 1$  is suitably close to 1, and similarly

$$B_3 - p_2 A_3 + p_4 (l_3 - 1) > 0, \tag{17}$$

if  $l_3 < 1$  is sufficiently close to 1. The Jansen inequalities for  $F_2$ ,  $F_3$  and  $F_{123}$  are just (16), (17) and (10).

It remains to check that there are no other fixed points on the boundary. In Fig. 3, we sketch the boundary faces  $x_1 = 0$ ,  $x_2 = 0$  and  $x_3 = 0$ . The points  $e_3$ ,  $F_{1y}$  and  $e_2$ , respectively, are the only saturated fixed points on the boundary of the resulting three-dimensional system. By the odd number theorem, there can be no fixed point in the interior of the corresponding three-space. Hence we have dealt with *all* boundary points.

**Theorem 4.** *A three competitors system with a heteroclinic attractor can be stabilized by the introduction of a suitable fourth competitor.*

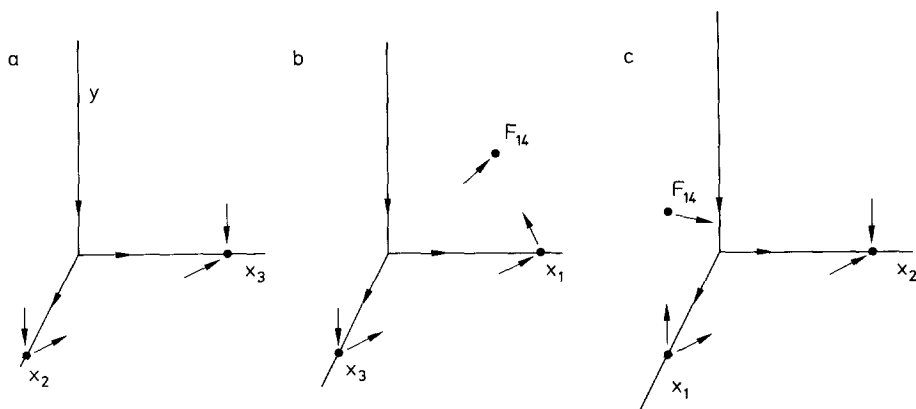


Fig. 3. The three-dimensional boundary faces for (9). a  $x_1 = 0$ ; b  $x_2 = 0$ ; c  $x_3 = 0$

We only sketch the proof. Let us consider a system of the form

$$\begin{aligned}
 \dot{x}_1 &= x_1 r_1 (1 - x_1 - \alpha_2 x_2 - \beta_3 x_3 - k_1 y), \\
 \dot{x}_2 &= x_2 r_2 (1 - \beta_1 x_1 - x_2 - \alpha_3 x_3), \\
 \dot{x}_3 &= x_3 r_3 (1 - \alpha_1 x_1 - \beta_2 x_2 - x_3), \\
 \dot{y} &= yr (1 - l_1 x_1 - l_2 x_2 - l_3 x_3 - y),
 \end{aligned}
 \tag{18}$$

where  $k_1$  and the  $l_i$  are to be suitably chosen. We shall obtain the same pattern of fixed points and transversal eigenvalues (with the addition of  $F_y = \underline{e}_4$ ) as in the proof of Theorem 3, by letting  $k_1 < 1, l_1 < 1, l_2 > 1, l_3 > 1$ . The transversal eigenvalues of the two species equilibrium  $F_{1,y} = ((1 - k_1 l_1)^{-1} (1 - k_1), 0, 0, (1 - k_1 l_1)^{-1} (1 - l_1))$  are given by Table 4. From  $1 - \beta_1 \bar{x}_1 - \bar{x}_2 - \alpha_3 \bar{x}_3 = 0$  follows that  $1 - l_1 \bar{x}_1 - l_2 \bar{x}_2 - l_3 \bar{x}_3 > 0$  if  $l_1$  is close to  $\beta_1 < 1, l_2$  close to 1 and  $l_3$  close to 1 ( $< \alpha_3$ ). Now we take  $p_1 = 1, p_2 < A_3^{-1} B_3$  and  $p_3 > B_2^{-1} A_2$  and choose  $p_4 > 0$  sufficiently large, so that the Jansen inequality for  $F_1$  is satisfied. Next we pick  $l_2$  and  $l_3$  smaller than 1, but so close to 1 that the inequalities for  $F_2$  and  $F_3$  are satisfied. Finally, we can find  $k_1 < 1$  such that  $1 - k_1 l_1 - \alpha_1 (1 - k_1)$  is negative, but so close to 0 that the Jansen inequality for

Table 4. Transversal eigenvalues for (18)

	$\frac{\dot{x}_1}{r_1 x_1}$	$\frac{\dot{x}_2}{r_2 x_2}$	$\frac{\dot{x}_3}{r_3 x_3}$	$\frac{\dot{x}_4}{r_4 x_4}$
0	1	1	1	1
$F_1$	0	$B_1$	$-A_1$	$1 - l_1 > 0$
$F_2$	$-A_2$	0	$B_2$	$1 - l_2 < 0$
$F_3$	$B_3$	$-A_3$	0	$1 - l_3 < 0$
$F_4$	$1 - k_1 > 0$	1	1	0
$F_{1,y}$	0	$1 - k_1 l_1 - \beta_1 (1 - k_1) > 0$	$1 - k_1 l_1 - \alpha_1 (1 - k_1) < 0$	0
$F_{123}$	0	0	0	$1 - l_1 \bar{x}_1 - l_2 \bar{x}_2 - l_3 \bar{x}_3 > 0$

$F_{1y}$ , holds. The inequalities for  $Q$ ,  $F_y$  and  $F_{123}$  are trivial. As in the previous proof one checks that there are no other fixed points.

## 5. Discussion

The examples discussed above are obviously meant as thought experiments rather than as descriptions of real ecological communities. It need not be stressed that a 'suitable predator' cannot be constructed at will. Real ecosystems are the result of a long history and the interaction terms are modelled by coevolution. Nevertheless, the models considered here show that even for very simple ecological systems, the removal of a predator or a competitor can have drastic effects (namely reduce the system to one species). These examples also point out the possibly important role of heteroclinic cycles in ecosystems. It is extremely difficult, of course, to conceive empirical studies which support the idea that a few extra competitors or predators can ensure a large increase in the diversity of an ecosystem, or that heteroclinic cycles can occur in 'real life'. On the other hand, it seems unjustified to dismiss these phenomena offhand as artificial spinoffs from oversimplified equations. Their biological possibility, if not plausibility, should be kept in mind.

Mathematically, several questions concerning Lotka–Volterra equations emerge in this context. It seems, for example, that there is a kind of equivalence between predator and prey: if a predating species stabilizes a community, then a competing species can also do the job, and vice versa. We know so far no explanation for this (except that the number of free parameters is the same). More generally, it would be interesting to find rules specifying the minimal number of additional predator species needed to stabilize a given ecosystem. In spite of recent progress (Kirlinger 1988), even the four-dimensional Lotka–Volterra equation is not completely understood from the viewpoint of permanence and invadability of subsystems. Recently developed tools, in particular the theorem of Jansen, seem to offer new opportunities for progress, however. An interesting question in this context concerns ecological networks with 'random interactions' (see Ginzburg et al. (1988) for a recent survey). So far, most authors seem to have addressed the question by looking for asymptotically stable fixed points in the interior of the state space. It seems more natural to check whether the permanence conditions are satisfied.

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## References

- Arneodo, A., Coulet, P., Tresser, C.: Occurrence of strange attractors in three dimensional Volterra equations. *Physics Letters* **79A**, 259–263 (1980)
- Chenciner, A.: Comportement asymptotique de systèmes différentiels du type 'compétition d'espèces'. *Comptes Rendus Acad. Sci. Paris* **284**, 313–315 (1977)

- Cramer, N. F., May, R. M.: Interspecific competition, predation and species diversity: a comment. *J. Theor. Biol.* **3**, 289–293 (1972)
- Fujii, K.: Complexity-stability relationship of two-prey one-predator species system model: local and global stability. *J. Theor. Biol.* **69**, 613–623 (1977)
- Ginzburg, L. R., Akcakaya, H. R., Kim, J.: Evolution of community structure: competition. *J. Theor. Biol.* **133**, 513–523 (1988)
- Hofbauer, J., Sigmund, K.: Permanence for replicator equations. In: Kurzhanski, A., Sigmund, K. (eds.) *Dynamical systems. (Lect. Notes Econ. Math. Syst., Vol. 287)* Berlin Heidelberg New York: Springer 1987
- Hofbauer, J., Sigmund, K.: *The theory of evolution and dynamical systems.* Cambridge: Cambridge University Press 1988
- Hsu, S. B. Predator-mediated coexistence and extinction. *Math. Biosci.* **54**, 231–248 (1981)
- Hutson, V., Vickers, G. T.: A criterion for permanent coexistence of species with an application to a two-prey one-predator system. *Math. Biosci.* **63**, 253–269 (1983)
- Jansen, W.: A permanence theorem for replicator and Lotka–Volterra systems. *J. Math. Biol.* **25**, 411–422 (1986)
- Kirlinger, G.: Permanence in Lotka–Volterra equations: linked predator-prey systems. *Math. Biosci.* **82**, 165–191 (1986)
- Kirlinger, G.: Permanence of some ecological systems with several predator and one prey species. *J. Math. Biol.* **26**, 217–232 (1988)
- May, R. M.: *Stability and complexity in model ecosystems.* Princeton: Princeton University Press 1973
- May, R. M., Leonard, W.: Nonlinear aspects of competition between three species. *SIAM J. Appl. Math.* **29**, 243–252 (1975)
- Paine, R. T.: Food web complexity and species diversity. *Am. Nat.* **100**, 65–76 (1966)
- Parish, J. D., Salla, S. B.: Interspecific competition, predation, and species diversity. *J. Theor. Biol.* **27**, 207–220 (1970)
- Schuster, P., Sigmund, K., Wolff, R.: Cooperative and competitive behaviour of hypercycles. *J. Differ. Equations* **32**, 357–368 (1979)
- Svirezhev, Y. M., Logofet, D. O.: *Stability of biological communities.* Moscow: Mir 1983
- Vance, R. R.: Predation and resource partitioning in one predator-two prey model communities. *Am. Nat.* **112**, 797–813 (1978)

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