

## COMPETITION IN THE CHEMOSTAT: SOME REMARKS

*This paper is dedicated to Paul Waltman on the occasion of his retirement*

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**1 Review of competition for a single substrate** Paul Waltman's chemostat-related work has had a large impact in population biology, ecology and bio-engineering. It has motivated and inspired the work of many other authors, including us. It seems appropriate to point out a major open problem which remains unresolved after more than thirty years and to touch on some other issues related to bacterial ecology in the chemostat.

The basic equations for mixed culture competition in the chemostat for a single growth-limiting substrate are given by [8, 26, 29]:

$$(1.1) \quad \begin{aligned} S' &= D(S^0 - S) - \sum_i \gamma_i^{-1} f_i(S) x_i \\ x_i' &= x_i(f_i(S) - D_i) \end{aligned}$$

where  $S$  is substrate concentration,  $S^0$  is the concentration of it in the feed, and  $x_i$  is  $i$ th population density.  $D$  is the dilution rate,  $\gamma_i$  is the yield of the organism  $i$ ,  $D_i$  is the removal rate (usually equal to  $D + k_i$ , where  $k_i$ , often neglected, is a death rate). All parameters are assumed to be positive. Specific growth rates of the  $i$ th organism are given by the  $f_i(S)$ . A typical form of the  $f_i$  are Monod functions

$$(1.2) \quad f(S) = \frac{mS}{a + S}$$

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although it is common to take a more general approach by restricting  $f_i$  to be continuously differentiable and to satisfy  $f_i(0) = 0$ . In many cases, one also assumes that  $f'_i(S) > 0$ , but see [3, 39] for notable exceptions. Here we adopt this assumption but we will remark on the more general case.

Assuming that  $f_i(S^0) > D_i$ , which we do since the alternative is extinction of the  $i$ th organism even in the absence of competition, and monotonicity of  $f_i$ , we may define the so-called “break-even concentration”  $\lambda_i$  by

$$(1.3) \quad f_i(\lambda_i) - D_i = 0$$

The **Competitive Exclusion Principle (CEP)** in this context is the following assertion: If  $\lambda_1 < \lambda_j$  for all  $j > 1$  then  $x_j(t) \rightarrow 0$  as  $t \rightarrow \infty$  and, if  $x_1(0) > 0$ , then  $x_1(t) \rightarrow \gamma_1(D/D_1)(S^0 - \lambda_1)$ .

CEP has been proved under a variety of hypotheses [1, 3, 12, 14, 20, 21, 39, 40] summarized crudely in the table below. In the table, “ $f_i$  monotone” means it is monotone increasing while mixed-monotone includes the broader class of functions that may assume a particular value at most twice. The meaning of “restricted to simplex” is that initial data were required to belong to the invariant simplex, which exists if  $D_i = D$ . Except for [39], which also applies to non-delay models, we have not cited any of the extensive literature on the chemostat model which include time delays. The most important open question remains: *is CEP true assuming only that the  $f_i$  are monotone with no restriction on the  $D_i$ ?*

Author(s) and Date	Hypotheses
Hsu, Hubbel, Waltman 1977	$D = D_i$ , $f_i$ Monod, restricted to simplex
Hsu 1978	$f_i$ Monod
Armstrong & McGehee 1980	$D_i = D$ , $f_i$ monotone, restricted to simplex
Butler & Wolkowicz 1985	$D_i = D$ , $f_i$ mixed-monotone
Wolkowicz & Lu 1992	$D_i \neq D$ , $f_i$ mixed-monotone, technical assumption
Wolkowicz & Xia 1997	$D_i - D$ small, $f_i$ monotone
Li 1998,1999	$D_i - D$ small, $f_i$ mixed-monotone, technical assumption

TABLE 1: Proofs of the Competitive Exclusion Principle.

**2 When does single substrate growth limitation hold?** One of the central tenets of the classical chemostat model of mixed culture competition for a single growth limiting nutrient is the assumption that all other nutrients required for growth are supplied in excess and therefore only one nutrient is growth limiting throughout the experiment [8, 26, 29]. This is an assumption that can only be justified within the context of a multi-resource model. In this section we aim to provide such justification using a standard model for multi-resource competition.

The equations for  $n$  species  $N_i$  competing for  $m$  resources  $R_j$  are

$$(2.1) \quad \begin{aligned} N_i' &= N_i[\mu_i(R) - D_i], \quad 1 \leq i \leq n \\ R_j' &= D[S_j - R_j] - \sum_k c_{jk} \mu_k(R) N_k, \quad 1 \leq j \leq m. \end{aligned}$$

Here,  $D_i > 0$  is the removal rate of the  $i$ th species,  $D > 0$  is the resource turnover rate and  $S_j > 0$  is the supply concentration of the  $j$ th resource. On re-scaling the  $N_i$ , we could assume that the  $c_{ji}$  satisfy  $\sum_j c_{ji} = 1$ ;  $c_{jk} > 0$  is the content of resource  $j$  in species  $k$ .

We restrict attention to essential resources  $R = (R_1, \dots, R_m)$  for which the Law of the Minimum applies

$$(2.2) \quad \mu_i(R) = \min_j \{f_{ji}(R_j)\},$$

where, typically,  $f_{ji}$  is a Monod function

$$(2.3) \quad f_{ji}(R_j) = \frac{r_i R_j}{K_{ji} + R_j},$$

although we really require only that  $f_{ji}$  is locally Lipschitz continuous, strictly increasing and satisfies

$$f_{ji}(0) = 0, \quad \text{and} \quad f_{ji}(\infty) = r_i.$$

See [6] for a derivation of (2.2) as well as alternatives to the law of the minimum. Model (2.1) with the law of the minimum has been tested and verified extensively using competition experiments with phytoplankton species [11, 15, 27, 31, 32, 35, 38]. The model also provides a conceptual framework for competitive interactions among terrestrial plants [36, 37]. A great deal of theoretical work has been devoted to system (2.1); see e.g., [19, 13, 4, 22, 2, 25, 23, 24, 15, 16, 17, 18].

In this paper, we are not interested in cases where a species becomes extinct in the absence of competition. Thus, we assume that  $D_i < r_i$  for all  $i$  so there exists positive real numbers  $\lambda_{ji}$  such that

$$f_{ji}(\lambda_{ji}) - D_i = 0.$$

Note  $\lambda_{ji}$  is the break-even concentration of resource  $R_j$  for the growth of species  $i$  when only resource  $R_j$  is growth limiting.

Our goal is to provide explicit conditions for resource  $R_1$  to be ultimately growth limiting. Mathematically, we seek conditions guaranteeing that for every solution of (2.1), we have

$$\mu_i(R(t)) = f_{1i}(R_1(t))$$

for all organisms  $i$  and all large  $t$ . If this is the case, then the asymptotic behavior of (2.1) is determined by that of the single-resource model

$$(2.4) \quad \begin{aligned} N'_i &= N_i[f_{1i}(R_1) - D_i], \quad 1 \leq i \leq n \\ R'_1 &= D[S_1 - R_1] - \sum_k c_{1k} f_{1k}(R_1) N_k. \end{aligned}$$

Without loss of generality, assume that organism  $N_1$  has the lowest break-even concentration for resource  $R_1$ :

$$(2.5) \quad \lambda_{11} < \lambda_{1i}, \quad i = 2, \dots, n.$$

If CEP holds for (2.4) then

$$(2.6) \quad \begin{aligned} N_j(t) &\rightarrow 0, \quad j > 1, \\ N_1(t) &\rightarrow \frac{D}{c_{11}D_1}(S_1 - \lambda_{11}), \\ R_1(t) &\rightarrow \lambda_{11}. \end{aligned}$$

Define

$$p_j := \max_k \frac{c_{jk}}{c_{1k}}$$

and, given  $S_1 > 0$ , define  $P_j = P_j(S_1)$  by

$$P_j := \max_k f_{jk}^{-1} \circ f_{1k}(S_1).$$

As  $f_{ji}([0, \infty)) = [0, r_i)$  for all  $j$ ,  $P_j > 0$  is well-defined. In particular, if the  $f_{ji}$  are Monod functions defined by (2.3), then

$$P_j = S_1 \max_k \frac{K_{jk}}{K_{1k}}.$$

**Theorem 1.** *Let  $S_1 > 0$  and*

$$(2.7) \quad S_j > P_j + p_j S_1, \quad j \geq 2.$$

*If  $(R(t), N(t))$  is any solution of (2.1), then*

$$(2.8) \quad \mu_i(R(t)) = f_{1i}(R_1(t))$$

*for all large  $t$  and all  $i$ . In other words,  $(R_1(t), N(t))$  satisfy (2.4) for all large  $t$ .*

*If, in addition CEP holds for (2.4),  $S_1 > \lambda_{11}$  and  $N_1(0) > 0$ , then (2.6) holds as  $t \rightarrow \infty$  and  $R_j(t) \rightarrow S_j - c_{j1}(D_1/D)N_1(\infty)$  for  $j \geq 2$ .*

*Moreover, (2.8) holds for all  $t \geq 0$  and all  $i$  if, in addition to (2.7),*

$$(2.9) \quad \begin{aligned} R_1(0) &\leq S_1, \\ R_j(0) &\geq P_j + p_j S_1, \quad j \geq 2. \end{aligned}$$

*Proof.* Fix  $j \geq 2$  and observe that  $p_j > 0$  satisfies  $p_j c_{1k} \geq c_{jk}$  for  $1 \leq k \leq n$ . The calculation

$$\begin{aligned} (R_j - p_j R_1)' &= D[(S_j - p_j S_1) - (R_j - p_j R_1)] - \sum_k (c_{jk} - p_j c_{1k}) \mu_k N_k \\ &\geq D[(S_j - p_j S_1) - (R_j - p_j R_1)] \end{aligned}$$

leads to

$$(2.10) \quad (R_j - p_j R_1)(t) \geq (R_j - p_j R_1)(0)e^{-Dt} + (S_j - p_j S_1)(1 - e^{-Dt}).$$

As  $S_j - p_j S_1 > P_j$  by hypothesis (2.7) we have  $R_j(t) > P_j$  for all large  $t$ . The sharper estimate,  $R_j(t) \geq S_j - (p_j/2)S_1$  holds if  $R_1(t) > S_1$  for all large  $t$ . The inequality

$$(2.11) \quad R_1' \leq D(S_1 - R_1)$$

implies that either  $R_1(t) \leq S_1$  for all large  $t$  or  $R_1(t) > S_1$  for all large  $t$  and, in the latter case,  $R_1(t) \rightarrow S_1$  as  $t \rightarrow \infty$ . In the former case, we have

$$(2.12) \quad f_{ji}(R_j(t)) > f_{ji}(P_j) \geq f_{1i}(S_1) \geq f_{1i}(R_1(t))$$

for all large  $t$ . In the latter case, since  $f_{ji}(P_j) \geq f_{1i}(S_1)$  and  $R_1(t) \rightarrow S_1$  we have

$$f_{ji}(R_j(t)) > f_{ji}(S_j - (p_j/2)S_1) > f_{ji}(P_j + (p_j/2)S_1) > f_{1i}(R_1(t))$$

for all large  $t$ . In either case (2.8) holds for all large  $t$  and all  $i$ .

The result (2.6) now follows from CEP.

Finally, assume that (2.9) holds. Then  $R_j(0) - p_j R_1(0) \geq P_j$  and (2.11) implies that  $R_1(t) \leq S_1$  for all  $t \geq 0$ . Inequality (2.10) implies that  $R_j(t) - p_j R_1(t) \geq P_j$  for all  $t \geq 0$ , and in particular,  $R_j(t) \geq P_j$  for  $t \geq 0$  and  $j \geq 2$ . The inequality (2.12) therefore holds for all  $t \geq 0$  so (2.8) also holds for all  $t \geq 0$ .  $\square$

We remark that if (2.3) holds, then (2.7) becomes

$$(2.13) \quad \frac{S_j}{S_1} > \max_k \frac{K_{jk}}{K_{1k}} + \max_k \frac{c_{jk}}{c_{1k}}, \quad j \geq 2.$$

The right hand side is small when resource  $R_1$  contributes the dominant fraction of each organisms make-up and when each organisms affinity ( $K_{1k}^{-1}$ ) for resource  $R_1$  is small relative to its affinity for the others.

Note that the first assertion of Theorem 1 depends only on the second equation of system (2.1) and not at all on the first.

**3 The turbidostat: feedback control of dilution rate** The present section is motivated by the work of de Leenheer and Smith [7] who considered two-species competition in the chemostat where the dilution rate is taken to be positive linear combination of the species densities. There, it was shown that coexistence of the two populations can occur in a robust manner. Control of the dilution rate by state feedback is not unknown to bio-engineers and biologists who commonly refer to it as a turbidostat. See Panikov [26] and Shuler and Kargi [28]. In the turbidostat, an optical sensor measures the turbidity of the fluid, a rough measure of population density, and this signal is used to control the dilution rate. The turbidostat is not nearly as popular as the chemostat, perhaps due to the fact that it more complicated to run and because it is not analogous to any natural ecosystem. However, it has been used for theoretical studies of competition for growth-limiting substrate by Flegr [5] whose work consists primarily of numerical simulations of two-species competition. Our aim in this brief section is to describe the model, to give a thorough analysis of the case of competition between two-species, and to give an essentially complete analysis of the three-species case.

In the turbidostat, an optical sensor measures the turbidity of the fluid, assumed to be related to the densities of the microbial densities  $x_i$  by  $\sum_i d_i x_i$ , where  $d_i$  reflects the turbidity weighting given to strain  $i$ . This signal is then used as a negative feedback to control the dilution rate of the reactor by setting  $D = D_0 + \sum_i d_i x_i$  where  $D_0 \geq 0$ ,  $d_i > 0$ . This leads to the system:

$$(3.1) \quad S' = D(S^0 - S) - \sum_i \gamma_i^{-1} f_i(S) x_i$$

$$(3.2) \quad x'_i = x_i [f_i(S) - D], \quad 1 \leq i \leq n$$

$$(3.3) \quad D = D_0 + \sum_i d_i x_i.$$

Flegr [5] takes  $D_0 = 0$ ; we allow  $D_0 \geq 0$  so as to include the classical chemostat ( $d_i = 0$ ) and the turbidostat ( $D_0 = 0$ ) in a single setting.

The usual scaling

$$(3.4) \quad \bar{S} = \frac{S}{S^0}, \quad \bar{x}_i = \frac{x_i}{\gamma_i S^0}, \quad \bar{f}_i(\bar{S}) = f_i(S^0 \bar{S}), \quad \bar{d}_i = d_i \gamma_i S^0.$$

leads to (on dropping the bars):

$$(3.5) \quad S' = D(1 - S) - \sum_i f_i(S) x_i$$

$$(3.6) \quad x'_i = x_i [f_i(S) - D], \quad 1 \leq i \leq n$$

$$(3.7) \quad D = D_0 + \sum_i d_i x_i.$$

Later it will be important to observe that the scaled  $d_i$  depend on the yield coefficients as well as on  $S^0$ . We will see that this allows these parameters to play a role that they do not in the ordinary chemostat.

If  $D_0 = 0$  then the entire  $S$ -axis consists of equilibria. However,

$$S' = \sum_i [d_i(1 - S) - f_i(S)] x_i > 0$$

for all small  $S \geq 0$  so there exists  $\epsilon > 0$  such that  $\liminf_{t \rightarrow \infty} S(t) \geq \epsilon$ . See [7] for details.

We still have the conservation of total substrate:

$$\left( S + \sum_i x_i \right)' = D \left( 1 - S - \sum_i x_i \right)$$

implying that, in the limit

$$S = 1 - \sum_i x_i.$$

The limiting equations are given by

$$(3.8) \quad x_i' = x_i \left[ f_i \left( 1 - \sum_j x_j \right) - D_0 - \sum_j d_j x_j \right], \quad 1 \leq i \leq n.$$

Hereafter, we work exclusively with the limiting equations. Standard techniques allow one to make the appropriate conclusions for (3.5). See [7].

There are uninteresting cases (but not if  $D_0 = 0!$ ).

**Lemma 1.** *If  $f_i(1) \leq D_0$ , then  $x_i(t) \rightarrow 0$ .*

The proof is a straightforward exercise in differential inequalities. Hereafter, we assume that  $f_i(1) > D_0$  for  $1 \leq i \leq n$ . For the pure turbidostat, this is no assumption at all.

If  $f_i(1) > D_0$  then there exists a unique root  $\hat{x}_i$  of  $f_i(1 - x_i) - D_0 - d_i x_i = 0$  satisfying  $0 < \hat{x}_i < 1$ . In that case,

$$E_i = (0, 0, \dots, \hat{x}_i, 0, \dots, 0)$$

is a steady state of (3.8). Define  $S_i := 1 - \hat{x}_i$ .

The Jacobian matrix  $J = (J_{ij})$  of the vector field (3.8) evaluated at  $E_1$  is easily seen to have non-zero entries only on the diagonal and the first row:

$$\begin{aligned} J_{1j} &= -\hat{x}_1 f_1'(S_1) - d_j \hat{x}_1, \quad 1 \leq j \leq n, \\ J_{kk} &= f_k(S_1) - f_1(S_1), \quad k \geq 2. \end{aligned}$$

Consequently,  $E_1$  is asymptotically stable in the linear approximation if and only if

$$f_k(S_1) < f_1(S_1), \quad k \geq 2.$$

Similarly, we have

**Lemma 2.**  *$E_i$  is asymptotically stable in the linear approximation if and only if*

$$(3.9) \quad f_k(S_i) < f_i(S_i), \quad k \neq i.$$

*$E_i$  is unstable if any of the strict inequalities is reversed.*



Observe that depending on the  $d_i$  and how the  $f_i$  intersect each other, it is quite possible for several of the  $E_i$  to be locally asymptotically stable. For example, suppose that there exists  $0 = u_0 < u_1 < u_2 < \dots < u_n = 1$  such that

$$f_i(S) > f_j(S), \quad u_{i-1} < S < u_i, \quad j \neq i, \quad 1 \leq i \leq n.$$

For each  $i$ , we can choose  $d_i > 0$  such that the graph of  $y = f_i(S)$  meets the line  $y = D_0 + d_i(1 - S)$  at a point with  $S = S_i \in (u_{i-1}, u_i)$ . Consequently,  $E_i$  is asymptotically stable for every  $i$ !

For simplicity, we make the following generic assumptions in the remainder of this section.

(A1)  $f_i(S) = f_j(S)$  for at most one  $S > 0$ ,  $i \neq j$ ; in this case  $f'_i(S) \neq f'_j(S)$ .

(A2)  $f_i(S) = f_j(S) = f_k(S)$  does not hold for any  $S > 0$  and distinct  $i, j$  and  $k$ .

(A3)  $f_i(S_i) \neq f_j(S_i)$  for  $i \neq j$ .

(A3) allows for at most two species to be present at positive density at equilibrium. If  $f_1(S^*) = f_2(S^*) := D^* > D_0$  at some  $1 > S^* > 0$  then there may exist a steady state  $E_{12}$  at which  $x_1, x_2 > 0$  and all other densities vanish. It is easily seen that  $x_1, x_2$  must satisfy

$$\begin{aligned} d_1x_1 + d_2x_2 &= D^* - D_0 \\ x_1 + x_2 &= 1 - S^*. \end{aligned}$$

This system has a positive solution given by

$$x_1^* = \frac{D^* - D_0 - d_2(1 - S^*)}{d_1 - d_2}, \quad x_2^* = \frac{D^* - D_0 - d_1(1 - S^*)}{d_2 - d_1}$$

if and only if  $(D^* - D_0)/(1 - S^*)$  lies strictly between  $d_1$  and  $d_2$ .

It is easily seen that, provided  $S^*$  exists and satisfies  $0 < S^* < 1$ , then  $S_i < S^*$  if and only if  $d_i < (D^* - D_0)/(1 - S^*)$ . Consequently,

$$(3.10) \quad d_1 < \frac{D^* - D_0}{1 - S^*} < d_2$$

is equivalent to

$$(3.11) \quad S_1 < S^* < S_2,$$

while

$$(3.12) \quad d_2 < \frac{D^* - D_0}{1 - S^*} < d_1$$

is equivalent to

$$(3.13) \quad S_2 < S^* < S_1.$$

The Jacobian matrix  $J = (J_{ij})$  of (3.8) at  $E_{12} = (x_1^*, x_2^*)$  has nonzero entries only in the first two rows and along the diagonal:

$$\begin{aligned} J_{1j} &= -x_1^*(f'_1 + d_j), \\ J_{2j} &= -x_2^*(f'_2 + d_j), \quad j = 1, 2, \\ J_{kk} &= f_k - D_0 - d_1x_1^* - d_2x_2^*, \quad k \geq 2. \end{aligned}$$

The two-by-two submatrix in the upper left corner has negative trace and determinant given by

$$(3.14) \quad J_{11}J_{22} - J_{12}J_{21} = x_1^*x_2^*(d_2 - d_1)(f'_1 - f'_2).$$

Only very limited results seem possible for the general case of  $n$  species. Hirsch's carrying simplex can be established following ideas in [23]. This means that there is an  $n - 1$  dimensional invariant manifold, homeomorphic to the standard simplex by radial projection, which attracts all non-zero initial data. We now turn to an analysis of two-population competition.

Whereas in the chemostat model, we typically order species  $i$  by their break-even concentrations  $\lambda_i$ , here it is more convenient to assume that  $f_1(S) > f_2(S)$  for all small positive  $S$  and, if  $S^*$  exists (we do not demand it!) and satisfies  $S^* < 1$ , we make the generic assumption (A1) that  $f'_2(S^*) > f'_1(S^*)$ .

**Theorem 2.** *Every solution of (3.8) where  $n = 2$  converges to one of  $E_1, E_2, E_{12}$ . There are four cases ( $S^* < 1$  is assumed in (b)–(d)):*

- (a) *If  $f_1 > f_2$  for all  $0 < S < 1$  or if  $S^* < 1$  and  $d_i < (D^* - D_0)/(1 - S^*)$  for  $i = 1, 2$ , then  $x_2(t) \rightarrow 0$  and  $x_1(t) \rightarrow \hat{x}_1$ . Competitive Exclusion.*
- (b) *If  $d_i > (D^* - D_0)/(1 - S^*)$  for  $i = 1, 2$ , then  $x_1(t) \rightarrow 0$  and  $x_2(t) \rightarrow \hat{x}_2$ . Competitive Exclusion.*
- (c) *If  $d_1 < (D^* - D_0)/(1 - S^*) < d_2$ , then both  $E_i$  are locally asymptotically stable and  $E_{12}$  is a saddle point. Bistability.*

(d) If  $d_2 < (D^* - D_0)/(1 - S^*) < d_1$ , then both  $E_i$  are unstable and  $E_{12}$  attracts all solutions satisfying  $x_i(0) > 0$ ,  $i = 1, 2$ . Coexistence.

*Proof.* The limiting system (3.8) is a planar competitive system so it follows that all solutions converge to equilibrium [30].

In case (a),  $f_1 > f_2$  at  $S_1, S_2$  so  $E_1$  is asymptotically stable and  $E_2$  is unstable by Lemma 2. There is no interior steady state so  $E_1$  attracts all positive initial data.

In case (b), since  $f_2 > f_1$  at  $S_1, S_2$ ,  $E_2$  is asymptotically stable and  $E_1$  is unstable by Lemma 2. As there is no interior steady state,  $E_2$  attracts all positive initial data.

In case (c),  $f_1(S_1) > f_2(S_1)$  and  $f_1(S_2) < f_2(S_2)$  so  $E_1$  and  $E_2$  are locally asymptotically stable. By (3.14),  $f'_2(S^*) > f'_1(S^*)$ , and  $d_1 < d_2$ ,  $E_{12}$  is a saddle point. It follows that there is a separatrix formed by the stable manifold of  $E_{12}$  which forms the common basin boundary of  $E_1$  and  $E_2$ .

In case (d),  $f_1(S_1) < f_2(S_1)$  and  $f_1(S_2) > f_2(S_2)$  so  $E_1$  and  $E_2$  are unstable. By (3.14),  $f'_2(S^*) > f'_1(S^*)$ , and  $d_2 < d_1$ ,  $E_{12}$  is locally asymptotically stable and hence must attract all positive solutions.  $\square$

In terms of the original, unscaled parameters, the crucial numbers that decide the outcome of competition are  $d_i\gamma_i S^0$  and  $S^0(D^* - D_0)/(S^0 - S^*)$ , the latter being meaningful if  $S^* < S^0$ . Dividing out the common factor  $S^0$ , we have  $d_i\gamma_i$  and  $(D^* - D_0)/(S^0 - S^*)$ , implying that the yield constants  $\gamma_i$  and the resource in the feed  $S^0$  can change the outcome of competition. We explore the case that  $D_0 = 0$ ,  $d_1\gamma_1 > d_2\gamma_2$ , and that  $S^*$  exists. For  $S^0 < S^*$  we have case (a) where  $x_1$  wins. In fact,  $x_1$  wins even when  $S^0 > S^*$  so long as  $D^*/(S^0 - S^*) > d_1\gamma_1$ , i.e., so long as  $S^0 < S^* + D^*/(d_1\gamma_1)$ . For  $S^* + D^*/(d_1\gamma_1) < S^0 < S^* + D^*/(d_2\gamma_2)$ , we have case (d), coexistence. Finally, for  $S^0 > S^* + D^*/(d_2\gamma_2)$ , case (b) holds so  $x_2$  wins. This scenario is drastically different from what occurs in the usual chemostat where the  $\gamma_i$  play no role in altering the outcome of competition and where a change in  $S^0$  can lead to extinction but otherwise cannot change the winner of competition.

We finally investigate the dynamics of three species competing for a resource in the turbidostat. Recall that (A2) implies that there is no positive equilibrium of (3.8) and it implies that if  $E_{ij}$  exists, then it is non-degenerate ( $f_k \neq f_i = f_j$  at  $E_{ij}$ ), i.e., the Jacobian is nonsingular. (A3) implies that each  $E_i$  is non-degenerate.

The question of interest is if three species can coexist on a single resource in the turbidostat. The following theorem provides a negative answer.

**Theorem 3.** *Every solution of (3.8) where  $n = 3$  converges to an  $E_i$  or an  $E_{ij}$ .*

The proof of this theorem is similar to that of Theorem 6.1 in [22] which is established by using the monotone theory for three dimensional competitive systems, as well as the Butler-McGehee Lemma. The proof in [22] requires considering all potential boundary phase portraits. In [22], the triangle method is used to describe boundary phase diagrams with vertices denoting  $E_i$ 's points (if any) on lateral sides  $E_i E_j$  denoting  $E_{ij}$ , and line segments with arrows denoting orbits (belonging to the boundary) that connect steady states. As  $E_0$  is always a source, each triangle does not include this aspect of the boundary dynamics. This triangle method is illustrated in Figure 1 as shown in [22]. As in [22], Figure 2–Figure 5 provide triangle diagrams according to the number of steady states other than  $E_0$  involved. All other possible triangle diagrams can be obtained from triangle diagrams in Figure 2–Figure 5 by symmetric rotations or reflections of the triangle. We will only need deal with the triangle diagrams in Figure 2–Figure 5.

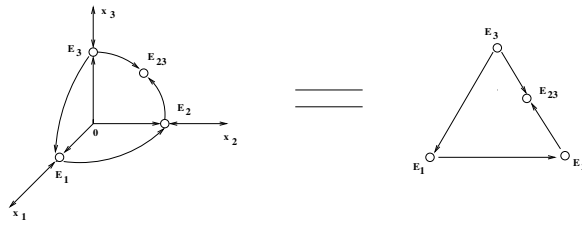


FIGURE 1: Triangle method of depicting boundary phase diagrams



FIGURE 2: Case 1: boundary phase diagrams involving 3 steady states.

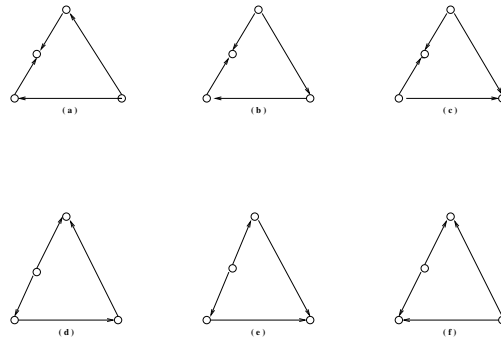


FIGURE 3: Case 2: boundary phase diagrams involving 4 steady states.

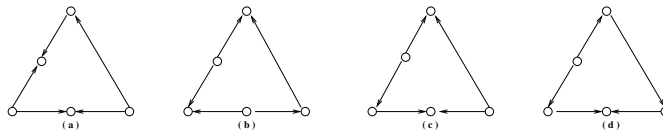


FIGURE 4: Case 3: boundary phase diagrams involving 5 steady states.

We give several useful lemmas below. They are either lemmas or modified versions of lemmas used in the proof of Theorem 6.1 of [22]. In each,  $\omega = \omega(p)$  is the omega limit set of a point  $p$  with  $p \in \mathbb{R}_+^3$  and  $p_i > 0, 1 \leq i \leq 3$ .

**Lemma 3.**  $\omega$  contains at least one steady state, and  $E_0 \notin \omega$ .

The proof of this lemma is similar to that of Lemma 6.9 of [22]. We omit it here.

**Lemma 4.**  $\omega$  does not contain any steady state with a one-dimensional stable manifold that lies in a boundary plane.

The proof of this lemma is the same as the proof of Lemma 6.10 of [22].

**Lemma 5.** Let  $i, j$  and  $k$  be distinct. (i) Assume that  $f_k > f_i$  at  $E_i$  and  $f_k > f_j$  at  $E_j$ , and  $E_i$  and  $E_j$  are asymptotically stable in the linear

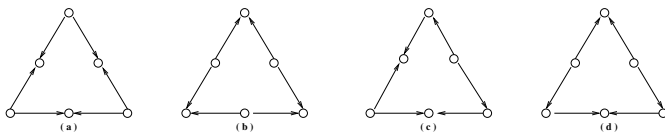


FIGURE 5: Case 4: boundary phase diagrams involving 6 steady states.

approximation in the  $x_i - x_j$  plane. Then  $f_k > f_i = f_j$  at  $E_{ij}$  if it exists.  
(ii) Assume that  $f_k < f_i$  at  $E_i$  and  $f_k < f_j$  at  $E_j$ . Then  $f_k < f_i = f_j$  at  $E_{ij}$  if it exists and is asymptotically stable in the linear approximation in the  $x_i - x_j$  plane.

*Proof.* We prove only the case  $i = 1$ ,  $j = 2$  and  $k = 3$ . The proofs of other cases are similar. Assume  $f_3 > f_1$  at  $E_1$  and  $f_3 > f_2$  at  $E_2$ . Then  $f_3(S_1) > f_1(S_1)$  and  $f_3(S_2) > f_2(S_2)$ . On the other hand, since  $E_i$  and  $E_j$  are asymptotically stable in the linear approximation in the  $x_i - x_j$  plane,  $f_1(S_1) > f_2(S_1)$  and  $f_2(S_2) > f_1(S_2)$ . It follows that  $f_3(S_1) > f_1(S_1) > f_2(S_1)$  and  $f_3(S_2) > f_2(S_2) > f_1(S_2)$ . Recall that  $E_{12}$  exists means  $S^*$  lies strictly between  $S_1$  and  $S_2$ . Because  $f_3$  meets each of  $f_1$  and  $f_2$  at most once for  $S > 0$ , it follows that  $f_3(S^*) > f_1(S^*) = f_2(S^*)$ , i.e.,  $f_3 > f_1 = f_2$  at  $E_{12}$ . Case (i) is established.

Assume  $f_3 < f_1$  at  $E_1$  and  $f_3 < f_2$  at  $E_2$ . Then  $f_3(S_1) < f_1(S_1)$  and  $f_3(S_2) < f_2(S_2)$ . Note that  $E_{12}$  exists and is asymptotically stable in the linear approximation in the  $x_i - x_j$  plane implies that  $S_2 < S^* < S_1$ ,  $f_2 > f_1$  at  $E_1$  and  $f_1 > f_2$  at  $E_2$ . Since  $f_1(S_2) > f_2(S_2)$  and  $f_1(S_1) < f_2(S_1)$ , we have  $f_3(S_1) < f_1(S_1) < f_2(S_1)$  and  $f_3(S_2) < f_2(S_2) < f_1(S_2)$ . Since  $f_3$  meets each of  $f_1$  and  $f_2$  at most once for  $S > 0$ ,  $f_3(S^*) < f_1(S^*) = f_2(S^*)$ , i.e.,  $f_3 < f_1 = f_2$  at  $E_{12}$ . The proof is complete.  $\square$

Lemma 5 is a modified version of Lemma 6.11 of [22].

**Lemma 6.** *Let  $i, j$  and  $k$  be distinct. Suppose that  $E_i$  and  $E_j$  are axial steady states in the plane  $x_k = 0$  and both are unstable in the  $x_k$ -direction. If either  $E_{ij}$  does not exist or  $E_{ij}$  exists and is unstable in the  $x_k$ -direction, then  $\omega$  contains no point with  $x_k = 0$ .*

Lemma 6 is a modified version of Lemma 6.12 of [22]. The proof of Lemma 6.12 of [22] is still valid to establish Lemma 6.

As in [22], we use the idea of a saturated equilibrium [10]. In view of (A3),  $E_i$  is saturated if and only if it is asymptotically stable, while, from (A2),  $E_{ij}$  is saturated if and only if it is stable in the  $x_k$ -direction, where

$i, j, k$  are distinct. The following lemma is a modified version of Lemma 6.13 of [22], which is an immediate consequence of [10] (Theorem 1, Sec. 19.4 and Exercise 3).

**Lemma 7.** *There exists an odd number of saturated equilibria for (3.8).*

*Proof of Theorem 3.* The strategy of the proof is simple. Let  $\omega$  denote the limit set of our solution with  $x(0) = p$  and  $p_i > 0$  for all  $i$ . By Lemma 3,  $\omega$  contains an equilibrium. We use the lemmas above to eliminate as many of the steady states as possible from belonging to  $\omega$ . We use the Butler-McGehee lemma to show that  $\omega$  must be either an asymptotically stable steady state or one of the  $E_{ij}$ . Following the proof of Theorem 6.1 of [22], we proceed in a case-by-case manner according to the phase diagrams in the Figures 2–Figures 5. Because Lemma 5 and Lemma 6 are essentially weaker than Lemma 6.11 and Lemma 6.12 in [22] respectively, the proof of Theorem 6.1 of [22] is no longer valid to prove Theorem 3. However, one can see that the cases 1a, 1b, 2b, 2f, 3b, 3c, 3d, 4b, and 4d can be still handled in the same way as in the proof of Theorem 6.1 of [22] with the lemmas used there replaced by the corresponding lemmas listed above, and with “ $f_k - D < 0 (> 0)$  at  $E_{ij}$ ” whenever it appears replaced by “ $E_{ij}$  is stable (unstable) in the  $x_k$ -direction”. So we will only deal with other cases.

**Case 2a:** Lemma 4 implies that  $E_2$  does not belong to  $\omega$ . If either  $E_1$  or  $E_3$  belongs to  $\omega$  an application of the Butler-McGehee lemma would force  $E_{13}$  to belong to  $\omega$ . By Lemma 7,  $E_{13}$  is the only saturated equilibrium, and thus locally asymptotically stable so  $E_{13}$  coincides with  $\omega$ .

**Case 2c:** Lemma 7 implies that  $E_2$  is the only saturated equilibrium. It follows that  $E_{12}$  is unstable in the  $x_3$ -direction. Lemma 6 implies that  $x_2 > 0$  on  $\omega$ . Lemma 3 implies that the locally asymptotically stable steady state  $E_2$  must belong to  $\omega$  so it coincides with  $\omega$ .

**Case 2d:** Lemma 7 implies that  $E_3$  is the only saturated equilibrium. It follows that  $E_{13}$  is unstable in the  $x_2$  direction. Since  $E_3$  is asymptotically stable, if  $\omega$  contains  $E_3$  then  $\omega = \{E_3\}$ . If  $E_2$  belongs to  $\omega$  an application of the Butler-McGehee lemma would force  $E_3$  to belong to  $\omega$ . Therefore  $\omega$  cannot contain  $E_2$ . If  $E_1$  belongs to  $\omega$  an application of the Butler-McGehee lemma would force  $E_2$  to belong to  $\omega$ . It follows that  $\omega$  cannot contain  $E_1$ . If  $E_{13}$  belongs to  $\omega$  an application of the Butler-McGehee lemma would force  $E_2$  or  $E_1$  to belong to  $\omega$ . So  $\omega$  cannot contain  $E_{13}$ . By Lemma 3,  $\omega = \{E_3\}$ .

**Case 2e:** Same argument as case 2d;  $\omega = \{E_2\}$ .

**Case 3a:** Lemma 4 and Lemma 6 indicate that none of  $E_1$ ,  $E_2$ , and  $E_3$  belong to  $\omega$ . If  $E_{13}$  is saturated, then Lemma 6 implies that  $E_{12}$  cannot belong to  $\omega$ , and by Lemma 3,  $\omega = \{E_{13}\}$ . If  $E_{13}$  is unsaturated, then Lemma 6 implies that  $E_{13}$  cannot belong to  $\omega$  and in this case by Lemma 3,  $\omega = \{E_{12}\}$ .

**Case 4a:** Lemma 4 implies that none of  $E_1$ ,  $E_2$ , and  $E_3$  belongs to  $\omega$ . By Lemma 3,  $\omega$  contains at least one of  $E_{12}$ ,  $E_{13}$ , and  $E_{23}$ . On the other hand, by Lemma 7, either  $E_{12}$ ,  $E_{23}$ ,  $E_{13}$  are all asymptotically stable or only one of them is asymptotically stable. In the first case, if  $\omega$  contains  $E_{ij}$  then  $\omega = \{E_{ij}\}$ . In the second case, assume first that  $E_{12}$  is asymptotically stable and  $E_{13}$  and  $E_{23}$  are not. Then by Lemma 6, only  $E_{12}$  can belong to  $\omega$ , and thus  $\omega = \{E_{12}\}$ . Other subcases in which  $E_{13}$  or  $E_{23}$  is the only asymptotically stable equilibrium can be treated in the same way.

**Case 4c:** The argument for Case 4c in [22] is essentially still valid if one can show  $x_1 > 0$  in  $\omega$ . Therefore it is sufficient to show  $x_1 > 0$ . If  $E_{23}$  is not saturated, then by Lemma 6,  $x_1 > 0$  in  $\omega$ . If  $E_{23}$  is saturated, by Lemma 7, there are two possibilities: either  $E_{12}$  and  $E_{13}$  are both saturated, or they are both not saturated. If  $E_{12}$ ,  $E_{23}$  and  $E_{13}$  are saturated, both  $E_{12}$  and  $E_{13}$  are asymptotically stable. If  $\omega$  contains one of  $E_2$ ,  $E_3$ ,  $E_{23}$ , then the Butler-McGehee lemma implies that  $\omega$  contains  $E_{12}$  or  $E_{13}$ , and thus  $\omega = \{E_{12}\}$  or  $\omega = \{E_{13}\}$ . If  $\omega$  contains none of  $E_2$ ,  $E_3$ , and  $E_{23}$ , the Butler-McGehee Lemma implies  $x_1 > 0$  in  $\omega$ .

Assume that  $E_{23}$  is saturated but  $E_{23}$  and  $E_{13}$  are not. Since  $E_1$  is unstable in the  $x_2$ -direction and  $x_3$ -direction, one obtains at  $E_1$

$$(3.15) \quad f_2(S_1) > f_1(S_1), f_3(S_1) > f_1(S_1).$$

$E_2$  is stable in the  $x_3$ -direction and unstable in the  $x_1$  direction. It follows that at  $E_2$

$$(3.16) \quad f_1(S_2) > f_2(S_2) > f_3(S_2).$$

$E_3$  is stable in the  $x_2$ -direction and unstable in the  $x_1$  direction. At  $E_3$

$$(3.17) \quad f_1(S_3) > f_3(S_3) > f_2(S_3).$$



Throughout this proof we use  $S_{ij}^*$  to denote the positive number at which  $f_i$  and  $f_j$  intercept.  $E_{12}$  exists, and is asymptotically stable in the  $x_1$ - $x_2$  plane and unstable in the  $x_3$ -direction. At  $E_{12}$ ,

$$(3.18) \quad \begin{aligned} & \text{(i)} \quad f'_2 > f'_1, \quad S_2 < S_{12}^* < S_1, \quad f_3(S_{12}^*) > f_1(S_{12}^*) = f_2(S_{12}^*); \\ & \text{or (ii)} \quad f'_2 < f'_1, \quad S_1 < S_{12}^* < S_2, \quad f_3(S_{12}^*) > f_1(S_{12}^*) = f_2(S_{12}^*). \end{aligned}$$

$E_{13}$  exists, and is asymptotically stable in the  $x_1$ - $x_3$  plane and unstable in the  $x_2$ -direction. At  $E_{13}$ ,

$$(3.19) \quad \begin{aligned} & \text{(i)} \quad f'_3 > f'_1, \quad S_3 < S_{13}^* < S_1, \quad f_2(S_{13}^*) > f_1(S_{13}^*) = f_3(S_{13}^*); \\ & \text{or (ii)} \quad f'_3 < f'_1, \quad S_1 < S_{13}^* < S_3, \quad f_2(S_{13}^*) > f_1(S_{13}^*) = f_3(S_{13}^*). \end{aligned}$$

$E_{23}$  exists, and is asymptotically stable in the  $x_1$  and is a saddle in the  $x_2, x_3$  plane. At  $E_{23}$ ,

$$(3.20) \quad \begin{aligned} & \text{(i)} \quad f'_3 > f'_2, \quad S_2 < S_{23}^* < S_3, \quad f_1(S_{23}^*) < f_2(S_{23}^*) = f_3(S_{23}^*); \\ & \text{or (ii)} \quad f'_3 < f'_2, \quad S_3 < S_{23}^* < S_2, \quad f_1(S_{23}^*) < f_2(S_{23}^*) = f_3(S_{23}^*). \end{aligned}$$

In the case that that  $E_{23}$  is saturated but  $E_{23}$  and  $E_{13}$  are not, one of the following eight sets of conditions is satisfied:

- (a) (3.15), (3.16), (3.17), (3.18)(i), (3.19)(i), (3.20)(i);
- (b) (3.15), (3.16), (3.17), (3.18)(i), (3.19)(i), (3.20)(ii);
- (c) (3.15), (3.16), (3.17), (3.18)(i), (3.19)(ii), (3.20)(i);
- (d) (3.15), (3.16), (3.17), (3.18)(i), (3.19)(ii), (3.20)(ii);
- (e) (3.15), (3.16), (3.17), (3.18)(ii), (3.19)(i), (3.20)(i);
- (f) (3.15), (3.16), (3.17), (3.18)(ii), (3.19)(i), (3.20)(ii);
- (g) (3.15), (3.16), (3.17), (3.18)(ii), (3.19)(ii), (3.20)(i);
- (h) (3.15), (3.16), (3.17), (3.18)(ii), (3.19)(ii), (3.20)(ii).

We prove that each of cases (a)–(h) cannot occur. As a result, it is impossible that  $E_{23}$  is saturated but  $E_{23}$  and  $E_{13}$  are not.

Case (a): Due to (3.16), (3.17) and (A1),  $f_1$  lies above  $f_2$  and  $f_3$  over the interval  $[S_2, S_3]$ . It follows that  $f_1(S_{23}^*) > f_2(S_{23}^*) = f_3(S_{23}^*)$ . This contradicts (3.20)(i).

Cases (b), (g), (h) can be handled using an argument similar to that for Case (1).

Case (c): It is easy to see  $S_3 > S_1 > S_2$ . Because of (3.15) and (3.16),  $f_1$  and  $f_2$  intercept in the interval  $(S_2, S_1)$ . On the other hand, because of (3.15) and (3.17),  $f_1$  and  $f_2$  intercept in the interval  $(S_1, S_3)$ . A contradiction follows from (A1).

Case (f) can be handled using an argument similar to that for Case (c).

Case (d): (3.18)(i) and (3.19)(ii) show that  $S_3 > S_2$  while (3.20) (ii) indicates  $S_3 < S_2$ . A contradiction follows.

Case (e): (3.18)(ii) and (3.19)(i) show that  $S_2 > S_3$  while (3.20)(i) indicates  $S_3 > S_2$ . A contradiction follows. The proof is complete.  $\square$

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