

Competitive Exclusion in a Discrete-time, Size-structured Chemostat Model

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Abstract Competitive exclusion is proved for a discrete-time, size-structured, nonlinear matrix model of m -species competition in the chemostat. The winner is the population able to grow at the lowest nutrient concentration. This extends the results of earlier work of the first author [11] where the case $m = 2$ was treated.

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1 Introduction

The classical chemostat model of microbial growth and competition for a limiting substrate has played a central role in population biology. See [12] for a treatment of chemostat models. However, the classical model ignores the size structure of the population

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and the observation that many microbes roughly double in size before dividing. Size-structured chemostat models formulated by Metz and Diekmann [10] and by Cushing [3, 4] (see also [12]) lead to hyperbolic partial differential equations with nonlocal boundary conditions. A conceptually simpler approach to modeling size structure was taken by Gage, Williams and Horton in [5] who formulated what is now referred to as a non-linear matrix model for the evolution, in discrete time steps, of a finite set of biomass classes (see Cushing [2] for a survey of such models). The first author gave a thorough mathematical analysis of this model for the case of two competing strains in [11]. There, it was shown that, like the classical chemostat model, competitive exclusion holds for two competing microbial populations. One population is driven to extinction while the winning strain approaches a stable equilibrium size distribution characterized by a uniform distribution of biomass among the size classes. The characteristic of the superior competitor is its ability to grow at the lowest nutrient concentration. The analysis in [11] made use of the fact that an associated reduced discrete dynamical system, which captures the time evolution of the total biomass of each strain, is order-preserving in the case of two competitors so that monotonicity arguments could be applied. This feature does not hold for more than two competitors. In the present paper, we extend the previous result to any number of competing populations, while at the same time simplifying the analysis. The discrete-time version of the LaSalle invariance principle is used in much the same way as in Armstrong and McGehee [1] for the classical chemostat system to provide a more elegant analysis.

The discrete-time, size-structured model of m -species competition in the chemostat is given by

$$\begin{aligned} x_{n+1}^i &= A_i(S_n)x_n^i, & 1 \leq i \leq m, \\ S_{n+1} &= (1 - E) \left(S_n - \sum_{j=1}^m f_j(S_n)U_n^j \right) + ES^0 \end{aligned} \quad (1.1)$$

where the vector $x_n^i \in \mathbb{R}_+^{r_i}$, $r_i > 0$, gives the distribution of biomass (in nutrient equivalent units) of the i -th microbial population among r_i size classes at the n -th time step and S_n is the nutrient concentration at the n -th time step. $S^0 > 0$ is the nutrient concentration in the input feed to the chemostat, $0 < E < 1$ is the turnover, or washout, rate for the chemostat. The total biomass of the i -th population at the n -th time step is given by $U_n^i = x_n^i \cdot \mathbf{1}$, the scalar product of x_n^i and $\mathbf{1} = (1, \dots, 1) \in \mathbb{R}^{r_i}$. The nutrient uptake rate for the i -th population is $f_i(S)$ and the $r_i \times r_i$ projection matrix for that population is given by

$$A_i(S) = (1 - E) \begin{bmatrix} 1 - P_i & 0 & \cdot & \cdot & \cdot & & M_i P_i \\ M_i P_i & 1 - P_i & 0 & & \dots & & 0 \\ 0 & M_i P_i & 1 - P_i & 0 & & \dots & 0 \\ & & & \ddots & & & \\ 0 & \cdot & \cdot & \cdot & \cdot & 0 & M_i P_i & 1 - P_i \end{bmatrix} \quad (1.2)$$

where

$$M_i = 2^{\frac{1}{r_i}}, \quad P_i = f_i(S)(M_i - 1)^{-1}, \quad 1 \leq i \leq m.$$

See [11] for further details of the model. Motivated by [5, 11], we make the following assumptions throughout this paper.

(H1) For each $1 \leq i \leq m$, $f_i \in C^1(\mathbb{R}_+, \mathbb{R})$, $f_i(0) = 0$, $f_i'(S) > 0$, $f_i'(S) \leq f_i'(0)$, $S \in \mathbb{R}_+$;

(H2) $f_i(+\infty)(M_i - 1)^{-1} < 1$, $1 \leq i \leq m$, and there exist $W > S^0$ and $\eta \in (0, 1)$ such that $W \sum_{i=1}^m f_i'(0) < \eta$.

Clearly, (H1) and the mean value theorem imply that $f_i(S) \leq f_i'(0)S$, for $S \geq 0$. The prototypical nutrient uptake rate, which satisfies (H1), is the Michaelis-Menten function

$$f(S) = \frac{mS}{a + S}, \quad S \in \mathbb{R}_+,$$

where m is the maximum uptake rate and $a > 0$ is the Michaelis-Menten (or half saturation) constant. In (H2), W is an appropriate upper bound on the total biomass of all species and the nutrient, and η an acceptable tolerance. We refer to [11] for a discussion of subtle issues involving the time step and growth rates in order that the model make biological sense.

In the following section we show that (1.1) leads to a lower-dimensional system of difference equations for the total biomass of each population and that conservation of total nutrient allows a further reduction to a limiting system where the nutrient is effectively eliminated. The dynamics of the resulting limiting system can be completely determined. A subsequent section is concerned with lifting the results for the limiting system dynamics to the dynamics of (1.1). This latter step is highly nontrivial.

2 Analysis of the limiting system

As in [11], the key to our analysis is the fact that the high-dimensional system (1.1) can be replaced by a lower dimensional system which tracks the total biomass of each competing strain. Using the fact that $\mathbf{1} = (1, \dots, 1) \in \mathbb{R}^m$, is the Perron-Frobenius (principal) eigenvector of the nonnegative, irreducible and primitive matrix $A_i(S)$ associated with its Perron-Frobenius (principal) eigenvalue $(1 - E)(1 + f_i(S))$ (see, e.g., [4, Theorem 1.1.1]), it follows that the total biomass $U_n^i = x_n^i \cdot \mathbf{1}$ satisfies the difference equations

$$U_{n+1}^i = (1 - E)(1 + f_i(S_n))U_n^i, \quad 1 \leq i \leq m. \quad (2.1)$$

Let $\Sigma_n = S_n + \sum_{i=1}^m U_n^i$, $n \geq 0$. Equation (2.1) and the second equation of (1.1) imply that the evolution of Σ_n can be decoupled from the rest of the system

$$\Sigma_{n+1} = (1 - E)\Sigma_n + ES^0, \quad n \geq 0, \quad (2.2)$$

resulting in

$$\Sigma_n = S^0 - (1 - E)^n(S^0 - \Sigma_0), \quad n \geq 0. \quad (2.3)$$

Clearly, (2.3) implies $\lim_{n \rightarrow \infty} \Sigma_n = S^0$. In order to study the dynamics of system (1.1), we may consider its population level dynamics described by equation (2.1) and the second equation in (1.1). In view of $S_n = \Sigma_n - \sum_{i=1}^m U_n^i$ and $\lim_{n \rightarrow \infty} \Sigma_n = S^0$, we may pass to the limiting system

$$U_{n+1}^i = (1 - E) \left(1 + f_i(S^0 - \sum_{j=1}^m U_n^j) \right) U_n^i, \quad 1 \leq i \leq m \quad (2.4)$$

with the initial value (U_0^1, \dots, U_0^m) in the domain

$$D := \{(U^1, \dots, U^m) \in \mathbb{R}_+^m : \sum_{i=1}^m U^i \leq S^0\}.$$

Denote by F the mapping determined by the right side of (2.4) so $(U_{n+1}^1, \dots, U_{n+1}^m) = F(U_n^1, \dots, U_n^m)$. Then the following result implies that D is positively invariant for system (2.4), and hence (2.4) defines a discrete dynamical system on D .

Lemma 2.1 $F(D) \subset \{(U^1, \dots, U^m) \in \mathbb{R}_+^m : \sum_{i=1}^m U^i \leq (1 - E)S^0\} \subset D$.

Proof. We use an argument similar to [11, Lemma 3.2]. For any $(U^1, \dots, U^m) \in D$, let $(V^1, \dots, V^m) = F(U^1, \dots, U^m)$ and $t = \sum_{i=1}^m U^i$. Then $V^i \geq 0$, $1 \leq i \leq m$, and $t \in [0, S^0]$. If $t > 0$, then

$$\begin{aligned} \sum_{i=1}^m V^i &= (1 - E)t \left(1 + \sum_{i=1}^m f_i(S^0 - t) \frac{U^i}{t} \right) \\ &\leq (1 - E)t \left(1 + \max_{1 \leq i \leq m} \{f_i(S^0 - t)\} \right) \\ &\leq (1 - E) \max_{1 \leq i \leq m} \{(1 + f_i(S^0 - t))t\}. \end{aligned} \quad (2.5)$$

By (H1) and (H2), we have

$$\begin{aligned} \frac{d}{dt} ((1 + f_i(S^0 - t))t) &= 1 + f_i(S^0 - t) - f_i'(S^0 - t)t \\ &\geq 1 - f_i'(0)W + f_i(S^0 - t) > 1 - \eta > 0. \end{aligned} \quad (2.6)$$

Consequently, the function $(1 + f_i(S^0 - t))t$ is strictly increasing with respect to $t \in [0, S^0]$, attaining its maximum value S^0 at $t = S^0$. Thus (2.5) yields $\sum_{i=1}^m V^i \leq (1 - E)S^0$. ■

As in [11], we define the break-even nutrient concentration for the i -th population as the solution, λ_i , of

$$(1 - E)(1 + f_i(S)) = 1$$

where $\lambda_i = +\infty$ if no such solution exists. If the supplied nutrient does not exceed the nutrient requirements of a population, then it is eliminated.

Lemma 2.2 If $\lambda_i \geq S^0$, then $\lim_{n \rightarrow \infty} U_n^i = 0$ for every solution (U_n^1, \dots, U_n^m) of (2.4).

Proof. $U_{n+1}^i \leq (1 - E)(1 + f_i(S^0 - U_n^i))U_n^i \equiv g(U_n^i)$ so, as g is increasing by (2.6), $U_n^i \leq V_n^i$ where $V_{n+1}^i = g(V_n^i)$ and $V_0^i = U_0^i$. We show that $V_n^i \rightarrow 0$. Our hypothesis ensures that $(1 - E)(1 + f_i(S^0 - U)) < 1$ if $U \in (0, S^0]$ so $g(U) < U$ for $U \in (0, S^0]$. Consequently, $V_{n+1}^i < V_n^i$ if $V_0^i > 0$ so V_n^i converges to the only fixed point of g , namely zero. ■

In view of (2.1), the biomass of the population having the lowest break-even nutrient concentration can grow at a lower nutrient concentration than the biomass of the other populations and consequently we expect that population is the superior competitor. The following result on the global dynamics of system (2.4) is, therefore, plausible.

Theorem 2.1 Assume that $\lambda_1 < S^0$, and $\lambda_1 < \lambda_i$ for all $i \geq 2$. Then for any $(U_0^1, \dots, U_0^m) \in D$ with $U_0^1 > 0$, the solution of (2.4) satisfies

$$\lim_{n \rightarrow \infty} (U_n^1, U_n^2, \dots, U_n^m) = (S^0 - \lambda_1, 0, \dots, 0).$$

Proof. For any $(U^1, \dots, U^m) \in D$, let $(V^1, \dots, V^m) = F(U^1, \dots, U^m)$. Define

$$D_1 := \{(U^1, \dots, U^m) \in D : \sum_{i=1}^m U^i \geq S^0 - \lambda_1\}$$

and $W_1(U^1, \dots, U^m) = \sum_{i=1}^m U^i$. If $(U^1, \dots, U^m) \in D_1$, then for system (2.4), there holds

$$\begin{aligned} \dot{W}_1(U^1, \dots, U^m) &:= W_1(F(U^1, \dots, U^m)) - W_1(U^1, \dots, U^m) \\ &= \sum_{i=1}^m V^i - \sum_{i=1}^m U^i \\ &= \sum_{i=1}^m \left[(1 - E) \left(1 + f_i \left(S^0 - \sum_{j=1}^m U^j \right) \right) - 1 \right] U^i \\ &\leq \sum_{i=1}^m [(1 - E)(1 + f_i(\lambda_1)) - 1] U^i \\ &= \sum_{i=2}^m [(1 - E)(1 + f_i(\lambda_1)) - 1] U^i \leq 0. \end{aligned} \tag{2.7}$$

Thus W_1 is a Liapunov function of (2.4) on D_1 (see [9, Definition 1.6.1]). By the fact that each term in large brackets in the third line of (2.7) is nonpositive in D_1 , it follows that

$$E_1 := \{(U^1, \dots, U^m) \in D_1 : \dot{W}_1(U^1, \dots, U^m) = 0\} = \{(S^0 - \lambda_1, 0, \dots, 0)\}. \quad (2.8)$$

Let $u_n = (U_n^1, \dots, U_n^m)$ be the solution of (2.4) with $u_0 \in D$, and let $\omega(u_0)$ be the omega limit of the positive orbit $\gamma^+(u_0) := \{u_n; n \geq 0\}$. If $\gamma^+(u_0) \subset D_1$, then the LaSalle invariance principle (see [9, Theorem 1.6.3]) implies that $\omega(u_0) = (S^0 - \lambda_1, 0, \dots, 0)$.

Define

$$D_2 := \{(U^1, \dots, U^m) \in \mathbb{R}_+^m : \sum_{i=1}^m U^i \leq S^0 - \lambda_1\}.$$

Clearly, $D_2 \subset D$. By (2.6), when $t = S^0 - \lambda_1$ the strictly increasing function $(1 + f_i(S^0 - t))t$ on $[0, S^0 - \lambda_1]$ attains its maximum value $(1 + f_i(\lambda_1))(S^0 - \lambda_1)$. Note that $(1 + f_i(\lambda_1)) \leq (1 + f_i(\lambda_i)) = \frac{1}{1-E}$, $1 \leq i \leq m$. Then (2.5) implies that $\sum_{i=1}^m V^i \leq S^0 - \lambda_1$. Thus $(V^1, \dots, V^m) \in D_2$, and hence D_2 is positively invariant for system (2.4). Define $W_2(U^1, \dots, U^m) = -U^1$. If $(U^1, \dots, U^m) \in D_2$, then for system (2.4), there holds

$$\begin{aligned} \dot{W}_2(U^1, \dots, U^m) &:= W_2(F(U^1, \dots, U^m)) - W_2(U^1, \dots, U^m) \\ &= -V^1 - (-U^1) = U^1 - V^1 \\ &= U^1 - (1 - E) \left(1 + f_1(S^0 - \sum_{j=1}^m U^j) \right) U^1 \\ &\leq U^1 [1 - (1 - E)(1 + f_1(\lambda_1))] = 0. \end{aligned} \quad (2.9)$$

Thus W_2 is a Liapunov function of (2.4) on D_2 . Let

$$L := \{(U^1, \dots, U^m) \in \mathbb{R}_+^m : U^1 = 0, \sum_{i=1}^m U^i < S^0 - \lambda_1\},$$

and

$$\Delta := \{(U^1, \dots, U^m) \in \mathbb{R}_+^m : \sum_{i=1}^m U^i = S^0 - \lambda_1\}.$$

By (2.9), we then have

$$E_2 := \{(U^1, \dots, U^m) \in D_2 : \dot{W}_2(U^1, \dots, U^m) = 0\} = L \cup \Delta. \quad (2.10)$$

If $u_0 = (U_0^1, \dots, U_0^m) \in D_2$ with $U_0^1 > 0$, then $\gamma^+(u_0) \subset D_2$. By the LaSalle invariance principle ([9, Theorem 1.6.3], $\omega(u_0) \subset L \cup \Delta$. Note that $0 \geq \dot{W}_2(u_n) = W_2(u_{n+1}) - W_2(u_n) = U_n^1 - U_{n+1}^1, \forall n \geq 0$. Then we get $U_{n+1}^1 \geq U_n^1, \forall n \geq 0$, and hence $U_n^1 \geq U_0^1 > 0, \forall n \geq 0$. Thus $\omega(u_0) \subset \Delta$. Clearly, (2.8) implies that for any $u \in \Delta \setminus \{(S^0 - \lambda_1, 0, \dots, 0)\}$, there holds $\dot{W}_1(u) < 0$, and hence $F(u) \subset \{(U^1, \dots, U^m) \in$

$D : \sum_{i=1}^m U^i < S^0 - \lambda_1\}$. So $(S^0 - \lambda_1, 0, \dots, 0)$ is the only invariant set in Δ . Thus $\omega(u_0) = (S^0 - \lambda_1, 0, \dots, 0)$.

For any $u_0 = (U_0^1, \dots, U_0^m) \in D$ with $U_0^1 > 0$, let $u_n = (U_n^1, \dots, U_n^m)$, $n \geq 0$, be the solution of (2.4). Clearly, $U_n^1 > 0$, $\forall n \geq 0$, and either $\gamma^+(u_0) \subset D_1$, or there is an $n_0 \geq 0$ such that $u_{n_0} \in D_2$. Note that $\omega(u_0) = \omega(u_{n_0})$. Then in either case, by what we have proved above, $\omega(u_0) = (S^0 - \lambda_1, 0, \dots, 0)$, and hence $\lim_{n \rightarrow \infty} u_n = (S^0 - \lambda_1, 0, \dots, 0)$. ■

Let (X, d) be a metric space and $h : X \rightarrow X$ be a continuous map. Recall that a nonempty invariant set A of h (i.e., $h(A) = A$) is said to be internally chain transitive if for any $a, b \in A$ and any $\epsilon > 0$, there is a finite sequence x_1, \dots, x_k in A with $x_1 = a, x_k = b$ such that $d(h(x_i), x_{i+1}) < \epsilon$, $1 \leq i \leq k - 1$. A typical example of internally chain transitive sets is the omega limit set of a precompact positive orbit for h (see [8, Lemma 2.1]).

Theorem 2.2 Assume that $\lambda_1 < \lambda_2 < \dots < \lambda_m$. Then every compact internally chain transitive set for F is a fixed point of it.

Proof. Let $e_0 = \mathbf{0} \in \mathbb{R}^m$, and let, in the case that $\lambda_i < S^0$, $e_i = (0, \dots, 0, S^0 - \lambda_i, 0, \dots, 0) \in \mathbb{R}^m$ with its i -th component being $(S^0 - \lambda_i)$ and the others being 0. Clearly, all these e_i are fixed points of $F : D \rightarrow D$. For any $v_0 \in D$ with $v_0 \neq e_0$, there exists a $1 \leq k \leq m$ such that $v_0 = (0, \dots, 0, V_0^k, \dots, V_0^m)$ with $V_0^k > 0$. Let $v_n = (V_n^1, \dots, V_n^m)$ be the solution of (2.4). Clearly, $V_n^i = 0$, $\forall n \geq 0, 1 \leq i < k$. If $\lambda_k < S^0$, then Theorem 2.1 implies that $\lim_{n \rightarrow \infty} v_n = e_k$; If $\lambda_k \geq S^0$, then $\lambda_i \geq S^0, \forall i \geq k$, and hence Lemma 2.2 implies that $\lim_{n \rightarrow \infty} v_n = e_0$. This convergence result also implies that each e_i is an isolated invariant set in $D \subset \mathbb{R}^m$ for F , and that no subset of e_i 's forms a cyclic chain in D . By a convergence theorem ([8, Theorem 3.2]), any compact internally chain transitive set for F is a fixed point of F . ■

3 Dynamics of the size-structured model

In this section, we first lift the result for the limiting system (2.4) to the reduced system at the total population level (see (3.1) below), and then consider the global dynamics of the full size-structured system (1.1).

The population level dynamics are described by

$$\begin{aligned} U_{n+1}^i &= (1 - E)(1 + f_i(S_n))U_n^i, \quad 1 \leq i \leq m, \\ S_{n+1} &= (1 - E) \left(S_n - \sum_{j=1}^m f_j(S_n)U_n^j \right) + ES^0 \end{aligned} \quad (3.1)$$

with the initial value $(U_0^1, \dots, U_0^m, S_0)$ in the domain

$$\Omega := \{(U^1, \dots, U^m, S) \in \mathbb{R}_+^{m+1} : \sum_{i=1}^m U^i + S \leq W\}.$$

Denote by G the mapping determined by the right side of (3.1) so $(U_{n+1}^1, \dots, U_{n+1}^m, S_{n+1}) = G(U_n^1, \dots, U_n^m, S_n)$. If $(U^1, \dots, U^m, S) \in \Omega$, then

$$S - \sum_{i=1}^m f_i(S)U^i \geq S \left(1 - \sum_{i=1}^m W f'_i(0)\right) > (1 - \eta)S \geq 0.$$

By the conservation principle (2.2) and the fact that $S^0 < W$, it then follows that $G(U^1, \dots, U^m, S) \in \Omega$, and hence $G(\Omega) \subset \Omega$. Thus system (3.1) defines a discrete dynamical system on Ω . The following result describes the competitive exclusion dynamics of (3.1).

Theorem 3.1 Assume that $\lambda_1 < S^0$ and $\lambda_1 < \lambda_2 < \dots < \lambda_m$. Then for any $(U_0^1, \dots, U_0^m, S_0) \in \Omega$ with $U_0^1 > 0$, the solution of (3.1) satisfies

$$\lim_{n \rightarrow \infty} (U_n^1, U_n^2, \dots, U_n^m, S_n) = (S^0 - \lambda_1, 0, \dots, 0, \lambda_1).$$

Proof. Fix $(U_0^1, \dots, U_0^m, S_0) \in \Omega$ with $U_0^1 > 0$, and let $(U_n^1, \dots, U_n^m, S_n)$ be the solution of system (3.1). Clearly, $U_n^1 > 0, \forall n \geq 0$. Let $\Sigma_n = S_n + \sum_{i=1}^m U_n^i, n \geq 0$. By (2.2), $u_n = (U_n^1, \dots, U_n^m, \Sigma_n)$ satisfies the following system

$$\begin{aligned} U_{n+1}^i &= (1 - E) \left(1 + f_i(\Sigma_n - \sum_{j=1}^m U_n^j)\right) U_n^i, \quad 1 \leq i \leq m, \\ \Sigma_{n+1} &= (1 - E)\Sigma_n + ES^0 \end{aligned} \quad (3.2)$$

Let $\omega = \omega(u_0)$ be the omega limit set of the positive orbit $\gamma^+(u_0)$ of (3.2). Then

$$\omega \subset \{(U^1, \dots, U^m, \Sigma) \in \mathbb{R}_+^{m+1} : \Sigma \leq W\}.$$

Note that $\Sigma_n - \sum_{i=1}^m U_n^i = S_n \geq 0, n \geq 0$, and $\lim_{n \rightarrow \infty} \Sigma_n = S^0$. It then follows that for any $(U^1, \dots, U^m, \Sigma) \in \omega$, there holds $\sum_{i=1}^m U^i \leq \Sigma$ and $\Sigma = S^0$. Thus there exists a set $\tilde{\omega} \subset D$ such that $\omega = \tilde{\omega} \times \{S^0\}$. Denote by H the mapping determined by the right side of (3.2) so $(U_{n+1}^1, \dots, U_{n+1}^m, \Sigma_{n+1}) = H(U_n^1, \dots, U_n^m, \Sigma_n)$. By [8, Lemma 2.1], ω is a compact, invariant and internally chain transitive set for H . Moreover, there holds

$$H|_{\omega}(U^1, \dots, U^m, S^0) = (F(U^1, \dots, U^m), S^0).$$

It then follows that $\tilde{\omega}$ is a compact, invariant and internally chain transitive set for $F : D \rightarrow D$. By Theorem 2.2, we get $\tilde{\omega} = e_l$ for some $0 \leq l \leq p$ where p is the maximal index such that $\lambda_p < S^0$, and hence, $\omega = \tilde{\omega} \times \{S^0\} = (e_l, S^0)$. Thus

$$\lim_{n \rightarrow \infty} u_n = \lim_{n \rightarrow \infty} (U_n^1, \dots, U_n^m, \Sigma_n) = (e_l, S^0). \quad (3.3)$$

It remains to prove that $l = 1$. Suppose that, by contradiction, $l \neq 1$. Let $\delta_l = \frac{1}{2}(1 + (1 - E)(1 + f_1(S^0)))$ if $l = 0$; and $\delta_l = \frac{1}{2}(1 + (1 - E)(1 + f_1(\lambda_l)))$ if $l \geq 2$. Since $\lambda_1 < S^0$ and $\lambda_l > \lambda_1$ if $l \geq 2$, we have

$$1 < \delta_0 < (1 - E)(1 + f_1(S^0)), \text{ and } 1 < \delta_l < (1 - E)(1 + f_1(\lambda_l)) \text{ if } l \geq 2.$$

By (3.3), it follows that

$$\lim_{n \rightarrow \infty} (1 - E) \left(1 + f_1 \left(\Sigma_n - \sum_{j=1}^m U_n^j \right) \right) = (1 - E)(1 + f_1(\lambda_l)) \text{ if } l \geq 2;$$

and

$$\lim_{n \rightarrow \infty} (1 - E) \left(1 + f_1 \left(\Sigma_n - \sum_{j=1}^m U_n^j \right) \right) = (1 - E)(1 + f_1(S^0)) \text{ if } l = 0.$$

Then there is an $n_0 > 0$ such that

$$(1 - E) \left(1 + f_1 \left(\Sigma_n - \sum_{j=1}^m U_n^j \right) \right) > \delta_l, \quad \forall n \geq n_0,$$

and hence, $U_{n+1}^1 \geq \delta_l U_n^1$, $\forall n \geq n_0$. In view of the fact that $\delta_l > 1$ and $U_n^1 > 0$, $\forall n \geq 0$, we get $\lim_{n \rightarrow \infty} U_n^1 = +\infty$, which contradicts the boundedness of $\{U_n^1 : n \geq 0\}$. By (3.3), it then follows that $\lim_{n \rightarrow \infty} (U_n^1, \dots, U_n^m, \Sigma_n) = (e_1, S^0)$, and hence

$$\lim_{n \rightarrow \infty} (U_n^1, \dots, U_n^m, S_n) = (e_1, \lambda_1) = (S^0 - \lambda_1, 0, \dots, 0, \lambda_1).$$

■

Let $r = \sum_{i=1}^m r_i$ and set

$$\Gamma := \{(x^1, \dots, x^m, S) \in \mathbb{R}_+^{r+1} : x^i \in \mathbb{R}^{r_i}, 1 \leq i \leq m, \text{ and } \sum_{i=1}^m x^i \cdot \mathbf{1} + S \leq W\}.$$

Clearly, the positive invariance of Ω for (3.1) implies that of Γ for (1.1). So (1.1) defines a discrete dynamical system on Γ . The next result shows that the surviving population asymptotically approaches a stable, uniform size distribution.

Theorem 3.2 Assume that $\lambda_1 < S^0$ and $\lambda_1 < \lambda_2 < \dots < \lambda_m$. Then for any $(x_0^1, \dots, x_0^m, S_0) \in \Gamma$ with $x_0^1 \neq \mathbf{0}$, the solution of (1.1) satisfies

$$\lim_{n \rightarrow \infty} (x_n^1, x_n^2, \dots, x_n^m, S_n) = \left(\frac{S^0 - \lambda_1}{r_1} \mathbf{1}, \mathbf{0}, \dots, \mathbf{0}, \lambda_1 \right).$$

Proof. Given $(x_0^1, \dots, x_0^m, S_0) \in \Gamma$ with $x_0^1 \neq \mathbf{0}$. Let $U_n^i = x_n^i \cdot \mathbf{1}$, $\forall 1 \leq i \leq m$, $n \geq 0$. Then $(U_0^1, \dots, U_0^m, S_0) \in \Omega$ with $U_0^1 > 0$. By Theorem 3.1, $\lim_{n \rightarrow \infty} (U_n^1, U_n^2, \dots, U_n^m, S_n) = (S^0 - \lambda_1, 0, \dots, 0, \lambda_1)$. Then $\lim_{n \rightarrow \infty} A_i(S_n) = A_i(\lambda_1)$, $1 \leq i \leq m$. As mentioned in Section 2, $A_i(S_n)$ and $A_i(\lambda_1)$ are nonnegative, irreducible and primitive and they have $e = \frac{1}{r_i} \mathbf{1}$ as their Perron-Frobenius eigenvectors with $e \cdot \mathbf{1} = 1$. By a weak ergodic theorem ([6, Corollary 3.2]), we then have

$$\lim_{n \rightarrow \infty} \frac{x_n^i}{x_n^i \cdot \mathbf{1}} = \lim_{n \rightarrow \infty} \frac{x_n^i}{U_n^i} = e = \frac{1}{r_i} \mathbf{1}, \quad 1 \leq i \leq m.$$

Since $\lim_{n \rightarrow \infty} U_n^1 = S^0 - \lambda_1$ and $\lim_{n \rightarrow \infty} U_n^i = 0$, $\forall 2 \leq i \leq m$, we conclude that

$$\lim_{n \rightarrow \infty} (x_n^1, x_n^2, \dots, x_n^m, S_n) = \left(\frac{S^0 - \lambda_1}{r_1} \mathbf{1}, \mathbf{0}, \dots, \mathbf{0}, \lambda_1 \right).$$

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