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GLOBAL ASYMPTOTIC BEHAVIOR OF A CHEMOSTAT MODEL WITH DISCRETE DELAYS*

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Abstract. This paper studies the global asymptotic behavior of an exploitative competition model between n species in a chemostat. The model incorporates discrete time delays to describe the delay in the conversion of nutrient consumed to viable biomass and hence includes delays simultaneously in variables of nutrient and species concentrations. In the case where only two species are engaged in competition, it is shown that competitive exclusion holds for any monotone growth response functions. Sufficient conditions are also obtained for the model to exhibit competitive exclusion in the n-species case. In regard to the delay effects on the qualitative outcome of competition, it is demonstrated that when the delays are relatively small, the predictions of the model are identical with the predictions given by corresponding models without time delays. However, including large delays in the model may alter the predicted outcome of competition. The techniques used also work when different removal rates are permitted, and in this case there are even new results in the no-delay case.

Key words. delayed growth response, competition in chemostat, competitive exclusion, global attractivity

AMS subject classifications. 92D25, 34D05, 34K15

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1. Introduction.

The main purpose of this paper is to study the global asymptotic behavior of the following model of n species of microorganisms competing exploitatively for a single growth-limiting nutrient in a well-stirred chemostat:

$$\begin{aligned} S'(t) &= \big(S^0 - S(t)\big)\, D - \sum_{i=1}^{n} p_i\big(S(t)\big)\, N_i(t), \\ N_i'(t) &= -DN_i(t) + \alpha_i\, p_i\big(S(t-\tau_i)\big)\, N_i(t-\tau_i),\ i = 1, 2, \ldots, n. \end{aligned} \tag{1.1}$$

Here $S(t)$ denotes the concentration of the nutrient external to cells in the growth vessel at time t. For each $i = 1, 2, \ldots, n$, $N_i(t)$ denotes the biomass of the ith species at time t, $p_i(S)$ represents the specific per-capita nutrient uptake function (functional response) of the ith species, the constant $\tau_i \geq 0$ stands for the time delay in conversion of nutrient to viable biomass for the ith species, and $\alpha_i = e^{-D\tau_i}$, and so $\alpha_i\, N_i(t-\tau_i)$ represents the biomass of those microorganisms in species N_i that consume nutrient τ_i units of time prior to time t and that survive in the chemostat the τ_i units of time necessary to complete the process of converting the nutrient to viable biomass at time t. S^0 and D are positive constants and denote, respectively, the concentration of the growth-limiting nutrient in the fresh inflowing medium and the flow rate of the chemostat. It is assumed that species-specific death rates are insignificant, compared to the flow rate, and hence can be ignored. The growth yield constants have been scaled out. In section 4 we study this model allowing differential removal rates.

Model (1.1), in the case where only two species are engaged in competition, first appeared in the literature in Freedman, So, and Waltman [12] and was recently studied

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in Ellermeyer [8], Ellermeyer and Hsu [9], and Hsu, Waltman, and Ellermeyer [21]. We have generalized the model by allowing n species to compete for a single growth-limiting nutrient. Following [8, 12], we make the assumptions below on the response functions p_i, $i = 1, 2, \ldots, n$, in model (1.1):

$$p_i : [0, \infty) \to [0, \infty) \quad \text{and} \quad p_i(0) = 0; \tag{1.2a}$$

$$p_i \text{ is locally Lipschitz and monotone increasing;} \tag{1.2b}$$

there exists a unique (possibly extended) real number $0 < \lambda_i \leq \infty$ such that

$$\begin{aligned} p_i(s) &< \frac{D}{\alpha_i} \quad \text{if } s < \lambda_i; \\ p_i(s) &> \frac{D}{\alpha_i} \quad \text{if } s > \lambda_i. \end{aligned} \tag{1.2c}$$

Generally, λ_i depends on τ_i. When the emphasis of the dependence of λ_i on τ_i is needed, we will use $\lambda_i(\tau_i)$ to mean λ_i. In the literature, the value $\lambda_i(0)$ has been referred to as the break-even concentration of the nutrient for the ith species, and it has played an important role in determining competitive ability.

It has long been recognized that there is a time delay in the growth response of a population to changes in the environment. In order to try to explain the transient oscillatory behavior in chemostat populations, many authors have included time delays explicitly in the modeling equations. The earliest attempt in this regard seems to have been by Finn and Wilson [10]. They observed sustained oscillations of a yeast population in a chemostat and discussed a linear model with discrete delays. In [4], Caperon utilized a distributed delay as well as a discrete delay in the growth response of *Isochrysis galbana*, and the resulting models successfully predicted the observed oscillatory transients in the experimental population growth. Droop [7] introduced the notion of an internal nutrient pool in cells in his model, assuming that only the internal substrate is available for cell growth and passage of the outside ambient nutrient to the inside of the cells inevitably leads to time delays. The model that was originally proposed by Droop is a system of three ordinary differential equations (ODEs), yet it bears a formal resemblance to a distributed infinite delay model using two equations (see MacDonald [26, 27] and compare with Stephens and Lyberatos [38]). Droop's model was adopted by Cunningham and Nisbet [6]. However, they noticed that the model cannot produce the oscillations in cell numbers that they observed in experiments in the chemostat and pointed out that an introduction of another lag in the equations is necessary (see also Cunningham and Maas [5], Nisbet and Gurney [30] for the use of the Droop model with delay, Lange and Oyarzun [24], Oyarzun and Lange [31], and Smith and Waltman [36] for more recent interesting results on the global asymptotic behavior of the Droop model). Chemostat models involving time delays are also seen in Powell [32], who utilizes delays in the maximum growth rate; MacDonald [25] and Thingstad and Langeland [40], who discuss the effect of delay in simple chemostat models; Bush and Cook [2], who explore delay influence on inhibitory specific growth response; and Freedman, So, and Waltman [11], who consider coexistence and sustained oscillations in two-species pure and simple competition (see also Ruan and Wolkowicz [33] and Zhao [48]). MacDonald [27] provides a thorough review and discussion on time delays in chemostat models and

their possible qualitative effects on transient dynamics. It is worth noting that all of the delay models mentioned in this paragraph are based on the classical Monod model [29] and, with the exception of [11], all involve only single-species growth on a single growth-limiting nutrient in a chemostat.

Model (1.1) appears to be the first time delay chemostat model that incorporates delays simultaneously in both variables of nutrient and species concentrations. It was initially studied in Freedman, So, and Waltman [12] for a single species N_1 feeding on a growth-limiting nutrient S, and it was shown that, by employing a Liapunov functional, if $\lambda_1 > S^0$, then $N_1(t) \to 0$ as $t \to \infty$ (washout). Two-species competition was recently considered by Ellermeyer [8], who proved that if $\lambda_1 < S^0 \leq \lambda_2$, species N_1 survives but species N_2 is washed out; if $\lambda_1 < \lambda_2 < S^0$, species N_1 continues to persist. No information was given about whether N_1 converges or about the ultimate fate of species N_2 in this latter case until Ellermeyer and Hsu [9] determined a sufficient condition (stronger than $\lambda_1 < \lambda_2 < S^0$ (see (3.5)) under which competitive exclusion occurs, in particular, $N_1(t) \to \alpha_1(S^0 - \lambda_1)$ and $N_2(t) \to 0$ as $t \to \infty$. More recently, Hsu, Waltman, and Ellermeyer [21] showed that for p_1 and p_2 of the Michaelis–Menten type, $\lambda_1 < \lambda_2 < S^0$ is actually enough to ensure competitive exclusion.

In the present paper, we extend the above studies in four aspects. First, we show that for $n = 2$, the species with the smaller $\lambda_i < S^0$ wins the competition and drives the other species to extinction for any monotone functional response p_i's satisfying (1.2). This generalizes the main result on time delay in the chemostat in [21], where each p_i was restricted to be of Michaelis–Menten type. Also, for response functions satisfying (1.2) and $n \geq 2$, we determine a sufficient condition that ensures that all species but one tend toward extinction (competitive exclusion). More specifically, if all λ_k's are less than S^0 and the sum of all $S^0 - \lambda_j$, $j \neq i$, is smaller than $S^0 - \lambda_i$, it is shown that species N_i survives, and all other species die out. Second, we prove that if the delays are relatively small (see (3.16)), model (1.1) gives the same predictions on the outcome of competition as the corresponding ODE model (see [1, 3, 19, 20, 45]). Therefore, our theory verifies the J-criterion (i.e., the λ_i values determine the relative competitive abilities; see [15]) in this particular case. Third, we show that if the differential death rates of all species are relatively small (see (4.8) or (4.20)), compared to the washout rate of the chemostat, they do not affect the outcome of competition and hence can be ignored. This result is even new for the corresponding ODE model that results in the case of differential death rates and no delay and complements the work of Wolkowicz and Lu [45]. Finally, we find that including large delays in the model can alter the predicted outcome of competition. An otherwise dominant species according to the J-criterion may lose the competition if the delay is sufficiently large, and as a consequence, competitive reversals [22, 41, 42] are possible. To the best of our knowledge, none of the previous studies on pure and simple competition in the chemostat has explored such delay effects on the outcome of competition (see also [26, 27] for discussions on the delay effects in other situations).

We remark that our method of showing the global asymptotic behavior of (1.1) is simpler than that in [21]. We avoid the theory of monotone dynamical systems (see Hirsch [17], Smith [34], and Smith and Thieme [35]). This is the main technique applied in [21]. Unfortunately, it cannot be used on model (1.1) when $n > 2$ (see [37]). We also avoid the theory of asymptotically autonomous differential equations (see [28] and [39]), which is frequently used in the study of chemostat models. The invariant set, which is technically constructed and plays an important role in [9], does not seem necessary for the proof of the global attractivity of (1.1). Because the delays appear in the variables of population concentrations, it would be difficult, if not impossible, to

apply the Liapunov functional method (or the Razumikhin technique) to model (1.1) in the case that all λ_i's are smaller than S^0. Our approach represents extensions of those techniques dealing with single-species delay population models (see Gopalsamy [13] and Kuang [23]) to a model with higher dimensions. It seems to us that the study of global attractivity in multispecies delay population models is overwhelmed by the method of Liapunov functionals [13, 23], and little work has been seen that merely uses simple arguments from mathematical analysis. Finally, it should be noted that, although the method used in this paper works for more general models, we have chosen to concentrate on model (1.1) in order not to obscure the basic simplicity of the method.

This paper is organized as follows. In section 2, we present some preliminary results about model (1.1). Our main results on the outcome of competition for (1.1) are stated and proven in section 3. These results are then extended in section 4 to the differential removal rates model. Finally, in section 5, we discuss some of the consequences of our results.

2. Preliminary results. We denote by C^+_{n+1} the nonnegative cone of the Banach space of continuous functions $C_{n+1} = \{\varphi = (\varphi_0, \varphi_1, \dots, \varphi_n) : [-r, 0] \to R^{n+1}$ continuous$\}$, where $r = \max\{\tau_1, \tau_2, \dots, \tau_n\}$, i.e., $C^+_{n+1} = \{\varphi \in C_{n+1} :\ \varphi_i(\theta) \geq 0$ for all $\theta \in [-r, 0], i = 0, 1, 2, \dots, n\}$. By using the method of steps, it can be shown that for each $\varphi \in C^+_{n+1}$, there is a unique solution of (1.1) $\pi(\varphi; t) = \big(S(\varphi; t), N_1(\varphi; t), \dots, N_n(\varphi; t)\big) \in R^+_{n+1}$ through φ that is well defined for all $t \geq 0$ and satisfies $\pi(\varphi; \cdot)|_{[-r,0]} = \varphi$. We will also denote by $\big(S(t), N_1(t), \dots, N_n(t)\big)$ the solution $\pi(\varphi; t)$ if no confusion can arise. Throughout, when we say a solution $\pi(\varphi; t)$ or $\big(S(t), N_1(t), \dots, N_n(t)\big)$ is positive, we mean that each component of the solution is positive for all $t > 0$.

Let $\varphi \in C^+_{n+1}$ be given. We set

$$W(t) = S^0 - S(\varphi; t) - \sum_{i=1}^{n} \frac{1}{\alpha_i} N_i(\varphi; t + \tau_i)$$

for all $t \geq 0$, where $\big(S(\varphi; t), N_1(\varphi; t), \dots, N_n(\varphi; t)\big)$ is the solution of (1.1) through φ. It follows from model (1.1) that $W'(t) = -DW(t)$ for all $t \geq 0$ and consequently

$$S(\varphi; t) + \sum_{i=1}^{n} \frac{1}{\alpha_i} N_i(\varphi; t + \tau_i) = S^0 + \epsilon(\varphi; t), \quad t \geq 0, \tag{2.1}$$

where $\epsilon(\varphi; t) \to 0$ exponentially as $t \to \infty$.

In what follows, we give three preliminary results. The proof of the following elementary but useful lemma due to Barbălat can be found in Gopalsamy [13].

LEMMA 2.1. *Let $a \in (-\infty, \infty)$ and $f : [a, \infty) \to R$ be a differentiable function. If $\lim_{t\to\infty} f(t)$ exists (finite) and the derivative function $f'(t)$ is uniformly continuous on (a, ∞), then $\lim_{t\to\infty} f'(t) = 0$.*

LEMMA 2.2. *For every $\varphi \in C^+_{n+1}$ with $\varphi_i(0) > 0$, $i = 1, 2, \dots, n$, the solution $\pi(\varphi; t)$ of (1.1) remains positive and bounded for $t > 0$. Moreover, if $\lambda_i < S^0$ for some $i \in \{1, 2, \dots, n\}$, then $S(t) < S^0$ for all sufficiently large t.*

Proof. First we note that if $S(\xi) = 0$ for some $\xi \geq 0$, then $S'(\xi) > 0$. This implies that $S(t) > 0$ for all $t > 0$. That $N_i(t)$ is positive for each $i \in \{1, 2, \dots, n\}$ can be seen from the formula

$$N_i(t) = \varphi_i(0)\, e^{-Dt} + \alpha_i \int_0^t e^{-D(t-\theta)}\, p_i\big(S(\theta - \tau_i)\big)\, N_i(\theta - \tau_i)\, d\theta$$

for $t \geq 0$. That $\pi(\varphi; t)$ is bounded follows immediately from (2.1).

We now prove that under the condition $\lambda_i < S^0$, $S(t) < S^0$ for all sufficiently large t. First note that if $S(\bar{t}) = S^0$ for some $\bar{t} \geq 0$, then $S'(\bar{t}) < 0$, and so if $S(T) \leq S^0$ for some $T \geq 0$, then $S(t) < S^0$ for all $t > T$.

Suppose that $S(t) > S^0$ for all large t. Then $S'(t) \leq (S^0 - S(t))D < 0$ and so $S(t) \downarrow S^* \geq S^0 > \lambda_i$ for some S^* as $t \to \infty$. (Since $S(t)$ is bounded below and satisfies (1.1), we must have $S^* = S^0$.) Thus $S(t) > \lambda_i$ for all large t. Define

$$z(t) = N_i(t) + \alpha_i \int_{t-\tau_i}^{t} p_i\big(S(\theta)\big)\, N_i(\theta)\, d\theta. \tag{2.2}$$

Then (1.1) and (1.2) imply that

$$z'(t) = N_i(t)\left[-D + \alpha_i\, p_i\big(S(t)\big)\right] > 0 \tag{2.3}$$

for all large t. Since $z(t)$ is clearly bounded above, this shows that $z(t) \uparrow z^* > 0$ exists as $t \to \infty$. From (2.3), we see that $z'(t)$ is uniformly continuous on $[0, \infty)$, since $S(t)$, $N_i(t)$, $S'(t)$, and $N_i'(t)$ are all bounded. Hence by Lemma 2.1, $\lim_{t\to\infty} z'(t) = 0$. Since $\lim_{t\to\infty} S(t) = S^0 > \lambda_i$, it follows that $\lim_{t\to\infty} N_i(t) = 0$, by (2.3). But (see (2.2)) this contradicts $z(t) \uparrow z^* > 0$ as $t \to \infty$. This completes the proof. □

Our next result shows that competition-independent extinction occurs for any population N_i with $\lambda_i \geq S^0$. In this case, species N_i is called an inadequate competitor. (See also Smith and Waltman [37].)

THEOREM 2.3. *For every positive solution $\pi(\varphi; t)$ of (1.1), if $\lambda_i \geq S^0$ for some $i \in \{1, 2, \ldots, n\}$, then $\lim_{t\to\infty} N_i(\varphi; t) = 0$.*

Proof. First it can be seen from the proof of Lemma 2.2 that either $S(t) \downarrow S^0$ as $t \to \infty$ or $S(t) < S^0$ for all large t. Suppose that $S(t) \downarrow S^0$ as $t \to \infty$. Since $\pi(\varphi; t)$ and its derivative $\pi'(\varphi; t)$ are bounded, from (1.1), $S'(t)$ is uniformly continuous. By Lemma 2.1, $\lim_{t\to\infty} S'(t) = 0$ and consequently

$$\lim_{t\to\infty} \sum_{j=1}^{n} p_j\big(S(t)\big)\, N_j(t) = 0.$$

This leads to $\lim_{t\to\infty} N_i(t) = 0$, as desired.

Suppose now that $S(t) < S^0 \leq \lambda_i$ for all large t. Then (1.2) gives

$$z'(t) = N_i(t)\left[-D + \alpha_i\, p_i\big(S(t)\big)\right] \leq 0 \tag{2.4}$$

for all large t, where $z(t)$ is defined as in (2.2). Thus $z(t) \downarrow z^*$ as $t \to \infty$ for some $z^* \geq 0$. Similarly, $z'(t)$ is uniformly continuous and so $\lim_{t\to\infty} z'(t) = 0$ by Lemma 2.1. In view of (2.4), it then follows that

$$\lim_{t\to\infty} N_i(t)\left[-D + \alpha_i\, p_i\big(S(t)\big)\right] = 0. \tag{2.5}$$

If there is a sequence $\{t_m\} \uparrow \infty$ such that $\lim_{m\to\infty} N_i(t_m) > 0$, then (2.5) forces $\lim_{m\to\infty} p_i(S(t_m)) = D/\alpha_i$, leading to $\lim_{m\to\infty} S(t_m) = \lambda_i$. But $S(t_m) < S^0$ for all large m and $\lambda_i \geq S^0$. This is a contradiction if $\lambda_i > S^0$. When $\lambda_i = S^0$, a contradiction can also be derived by using (2.1) and the fact that $\lim_{m\to\infty} S(t_m) = \lambda_i = S^0$. This shows that $\lim_{t\to\infty} N_i(t) = 0$, and this completes the proof. □

The following corollary of Theorem 2.3 describes outcomes of continuous culture where all populations are eliminated from the chemostat because the nutrient is insufficient (or the flow rate is too high) for any of the populations to survive.

COROLLARY 2.4. *If $\lambda_i \geq S^0$ for all $i \in \{1, 2, \ldots, n\}$, then every positive solution $\pi(\varphi; t)$ of (1.1) satisfies*

$$\lim_{t\to\infty} \pi(\varphi; t) = (S^0, 0, \ldots, 0).$$

Proof. The result is a direct consequence of Theorem 2.3 and formula (2.1). □

3. Main results. In this section, we consider the global asymptotic behavior of the positive solutions of (1.1) when none of the λ_i's is larger than or equal to S^0. Without loss of generality, we assume throughout this section that

$$\lambda_1 < \lambda_j < S^0 \quad \text{for all} \quad j = 2, 3, \ldots, n. \tag{3.1}$$

We will also need the following assumption:

$$\sum_{j=2}^{n} (S^0 - \lambda_j) < S^0 - \lambda_1. \tag{3.2}$$

Clearly, if $n \geq 3$, (3.2) is stronger than (3.1), but they are equivalent when $n = 2$.

Our first result in this section can be stated as follows.

THEOREM 3.1. *If* (3.2) *holds, then every positive solution* $\pi(\varphi; t) = \big(S(\varphi; t), N_1(\varphi; t), \ldots, N_n(\varphi; t)\big)$ *of* (1.1) *satisfies*

$$\lim_{t\to\infty} \pi(\varphi; t) = \big(\lambda_1, \alpha_1(S^0 - \lambda_1), 0, \ldots, 0\big). \tag{3.3}$$

The following corollary, which gives a complete description of the global dynamics of (1.1) when (3.1) is satisfied and there are only two populations of microorganisms engaged in competition, is an immediate consequence of Theorem 3.1.

COROLLARY 3.2. *If* $\lambda_1 < \lambda_2 < S^0$, *then every positive solution of the delay differential equations*

$$\begin{aligned} S'(t) &= \big(S^0 - S(t)\big)\, D - p_1\big(S(t)\big)\, N_1(t) - p_2\big(S(t)\big)\, N_2(t), \\ N_1'(t) &= -DN_1(t) + \alpha_1\, p_1\big(S(t-\tau_1)\big)\, N_1(t-\tau_1), \\ N_2'(t) &= -DN_2(t) + \alpha_2\, p_2\big(S(t-\tau_2)\big)\, N_2(t-\tau_2) \end{aligned} \tag{3.4}$$

satisfies

$$\lim_{t\to\infty} \big(S(t), N_1(t), N_2(t)\big) = \big(\lambda_1, \alpha_1(S^0 - \lambda_1), 0\big).$$

The corollary improves the main result of Ellermeyer and Hsu [9], where the following additional condition is assumed:

$$\begin{aligned} &\text{Either } \tau_1 \leq \tau_2 \text{ and } p_1^{-1}(D\, e^{D\tau_2}) < \lambda_2 < S^0 \text{ or} \\ &\tau_1 < \tau_2 \text{ and } p_1^{-1}(D\, e^{D\tau_2}) \leq \lambda_2 < S^0. \end{aligned} \tag{3.5}$$

We remove assumption (3.5). The corollary also generalizes a result of Hsu, Waltman, and Ellermeyer [21]. They prove the corollary in the case of Michaelis–Menten-type functional responses by using the monotone dynamical systems theory [17, 34, 35]. Here we take a different and more elementary approach.

Let $\big(S(t), N_1(t), \ldots, N_n(t)\big)$ be an arbitrarily fixed positive solution of (1.1). We define

$$x_i(t) = \frac{1}{\alpha_i} N_i(t + \tau_i), \quad i = 1, 2, \ldots, n. \tag{3.6}$$

It follows from (2.1) that

$$S(t) = S^0 - \sum_{j=1}^{n} x_j(t) + \epsilon(t), \quad t \geq 0, \tag{3.7}$$

where $\epsilon(t) \to 0$ exponentially as $t \to \infty$. Therefore $\big(x_1(t), x_2(t), \ldots, x_n(t)\big)$ satisfies the following n delay differential equations:

$$x_i'(t) = -D\,x_i(t) + \alpha_i\,p_i\left(S^0 - \sum_{j=1}^{n} x_j(t) + \epsilon(t)\right) x_i(t-\tau_i), \quad i = 1, 2, \ldots, n. \tag{3.8}$$

Notice that by (3.6) and (3.7), $\sum_{i=1}^{n} x_i(t) \le S^0 + \epsilon(t)$ for all $t \ge 0$. For each $i = 1, 2, \ldots, n$, we can define the numbers

$$\delta_i = \liminf_{t\to\infty} x_i(t), \quad \gamma_i = \limsup_{t\to\infty} x_i(t).$$

Clearly, $0 \le \delta_i \le \gamma_i \le S^0$ for all $i = 1, 2, \ldots, n$.

The proof of Theorem 3.1 is based on a series of lemmas. We begin with the following fluctuation lemma. For a proof, see Hirsch, Hanisch, and Gabriel [18].

LEMMA 3.3. *Let $f : R^+ \to R$ be a differentiable function. If $\liminf_{t\to\infty} f(t) < \limsup_{t\to\infty} f(t)$, then there are sequences $\{t_m\} \uparrow \infty$ and $\{s_m\} \uparrow \infty$ such that for all m*

$$f(t_m) \to \limsup_{t\to\infty} f(t) \;\; as \;\; m \to \infty, \;\; f'(t_m) = 0,$$
$$f(s_m) \to \liminf_{t\to\infty} f(t) \;\; as \;\; m \to \infty, \;\; f'(s_m) = 0.$$

It is interesting to note that the lemmas that follow are proven by repeatedly appealing to Lemmas 2.1 and 3.3.

LEMMA 3.4. *For every $i \in \{1, 2, \ldots, n\}$, $\gamma_i \le S^0 - \lambda_i$.*

Proof. We first assume that $\delta_i < \gamma_i$. By Lemma 3.3, for any $\varepsilon > 0$ there is a sequence $\{t_m\} \uparrow \infty$ such that

$$\lim_{m\to\infty} x_i(t_m) = \gamma_i, \quad x_i'(t_m) = 0, \quad \text{and} \quad x_i(t_m - \tau_i) \le \gamma_i + \varepsilon.$$

It then follows from (3.8) that

$$\begin{aligned} D\,x_i(t_m) &= \alpha_i\,p_i\left(S^0 - \sum_{j=1}^{n} x_j(t_m) + \epsilon(t_m)\right) x_i(t_m - \tau_i) \\ &\le \alpha_i\,p_i\big(S^0 - x_i(t_m) + \epsilon(t_m)\big)\,(\gamma_i + \varepsilon). \end{aligned}$$

Let $m \to \infty$. We obtain

$$D\,\gamma_i \le \alpha_i\,p_i(S^0 - \gamma_i)\,(\gamma_i + \varepsilon).$$

Since $\varepsilon > 0$ is arbitrary, letting $\varepsilon \to 0$ we obtain

$$D\,\gamma_i \le \alpha_i\,p_i(S^0 - \gamma_i)\,\gamma_i,$$

and hence $S^0 - \gamma_i \ge \lambda_i$, i.e., $\gamma_i \le S^0 - \lambda_i$, as desired.

Suppose now that $\delta_i = \gamma_i$. Then $\lim_{t\to\infty} x_i(t) = \gamma_i$ exists, and appealing to Lemma 2.1 gives $\lim_{t\to\infty} x_i'(t) = 0$. Let $\varepsilon > 0$ be arbitrary. Find $T > 0$ such that $x_i(t - \tau_i) \le \gamma_i + \varepsilon$ for all $t \ge T$. By (3.8), it follows that

$$\begin{aligned} D\,\gamma_i &= \lim_{t\to\infty} \alpha_i\,p_i\left(S^0 - x_i(t) - \sum_{j\ne i} x_j(t) + \epsilon(t)\right) x_i(t - \tau_i) \\ &\le \alpha_i\,p_i(S^0 - \gamma_i)\,(\gamma_i + \varepsilon). \end{aligned}$$

Letting $\varepsilon \to 0$, we obtain

$$D\,\gamma_i \le \alpha_i\, p_i(S^0 - \gamma_i)\,\gamma_i.$$

If $\gamma_i = 0$, there is nothing to prove. If $\gamma_i \neq 0$, the above inequality again gives $S^0 - \gamma_i \ge \lambda_i$, i.e., $\gamma_i \le S^0 - \lambda_i$. This completes the proof. □

Our next lemma shows that under assumption (3.2), the first population N_1 survives. Its proof uses the main idea of Ellermeyer [8].

LEMMA 3.5. *Let* (3.2) *hold. Then* $\delta_1 > 0$.

Proof. Let $0 < \varepsilon < S^0 - \lambda_1 - \sum_{j=2}^{n}(S^0 - \lambda_j)$. By Lemma 3.4, there is $T > \tau_1$ such that for $t \ge T,\ \epsilon(t) > -\frac{\varepsilon}{3}$, and $x_j(t) \le (S^0 - \lambda_j) + \frac{\varepsilon}{3(n-1)},\ j = 2, 3, \ldots, n$. Suppose that $\delta_1 = 0$. We then can find $t_0 \ge T$ such that $x_1(t_0) < \frac{\varepsilon}{3}$. Define

$$\begin{aligned}
&\sigma = \min_{t\in[t_0-\tau_1,t_0]} x_1(t) > 0,\\
&\bar{t} = \sup\{\, t \ge t_0 - \tau_1 :\ x_1(s) \ge \sigma \ \text{ for all } \ \ s \in [t_0 - \tau_1, t]\,\}.
\end{aligned}$$

Then $t_0 \le \bar{t} < \infty,\ \sigma \le \frac{\varepsilon}{3}$, and

$$\begin{aligned}
&x_1(t) \ge \sigma \ \text{ for all } \ \ t \in [t_0 - \tau_1, \bar{t}\,],\\
&x_1(\bar{t}) = \sigma,\ \ x_1'(\bar{t}) \le 0.
\end{aligned} \tag{3.9}$$

Notice that

$$\begin{aligned}
S^0 - &x_1(\bar{t}) - x_2(\bar{t}) - \cdots - x_n(\bar{t}) + \epsilon(\bar{t})\\
&\ge S^0 - \sigma - \sum_{j=2}^{n}\left(S^0 - \lambda_j + \frac{\varepsilon}{3(n-1)}\right) - \frac{\varepsilon}{3}\\
&\ge S^0 - \frac{\varepsilon}{3} - \sum_{j=2}^{n}(S^0 - \lambda_j) - \frac{\varepsilon}{3} - \frac{\varepsilon}{3}\\
&= S^0 - \sum_{j=2}^{n}(S^0 - \lambda_j) - \varepsilon > \lambda_1.
\end{aligned}$$

We deduce that $p_1\big(S^0 - x_1(\bar{t}) - x_2(\bar{t}) - \cdots - x_n(\bar{t}) + \epsilon(\bar{t})\big) > \frac{D}{\alpha_1}$ and

$$\begin{aligned}
x_1'(\bar{t}) &= -D\,x_1(\bar{t}) + \alpha_1\, p_1\left(S^0 - \sum_{j=1}^{n} x_j(\bar{t}) + \epsilon(\bar{t})\right) x_1(\bar{t} - \tau_1)\\
&> -D\,\sigma + D\,\sigma = 0,
\end{aligned}$$

contradicting (3.9). Therefore, $\delta_1 > 0$ and the proof is complete. □

The following lemma is concerned with the asymptotic behavior of the other populations.

LEMMA 3.6. *If* (3.2) *is satisfied, then* $\delta_j = \gamma_j$ *for all* $j \ge 2$*; i.e.,* $\lim_{t\to\infty} x_j(t)$ *exists for every* $j = 2, 3, \ldots, n$.

Proof. Suppose to the contrary that there is a $j \in \{2, 3, \ldots, n\}$ such that $\delta_j < \gamma_j$. Let $\varepsilon > 0$ be given. Lemma 3.3 gives us a sequence $\{t_m\} \uparrow \infty$ such that

$$\begin{aligned}
&\lim_{m\to\infty} x_j(t_m) = \gamma_j, \quad x_j'(t_m) = 0,\\
&x_j(t_m - \tau_j) < \gamma_j + \varepsilon,\ \ x_k(t_m) \ge \delta_k - \frac{\varepsilon}{n-1} \ \text{ for } \ k \neq j.
\end{aligned}$$

Again, (3.8) implies that

$$D\,x_j(t_m) = \alpha_j\,p_j\left(S^0 - x_1(t_m) - x_j(t_m) - \sum_{k\neq 1,j} x_k(t_m) + \epsilon(t_m)\right)\,x_j(t_m-\tau_j)$$
$$\leq \alpha_j\,p_j\left(S^0 - \delta_1 - x_j(t_m) - \sum_{k\neq 1,j}\delta_k + \epsilon(t_m) + \varepsilon\right)\,(\gamma_j+\varepsilon).$$

Letting $m\to\infty$ and $\varepsilon\to 0$, we obtain

$$D \leq \alpha_j\,p_j\left(S^0 - \delta_1 - \gamma_j - \sum_{k\neq 1,j}\delta_k\right).$$

Consequently,

$$S^0 - \delta_1 - \gamma_j - \sum_{k\neq 1,j}\delta_k \geq \lambda_j. \tag{3.10}$$

On the other hand, for any given $\varepsilon>0$, we apply Lemmas 2.1 and 3.3 to obtain a sequence $\{s_m\}\uparrow\infty$ such that

$$\lim_{m\to\infty} x_1(s_m) = \delta_1, \quad \lim_{m\to\infty} x_1'(s_m) = 0,$$
$$x_1(s_m-\tau_1) \geq \delta_1 - \varepsilon, \;\; x_k(s_m) \leq \gamma_k + \frac{\varepsilon}{n-1} \;\text{ for }\; k\neq 1.$$

From (3.8), it follows that

$$D\,\delta_1 = \lim_{m\to\infty} D\,x_1(s_m)$$
$$= \lim_{m\to\infty}\left[\alpha_1\,p_1\left(S^0 - x_1(s_m) - \sum_{k=2}^{n} x_k(s_m) + \epsilon(s_m)\right)\,x_1(s_m-\tau_1)\right]$$
$$\geq \alpha_1\,p_1\left(S^0 - \delta_1 - \gamma_j - \sum_{k\neq 1,j}\gamma_k - \varepsilon\right)\,(\delta_1-\varepsilon).$$

Notice that by Lemma 3.5, we have $\delta_1>0$. Let $\varepsilon\to 0$. We obtain

$$D \geq \alpha_1\,p_1\left(S^0 - \delta_1 - \gamma_j - \sum_{k\neq 1,j}\gamma_k\right).$$

This implies that

$$S^0 - \delta_1 - \gamma_j - \sum_{k\neq 1,j}\gamma_k \leq \lambda_1. \tag{3.11}$$

Now (3.10) in conjunction with (3.11) yields

$$\sum_{k\neq 1,j}(\gamma_k - \delta_k) \geq \lambda_j - \lambda_1. \tag{3.12}$$

However, applying Lemma 3.4 directly, we obtain

$$\sum_{k\neq 1,j}(\gamma_k-\delta_k)\le\sum_{k\neq 1,j}\gamma_k\le\sum_{k\neq 1,j}(S^0-\lambda_k). \tag{3.13}$$

Combining (3.12) and (3.13) now gives

$$\lambda_j-\lambda_1\le\sum_{k\neq 1,j}(S^0-\lambda_k)$$

or equivalently

$$\sum_{k=2}^{n}(S^0-\lambda_k)\ge(S^0-\lambda_1).$$

This contradicts assumption (3.2). Therefore, $\delta_j=\gamma_j$ and the proof is complete. □

Our next lemma is related to a condition that guarantees competitive exclusion.

LEMMA 3.7. *For every $j\ge 2$, if $\delta_1>0$ and $\delta_j=\gamma_j$, then $\delta_j=\gamma_j=0$.*

Proof. Suppose that $\delta_j>0$. Note that $\lim_{t\to\infty}x_j(t)=\delta_j$. By Lemma 2.1, $\lim_{t\to\infty}x_j'(t)=0$. Then (3.8) gives us

$$D\,\delta_j=\lim_{t\to\infty}D\,x_j(t)=\lim_{t\to\infty}\alpha_j\,p_j\left(S^0-\sum_{k\neq j}x_k(t)-x_j(t)+\epsilon(t)\right)x_j(t-\tau_j).$$

It follows that $x^*=\lim_{t\to\infty}\sum_{k\neq j}x_k(t)$ exists and

$$S^0-x^*-\delta_j=\lambda_j. \tag{3.14}$$

On the other hand, let $0<\varepsilon<\delta_1$ be given. Select $T>0$ such that for $t\ge T$, $x_1(t-\tau_1)\ge\delta_1-\varepsilon$, $\sum_{k\neq j}x_k(t)\le x^*+\frac{\varepsilon}{3}$, $x_j(t)\le\delta_j+\frac{\varepsilon}{3}$, and $\epsilon(t)>-\frac{\varepsilon}{3}$. We then have that for $t\ge T$,

$$\begin{aligned}x_1(t)&=x_1(T)\,e^{-D\,(t-T)}\\&\quad+\alpha_1\int_T^t e^{-D\,(t-s)}\,p_1\left(S^0-\sum_{k\neq j}x_k(s)-x_j(s)+\epsilon(s)\right)x_1(s-\tau_1)\,ds\\&\ge x_1(T)\,e^{-D\,(t-T)}+\alpha_1\int_T^t e^{-D\,(t-s)}\,p_1\big(S^0-x^*-\delta_j-\varepsilon\big)\,(\delta_1-\varepsilon)\,ds\\&=x_1(T)\,e^{-D\,(t-T)}+\frac{\alpha_1}{D}\,p_1\big(S^0-x^*-\delta_j-\varepsilon\big)\,(\delta_1-\varepsilon)\,[1-e^{-D\,(t-T)}].\end{aligned}$$

Let $t\to\infty$ and $\varepsilon\to 0$. We are led to

$$\delta_1\ge\frac{\alpha_1}{D}\,p_1(S^0-x^*-\delta_j)\,\delta_1,$$

which is equivalent to

$$S^0-x^*-\delta_j\le\lambda_1. \tag{3.15}$$

Notice that $\lambda_1<\lambda_j$. The inequality (3.15) is incompatible with (3.14). Therefore, we must have $\delta_j=0$. This completes the proof. □

When combined with Theorem 2.3 and equation (2.1), our next lemma represents generalizations of Theorems 3.4 and 3.5 of Ellermeyer [8].

LEMMA 3.8. *If* $\lim_{t\to\infty} x_j(t) = 0$ *for all* $j \in \{2, 3, \ldots, n\}$, *then* $\delta_1 = \gamma_1 = S^0 - \lambda_1$.

Proof. We first show that $\delta_1 > 0$. For the sake of contradiction, suppose that $\delta_1 = 0$. Let $0 < \varepsilon < S^0 - \lambda_1$ and find $T > 0$ such that $\epsilon(t) > -\frac{\varepsilon}{3}$ and $\sum_{j=2}^{n} x_j(t) \le \frac{\varepsilon}{3}$. Arguing as in the proof of Lemma 3.5, we have numbers $t_0 \ge T$, $0 < \sigma < \frac{\varepsilon}{3}$, and $\bar{t} \ge t_0$ such that $x_1(\bar{t}) \ge \sigma$ on $[t_0 - \tau_1, \bar{t}]$, $x_1(\bar{t}) = \sigma$, and $x_1'(\bar{t}) \le 0$. Moreover,

$$\begin{aligned} S^0 - x_1(\bar{t}) - \sum_{j=2}^{n} x_j(\bar{t}) + \epsilon(\bar{t}) &\ge S^0 - \sigma - \frac{2\varepsilon}{3} \\ &> S^0 - \varepsilon > \lambda_1. \end{aligned}$$

This will lead to $x_1'(\bar{t}) > 0$, a contradiction. Therefore, $\delta_1 > 0$.

We now demonstrate that $\delta_1 = \gamma_1$. Suppose that $\delta_1 < \gamma_1$. Let $\varepsilon > 0$ be given. By Lemma 3.3, there is a sequence $\{s_m\} \uparrow \infty$ such that

$$\begin{gathered} \lim_{m\to\infty} x_1(s_m) = \delta_1, \quad x_1'(s_m) = 0, \\ x_1(s_m - \tau_1) \ge \delta_1 - \varepsilon, \quad \sum_{j=2}^{n} x_j(s_m) < \varepsilon. \end{gathered}$$

Now (3.8) gives us

$$\begin{aligned} D\, x_1(s_m) &= \alpha_1\, p_1 \left(S^0 - x_1(s_m) - \sum_{j=2}^{n} x_j(s_m) + \epsilon(s_m) \right) x_1(s_m - \tau_1) \\ &\ge \alpha_1\, p_1 \big(S^0 - x_1(s_m) - \varepsilon + \epsilon(s_m) \big)\, (\delta_1 - \varepsilon). \end{aligned}$$

Letting $m \to \infty$ and $\varepsilon \to 0$, we obtain

$$D\, \delta_1 \ge \alpha_1\, p_1 (S^0 - \delta_1)\, \delta_1,$$

which leads to $S^0 - \delta_1 \le \lambda_1$, i.e., $\delta_1 \ge S^0 - \lambda_1$. Note that we have $\gamma_1 \le S^0 - \lambda_1$ by Lemma 3.4. We arrive at $\gamma_1 \le \delta_1$, a contradiction. Therefore $\delta_1 = \gamma_1$ and $\lim_{t\to\infty} x_1(t)$ exists. Now applying Lemma 2.1 once more, we obtain $\lim_{t\to\infty} x_1'(t) = 0$ and consequently

$$\lim_{t\to\infty} \left[-D\, x_1(t) + \alpha_1\, p_1 \left(S^0 - x_1(t) - \sum_{j=2}^{n} x_j(t) + \epsilon(t) \right) x_1(t - \tau_1) \right] = 0.$$

This implies that $D\, \delta_1 = \alpha_1\, p_1 (S^0 - \delta_1)$ and thus $\delta_1 = S^0 - \lambda_1$. The proof is now complete. □

We are now in a position to prove Theorem 3.1.

Proof of Theorem 3.1. Define $x_i(t)$, $i = 1, 2, \ldots, n$, as in (3.6). By (3.7), it suffices to show that $(x_1(t), x_2(t), \ldots, x_n(t))$ satisfies $(x_1(t), x_2(t), \ldots, x_n(t)) \to (S^0 - \lambda_1, 0, \ldots, 0)$ as $t \to \infty$. To see this, we first note that by Lemma 3.5, $\delta_1 > 0$ under assumption (3.2). Moreover, it follows from Lemma 3.6 that $\delta_j = \gamma_j$ for all $j \ge 2$. Since $\delta_1 > 0$, Lemma 3.7 gives us $\delta_j = \gamma_j = 0$ for all $j = 2, 3, \ldots n$. Now we apply Lemma 3.8 to conclude that $\lim_{t\to\infty} x_j(t) = 0$, $j \ge 2$, and $\lim_{t\to\infty} x_1(t) = S^0 - \lambda_1$, as desired. This completes the proof. □

Note that the sufficient condition (3.2) in Theorem 3.1 for the global attractivity of $(\lambda_1, \alpha_1(S^0 - \lambda_1), 0, \dots, 0)$ actually depends on the number of populations engaged in competition. If the number is large, condition (3.2) is severe. In what follows, we present another condition that is weaker than (3.2) and can be applied when the delays are close to each other.

Let $\tau \geq 0$ be arbitrarily given. We set

$$\gamma = \sum_{j=2}^{n} \alpha_j \, p_j(S^0) \, (S^0 - \lambda_j) \, |\tau_j - \tau|.$$

For every $j \geq 2$, we denote by x_j^* the unique solution of $\alpha_j \, p_j(S^0 - x) = \frac{Dx}{\gamma + x}$ on the interval $(0, S^0)$. Define $\ell_j = S^0 - x_j^*$. We assume

$$\lambda_1 < \ell_j < S^0 \quad \text{for all} \quad j = 2, 3, \dots, n. \tag{3.16}$$

We remark that all ℓ_j's are continuous functions of $(\tau_2, \tau_3, \dots, \tau_n)$ and $0 \leq \lambda_j - \ell_j \to 0$ for each $j \geq 2$, as $(\tau_2, \tau_3, \dots, \tau_n) \to (\tau, \tau, \dots, \tau)$. Thus (3.16) is generally stronger than (3.1), and (3.16) can be satisfied if (3.1) holds for $\tau_j = \tau$, $j = 2, 3, \dots, n$, and $\bar{\tau} = \max_{2 \leq j \leq n} \{ \, |\tau_j - \tau| \, \}$ is small. (By continuity this will imply that (3.1) still holds for those τ_j's such that $\bar{\tau}$ is small and so does (3.16).) In particular, if $\lambda_1(0) < \lambda_j(0) < S^0$ for all $j \geq 2$, (3.16) then holds, provided that all τ_j's are small. Obviously, if all τ_j's, $j \geq 2$, are equal, then by choosing $\tau = \tau_j$, $j \geq 2$, we have $\ell_j = \lambda_j$. In this case, (3.16) is simply the familiar condition (3.1). As a consequence, assumption (3.16) is weaker than (3.2) if all τ_j's, $j \geq 2$, are close to each other. To be more concrete, let us consider the three-species competition case where $\lambda_1 < \lambda_2 \leq \lambda_3 < S^0$. If $\lambda_2 + \lambda_3 - \lambda_1 \leq S^0$, then there is no way that we can apply Theorem 3.1, since the main assumption (3.2) fails to hold. In contrast, assumption (3.16) can be satisfied in the case where $\tau_2 - \tau_3$ is sufficiently small, and hence it is still possible to determine the outcome of competition, as the following theorem shows. However, it is also interesting to note that even if the differences between the delays are small or even if the delays are all identical, it might still be the case that large enough delays alter the outcome. Recall that each λ_i is actually a function of τ_i, and so for example, even if $\lambda_1(0) < \lambda_i(0)$ for all $i = 2, 3, \dots, n$, if $\tau_i = \tau$ for all $i = 1, 2, \dots, n$, it could still be the case that $\lambda_j(\tau) < \lambda_1(\tau)$ for at least one j, and hence x_1 would no longer be the survivor.

THEOREM 3.9. *Assume that there is a $\tau \geq 0$ such that* (3.16) *holds. Then every positive solution $(S(t), N_1(t), \dots, N_n(t))$ of* (1.1) *satisfies*

$$\lim_{t \to \infty} \big(S(t), N_1(t), \dots, N_n(t) \big) = \big(\lambda_1, \alpha_1(S^0 - \lambda_1), 0, \dots, 0 \big).$$

Proof. Define $x_i(t)$, $i = 1, 2, \dots, n$, as in (3.6). By (3.7), it suffices to show that

$$\lim_{t \to \infty} \big(x_1(t), x_2(t), \dots, x_n(t) \big) = (S^0 - \lambda_1, 0, \dots, 0). \tag{3.17}$$

We argue as in the proof of Theorem 3.1.

Let $u(t) = \sum_{j=2}^{n} x_j(t)$. We define

$$\alpha = \liminf_{t \to \infty} \, u(t) \quad \text{and} \quad \beta = \limsup_{t \to \infty} \, u(t).$$

Obviously, $0 \leq \alpha \leq \beta$. We claim that $\beta \leq S^0 - \ell_k$ for some $k \in \{ \, 2, 3, \dots, n \, \}$. To see this, we assume $\alpha < \beta$. The case $\alpha = \beta$ can be dealt with similarly.

Let $\{\varepsilon_q\}$ be a positive sequence such that $\varepsilon_q \to 0$ as $q \to \infty$. Fix any $q > 0$. By Lemma 3.3, there is a sequence $\{t_m\} \uparrow \infty$ satisfying $\epsilon(t_m) < \frac{\varepsilon_q}{2}$,

$$\lim_{m\to\infty} u(t_m) = \beta, \quad u'(t_m) = 0,$$
$$u(t_m - \tau) \le \beta + \varepsilon_q, \quad u(t_m) \ge \beta - \frac{\varepsilon_q}{2}.$$

It follows from (3.8) and the mean value theorem that

$$\begin{aligned} D\,u(t_m) &= \sum_{j=2}^{n} \alpha_j\, p_j\big(S^0 - x_1(t_m) - u(t_m) + \epsilon(t_m)\big)\, x_j(t_m - \tau_j) \\ &\le \sum_{j=2}^{n} \alpha_j\, p_j(S^0 - \beta + \varepsilon_q)\, x_j(t_m - \tau_j) \\ &\le \alpha_{k_q}\, p_{k_q}(S^0 - \beta + \varepsilon_q) \left[\sum_{j=2}^{n} \big(x_j(t_m - \tau_j) - x_j(t_m - \tau)\big) + u(t_m - \tau) \right] \\ &\le \alpha_{k_q}\, p_{k_q}(S^0 - \beta + \varepsilon_q) \left[\sum_{j=2}^{n} \big|x_j'(\xi_m^j)\big|\, \big|\tau_j - \tau\big| + \beta + \varepsilon_q \right], \end{aligned} \tag{3.18}$$

where $k_q \in \{\,2, 3, \ldots, n\,\}$ is such that $\alpha_{k_q}\, p_{k_q}(S^0 - \beta + \varepsilon_q) \ge \alpha_j\, p_j(S^0 - \beta + \varepsilon_q)$ for all $j \ge 2$ and ξ_m^j lies between $t_m - \tau_j$ and $t_m - \tau$. Note that $\lambda_1 < \lambda_j$ and by Lemma 3.4, $\limsup_{t\to\infty} x_j(t) \le S^0 - \lambda_j$ for every $j \ge 2$. We deduce that for all large t, $x_j(t) < S^0 - \lambda_j + \bar\varepsilon_q$, where $\bar\varepsilon_q > 0$ and satisfies

$$\bar\varepsilon_q \sum_{j=2}^{n} \alpha_j\, p_j(S^0)\big|\tau_j - \tau\big| \le \varepsilon_q.$$

Therefore, for all large t,

$$\begin{aligned} \big|x_j'(t)\big| &= \big|-D\,x_j(t) + \alpha_j\, p_j\big(S^0 - x_1(t) - u(t) + \epsilon(t)\big)\, x_j(t - \tau_j)\big| \\ &\le \max\{\, D\,x_j(t),\, \alpha_j\, p_j\big(S^0 - x_1(t) - u(t) + \epsilon(t)\big)\, x_j(t - \tau_j)\,\} \\ &\le \max\{\, D\,(S^0 - \lambda_j + \bar\varepsilon_q),\, \alpha_j\, p_j(S^0)\,(S^0 - \lambda_j + \bar\varepsilon_q)\,\} \\ &= \alpha_j\, p_j(S^0)\,(S^0 - \lambda_j + \bar\varepsilon_q). \end{aligned} \tag{3.19}$$

Here we have used the fact that $S(t) = S^0 - x_1(t) - u(t) + \epsilon(t) < S^0$ for all large t (see Lemma 2.2). Substituting (3.19) into (3.18), for all large m, we obtain

$$\begin{aligned} D\,u(t_m) &\le \alpha_{k_q}\, p_{k_q}(S^0 - \beta + \varepsilon_q) \left[\sum_{j=2}^{n} \alpha_j\, p_j(S^0)\,(S^0 - \lambda_j + \bar\varepsilon_q)\,\big|\tau_j - \tau\big| + \beta + \varepsilon_q \right] \\ &\le \alpha_{k_q}\, p_{k_q}(S^0 - \beta + \varepsilon_q)\,(\gamma + \beta + 2\varepsilon_q). \end{aligned}$$

Let $m \to \infty$. We then obtain

$$D\,\beta \le \alpha_{k_q}\, p_{k_q}(S^0 - \beta + \varepsilon_q)\,(\gamma + \beta + 2\varepsilon_q). \tag{3.20}$$

Note that $\{k_q\}$ is a bounded sequence. We can assume, by selecting the appropriate subsequence, that $k_q \to k$ as $q \to \infty$ for some $k \in \{\,2, 3, \ldots, n\,\}$. By letting $q \to \infty$, (3.20) yields

$$D\,\beta \le \alpha_k\, p_k(S^0 - \beta)\,(\gamma + \beta). \tag{3.21}$$

This implies that $\beta \le x_k^* = S^0 - \ell_k$, as claimed.

We next show that under (3.16), $\delta_1 > 0$. To see this, let $0 < \varepsilon < \ell_k - \lambda_1$ and find $T > 0$ such that $\epsilon(\bar{t}) > \frac{\varepsilon}{3}$ and $u(t) \le S^0 - \ell_k + \frac{\varepsilon}{3}$ for all $t \ge T$. We proceed as in the proof of Lemma 3.5. We can find $t_0 \ge T$, a number $0 < \sigma < \frac{\varepsilon}{3}$ and $\bar{t} \ge t_0$ such that $x_1(t) \ge \sigma$ on $[t_0 - \tau_1, \bar{t}]$, $x_1(\bar{t}) = \sigma$, and $x_1'(\bar{t}) \le 0$. Now

$$\begin{aligned} S^0 - x_1(\bar{t}) - x_2(\bar{t}) - \cdots - x_n(\bar{t}) + \epsilon(\bar{t}) &\ge S^0 - \sigma - u(\bar{t}) + \epsilon(\bar{t}) \\ &\ge S^0 - \frac{\varepsilon}{3} - \Big(S^0 - \ell_k + \frac{\varepsilon}{3}\Big) - \frac{\varepsilon}{3} \\ &= \ell_k - \varepsilon > \lambda_1, \end{aligned}$$

which will lead to $x_1'(\bar{t}) > 0$, a contradiction. This shows that $\delta_1 > 0$.

We then prove that $\alpha = \beta$. For the sake of contradiction, we assume $\alpha < \beta$. For a given sequence $\{\varepsilon_q\} \downarrow 0$, by Lemma 3.3 we can find another sequence $\{t_m\} \uparrow \infty$ for each q, which satisfies $\epsilon(t_m) < \frac{\varepsilon_q}{2}$,

$$\begin{aligned} &\lim_{m\to\infty} u(t_m) = \beta, \;\; u'(t_m) = 0, \\ &u(t_m - \tau) < \beta + \varepsilon_q, \;\; u(t_m) \ge \beta - \frac{\varepsilon_q}{2}. \end{aligned}$$

As in (3.18), using (3.19) yields

$$\begin{aligned} D\,u(t_m) &\le \sum_{j=2}^{n} \alpha_j\, p_j(S^0 - \delta_1 - \beta + \varepsilon_q)\, x_j(t_m - \tau_j) \\ &\le \alpha_{k_q}\, p_{k_q}(S^0 - \delta_1 - \beta + \varepsilon_q)\,(\gamma + \beta + 2\varepsilon_q) \end{aligned}$$

for some $k_q \in \{\,2, 3, \ldots, n\,\}$. A similar argument to that following (3.20) gives

$$D\,\beta \le \alpha_k\, p_k(S^0 - \delta_1 - \beta)\,(\gamma + \beta)$$

for some $k \ge 2$. This further implies that

$$S^0 - \delta_1 - \beta \ge \ell_k. \tag{3.22}$$

On the other hand, using the fact that $\delta_1 > 0$ and the argument following (3.10), we can show that

$$S^0 - \delta_1 - \beta \le \lambda_1. \tag{3.23}$$

Since $\lambda_1 < \ell_k$, the inequality (3.23) is incompatible with (3.22). This proves $\alpha = \beta$.

Finally, we show that $\alpha = \beta = 0$. To this end, first note that by Lemma 2.1, $\lim_{t\to\infty} u'(t) = 0$. Thus

$$D\,\alpha = \lim_{t\to\infty} D\,u(t) = \lim_{t\to\infty} \sum_{j=2}^{n} \alpha_j\, p_j\big(S^0 - x_1(t) - u(t) + \epsilon(t)\big)\, x_j(t - \tau_j).$$

As in (3.18)–(3.21), there is $k \ge 2$ such that

$$D\,\alpha \le \alpha_k\, p_k(S^0 - \delta_1 - \alpha)(\gamma + \alpha).$$

If $\alpha > 0$, this would lead to $S^0 - \delta_1 - \alpha \ge \ell_k$, contradicting (3.23). Therefore, $\alpha = \beta = 0$.

Now we have shown that $\lim_{t\to\infty} \sum_{j=2}^{n} x_j(t) = 0$. Since $x_j(t) > 0$ for all $j \ge 2$, $\lim_{t\to\infty} x_j(t) = 0$ for every $j \ge 2$. Lemma 3.8 then yields (3.17), completing the proof. ∎

4. Extensions. In this section, we extend the results in previous sections to allow for differential removal rates:

$$\begin{aligned} S'(t) &= \big(S^0 - S(t)\big)\, D - \sum_{i=1}^{n} p_i\big(S(t)\big)\, N_i(t), \\ N_i'(t) &= -D_i\, N_i(t) + \alpha_i\, p_i\big(S(t-\tau_i)\big)\, N_i(t-\tau_i), \quad i = 1, 2, \dots, n. \end{aligned} \tag{4.1}$$

Here we use the same notation as in model (1.1), except that each constant D_i, $i = 1, 2, \dots, n$, now represents the specific removal rate of species N_i and $\alpha_i = e^{-D_i\,\tau_i}$. A model incorporating differential removal rates that neglects the time delays and hence involves only ODEs was discussed by Hsu [19] for p_i's of Michaelis–Menten type and by Wolkowicz and Lu [45] for general (not necessarily monotone) functional responses. In practice, one would expect $D_i > D$ if the specific death rate of the species is significant and $D_i < D$ if a filter on the output slows the washout of the species but not the nutrient (see Smith and Waltman [37]).

Throughout this section, we assume that the response functions $p_i,\ i = 1, 2, \dots, n$, satisfy (1.2) with D replaced by D_i. As in section 2, for every $\varphi \in C_{n+1}^{+}$, system (4.1) has a unique solution $\pi(\varphi; t) = \big(S(\varphi; t), N_1(\varphi; t), \dots, N_n(\varphi; t)\big) \in R_{n+1}^{+}$, that exists for all $t \geq 0$ and satisfies $\pi(\varphi; \cdot)|_{[-r,0]} = \varphi$. Similarly, if $\varphi \in C_{n+1}^{+}$ with $\varphi_i(0) > 0$, $i = 1, 2, \dots, n$, then the solution $\pi(\varphi; \cdot)$ remains positive for all $t > 0$. Moreover, if $\lambda_i < S^0$ for some $i \in \{1, 2, \dots, n\}$, then $S(\varphi; t) < S^0$ for all sufficiently large t.

Let $\big(S(t), N_1(t), \dots, N_n(t)\big)$, $t \geq 0$, be an arbitrary positive solution of (4.1). We define

$$V(t) = S(t) + \sum_{i=1}^{n} \frac{1}{\alpha_i}\, N_i(t + \tau_i), \quad t \geq 0. \tag{4.2}$$

Then it follows from (4.1) that

$$S^0 D - D_{\max}\, V(t) \leq V'(t) \leq S^0 D - D_{\min}\, V(t), \quad t \geq 0, \tag{4.3}$$

where $D_{\max} = \max\{D, D_1, \dots, D_n\}$ and $D_{\min} = \min\{D, D_1, \dots, D_n\}$. Solving the differential inequalities in (4.3) now gives

$$\frac{S^0 D}{D_{\max}} + \varepsilon_1(t) \leq V(t) \leq \frac{S^0 D}{D_{\min}} + \varepsilon_2(t), \quad t \geq 0, \tag{4.4}$$

where for $i = 1, 2,\ \varepsilon_i(t) \to 0$ exponentially as $t \to \infty$. This leads to the well-defined numbers

$$\alpha = \liminf_{t\to\infty} V(t) \quad \text{and} \quad \beta = \limsup_{t\to\infty} V(t),$$

and by (4.4)

$$\frac{S^0 D}{D_{\max}} \leq \alpha \leq \beta \leq \frac{S^0 D}{D_{\min}}. \tag{4.5}$$

Therefore, $V(t)$ is bounded, and all positive solutions of (4.1) are also bounded.

We also have the following result for model (4.1).

THEOREM 4.1. *Let $\pi(\varphi; t)$ be an arbitrary positive solution of* (4.1). *If $\lambda_i > S^0$ for some $i \geq 1$, then $\lim_{t\to\infty} N_i(\varphi; t) = 0$. Consequently, if $\lambda_i > S^0$ for all $i \geq 1$, then*

$$\lim_{t\to\infty} \pi(\varphi; t) = (S^0, 0, \dots, 0). \tag{4.6}$$

Proof. The proof for the first part is the same as that for Theorem 2.3, with D_i in place of D. To see that (4.6) is true, we note that $\lim_{t\to\infty} N_i(\varphi;t) = 0$ for all $i = 1, 2, \ldots, n$. Hence it suffices to show that $\lim_{t\to\infty} S(\varphi;t) = S^0$. In what follows, we drop φ in $S(\varphi;t)$ and $N_i(\varphi;t)$.

Since $S(t)$ is bounded, $\lim_{t\to\infty} \sum_{i=1}^n p_i\big(S(t)\big)\, N_i(t) = 0$. By Lemmas 2.1 and 3.3, there is a sequence $\{t_m\} \uparrow \infty$ such that

$$\lim_{m\to\infty} S(t_m) = \limsup_{t\to\infty} S(t) \quad \text{and} \quad \lim_{m\to\infty} S'(t_m) = 0.$$

Now the first equation of (4.1) gives

$$\lim_{m\to\infty} \big(S^0 - S(t_m)\big)\, D = \lim_{m\to\infty} \sum_{i=1}^n p_i\big(S(t_m)\big)\, N_i(t_m) = 0;$$

thus $\limsup_{t\to\infty} S(t) = \lim_{m\to\infty} S(t_m) = S^0$. Similarly, by using Lemmas 2.1 and 3.3 once more, we obtain a sequence $\{s_m\} \uparrow \infty$ such that

$$\lim_{m\to\infty} S(s_m) = \liminf_{t\to\infty} S(t) \quad \text{and} \quad \lim_{m\to\infty} S'(s_m) = 0.$$

Reasoning as before, we obtain $\liminf_{t\to\infty} S(t) = \lim_{m\to\infty} S(s_m) = S^0$. Therefore, we must have $\lim_{t\to\infty} S(t) = S^0$, and (4.6) follows. This completes the proof. □

In view of Theorem 4.1, we now make the following assumption:

$$\lambda_1 < \lambda_j < S^0 \quad \text{for all} \quad j = 2, 3, \ldots, n. \tag{4.7}$$

For technical reasons we also need the following assumption:

$$\sum_{j=2}^n \left(\frac{S^0 D}{D_{\min}} - \lambda_j\right) < \frac{S^0 D}{D_{\max}} - \lambda_1. \tag{4.8}$$

Under assumptions (4.7) and (4.8), we can extend Theorem 3.1 to model (4.1). But first we require a couple of lemmas.

Let $\pi(\varphi;t) = (S(t), N_1(t), \ldots, N_n(t))$ be a fixed positive solution of (4.1). Define $V(t)$ and $x_i(t)$, $i = 1, 2, \ldots, n$, as in (4.2) and (3.6). Then $\big(V(t), x_1(t), \ldots, x_n(t)\big)$ satisfies

$$\begin{aligned} x_i'(t) = &- D_i\, x_i(t) + \alpha_i\, p_i \left(V(t) - \sum_{j=1}^n x_j(t)\right) x_i(t-\tau_i), \\ &i = 1, 2, \ldots, n. \end{aligned} \tag{4.9}$$

Note that since $\pi(\varphi;t)$ is bounded, the following numbers are finite:

$$\delta_i = \liminf_{t\to\infty} x_i(t), \quad \gamma_i = \limsup_{t\to\infty} x_i(t),$$

where $i = 1, 2, \ldots, n$.

LEMMA 4.2. *Let* (4.7) *and* (4.8) *hold. Then* $\delta_1 > 0$ *and* $\lim_{t\to\infty} N_j(t) = 0$ *for all* $j \geq 2$.

Proof. We proceed as in the proofs of Lemmas 3.4–3.7. We first claim that

$$\gamma_i \leq \frac{S^0 D}{D_{\min}} - \lambda_i \quad \text{for every} \quad i = 1, 2, \ldots, n. \tag{4.10}$$

In fact, by (4.5) and Lemmas 2.1 and 3.3, for any $\varepsilon > 0$ there is a sequence $\{t_m\} \uparrow \infty$ such that

$$\lim_{m\to\infty} x_i(t_m) = \gamma_i, \ \lim_{m\to\infty} x_i'(t_m) = 0,$$
$$x_i(t_m - \tau_i) \le \gamma_i + \varepsilon, \ \ V(t_m) \le \frac{S^0 D}{D_{\min}} + \varepsilon.$$

It follows from (4.9) that

$$\begin{aligned} D_i\,\gamma_i &= \lim_{m\to\infty} \alpha_i\, p_i \left(V(t_m) - x_i(t_m) - \sum_{j\neq i} x_j(t_m) \right) x_i(t_m - \tau_i) \\ &\le \alpha_i\, p_i \left(\frac{S^0 D}{D_{\min}} + \varepsilon - \gamma_i \right) (\gamma_i + \varepsilon). \end{aligned}$$

Letting $\varepsilon \to 0$, we obtain

$$D_i\,\gamma_i \le \alpha_i\, p_i \left(\frac{S^0 D}{D_{\min}} - \gamma_i \right) \gamma_i.$$

This yields (4.10), as required.

We now prove that $\delta_1 > 0$. As in the proof of Lemma 3.5, we choose $0 < \varepsilon < \frac{S^0 D}{D_{\max}} - \lambda_1 - \sum_{j=2}^n (\frac{S^0 D}{D_{\min}} - \lambda_j)$. Clearly, $x_j(t) \le (\frac{S^0 D}{D_{\min}} - \lambda_j) + \frac{\varepsilon}{3(n-1)}$, $j = 2, 3, \ldots, n$, for all sufficiently large t. Find t_0, σ, and $\bar{t}$ such that (3.9) holds and $V(\bar{t}) \ge \frac{S^0 D}{D_{\max}} - \frac{\varepsilon}{3}$. Using (4.10), we find that

$$\begin{aligned} &V(\bar{t}) - x_1(\bar{t}) - \cdots - x_n(\bar{t}) \\ &\quad \ge \frac{S^0 D}{D_{\max}} - \frac{\varepsilon}{3} - \sigma - \sum_{j=2}^n \left(\frac{S^0 D}{D_{\min}} - \lambda_j + \frac{\varepsilon}{3(n-1)} \right) \\ &\quad \ge \frac{S^0 D}{D_{\max}} - \sum_{j=2}^n \left(\frac{S^0 D}{D_{\min}} - \lambda_j \right) - \varepsilon > \lambda_1, \end{aligned}$$

and therefore $x_1'(\bar{t}) = -D_1\, x_1(\bar{t}) + \alpha_1\, p_1\big(V(\bar{t}) - \sum_{j=1}^n x_j(\bar{t})\big)\, x_1(\bar{t} - \tau_1) > 0$, a contradiction. Hence, $\delta_1 > 0$.

We finally prove that $\lim_{t\to\infty} N_j(t) = 0$ by showing that $\delta_j = \gamma_j = 0$ for all $j = 2, 3, \ldots, n$. First, under assumptions (4.7) and (4.8), we can show that $\delta_j = \gamma_j$ for all $j \ge 2$ by a proof similar to that of Lemma 3.6. The main difference is that the role played by (2.1) and Lemma 3.4 is now played by (4.5) and (4.10). We omit the details.

It now suffices to show that $\delta_j = \gamma_j = 0$, $j \ge 2$. By way of contradiction, assume $\gamma_j \neq 0$. We apply Lemma 2.1 to obtain

$$D_j\,\gamma_j = \lim_{t\to\infty} \alpha_j\, p_j \left(V(t) - \sum_{k\neq j} x_k(t) - x_j(t) \right) x_j(t - \tau_j).$$

This implies that $z^* = \lim_{t\to\infty} V(t) - \sum_{k\neq j} x_k(t)$ exists and $z^* = \lambda_j + \gamma_j$. On the other hand, by Lemmas 2.1 and 3.3, for any $\varepsilon > 0$, there is a sequence $\{s_m\} \uparrow \infty$ such that

$$\lim_{m\to\infty} x_1(s_m) = \delta_1, \ \ \lim_{m\to\infty} x_1'(s_m) = 0, \ \text{ and } \ x_1(s_m - \tau_1) \ge \delta_1 - \varepsilon.$$

Using (4.9),

$$\begin{aligned} D_1\,\delta_1 &= \lim_{m\to\infty}\ \alpha_1\,p_1\left(V(s_m)-\sum_{k\neq j}x_k(s_m)-x_j(s_m)\right)\,x_1(s_m-\tau_1)\\ &\geq \alpha_1\,p_1(z^*-\delta_j)\,(\delta_1-\varepsilon)\\ &= \alpha_1\,p_1(\lambda_j+\gamma_j-\delta_j)\,(\delta_1-\varepsilon). \end{aligned}$$

Letting $\varepsilon\to 0$ and recalling that $\delta_1>0$, it follows that

$$\lambda_j+\gamma_j-\delta_j\leq\lambda_1.$$

This contradicts (4.7) since $\gamma_j=\delta_j$. Therefore, $\delta_j=\gamma_j=0$ and the proof is complete. □

LEMMA 4.3. *If* $\delta_1>0,\ 0<D_1<2D$, *and* $\lim_{t\to\infty}N_j(t)=0$ *for all* $j\geq 2$, *then*

$$\lim_{t\to\infty}\ \pi(\varphi;t)=\left(\lambda_1,\frac{\alpha_1(S^0-\lambda_1)D}{D_1},0,\ldots,0\right).$$

Proof. It suffices to show that

$$\lim_{t\to\infty}\big(V(t),x_1(t)\big)=\left(S^0+\frac{(D-D_1)\,(S^0-\lambda_1)}{D_1},\frac{(S^0-\lambda_1)\,D}{D_1}\right). \tag{4.11}$$

Note that $(V(t),x_1(t))$ satisfies the following two-dimensional asymptotically autonomous differential equations

$$\begin{aligned} V'(t)&=-D\,V(t)+(D-D_1)\,x_1(t)+S^0D-\varepsilon_1(t),\\ x_1'(t)&=-D_1\,x_1(t)+\alpha_1\,p_1\big(V(t)-x_1(t)-\varepsilon_2(t)\big)\,x_1(t-\tau_1), \end{aligned} \tag{4.12}$$

where

$$\varepsilon_1(t)=\sum_{j=2}^{n}\frac{D_j-D}{\alpha_j}\,N_j(t+\tau_j)\quad\text{and}\quad 0\leq\varepsilon_2(t)=\sum_{j=2}^{n}\frac{1}{\alpha_j}\,N_j(t+\tau_j).$$

By assumption, $\lim_{t\to\infty}\varepsilon_k(t)=0,\ k=1,2$. We claim that

$$\beta-\alpha\geq\gamma_1-\delta_1. \tag{4.13}$$

In fact, applying Lemmas 2.1 and 3.3, for every $\varepsilon>0$, we can find a sequence $\{t_m\}\uparrow\infty$ such that $\lim_{m\to\infty}x_1(t_m)=\gamma_1,\ \lim_{m\to\infty}x_1'(t_m)=0,\ x_1(t_m-\tau_1)\leq\gamma_1+\varepsilon$, and $V(t_m)\leq\beta+\varepsilon$. By (4.12), it follows that

$$\begin{aligned} \lim_{m\to\infty}\ D_1\,x_1(t_m)&=\lim_{m\to\infty}\ \alpha_1\,p_1\big(V(t_m)-x_1(t_m)-\varepsilon_2(t_m)\big)\,x_1(t_m-\tau_1)\\ &\leq\alpha_1\,p_1(\beta+\varepsilon-\gamma_1)\,(\gamma_1+\varepsilon). \end{aligned}$$

Letting $\varepsilon\to 0$, we obtain

$$D_1\,\gamma_1\leq\alpha_1\,p_1(\beta-\gamma_1)\,\gamma_1.$$

Since $\delta_1>0$, $\gamma_1\neq 0$ and the above inequality gives $\beta-\gamma_1\geq\lambda_1$, i.e.,

$$\beta\geq\gamma_1+\lambda_1. \tag{4.14}$$

Similarly, for any $\varepsilon > 0$, there is a sequence $\{s_m\} \uparrow \infty$ such that $\lim_{m\to\infty} x_1(s_m) = \delta_1$, $\lim_{m\to\infty} x_1'(s_m) = 0$, $x_1(s_m - \tau_1) \geq \delta_1 - \varepsilon$, and $V(s_m) \geq \alpha - \varepsilon$. We use (4.12) once more to obtain

$$D_1\,\delta_1 \geq \alpha_1\,p_1(\alpha - \varepsilon - \delta_1)\,(\delta_1 - \varepsilon).$$

Let $\varepsilon \to 0$ and notice that $\delta_1 > 0$. We find that $\alpha - \delta_1 \leq \lambda_1$, i.e.,

$$\alpha \leq \delta_1 + \lambda_1. \tag{4.15}$$

Now (4.13) follows immediately from (4.14) and (4.15).

We next show that $\delta_1 = \gamma_1$. By way of contradiction, we suppose that $\delta_1 < \gamma_1$. Observe that $\alpha < \beta$ from (4.13). We consider two cases.

Case 1. $D < D_1 < 2D$. By Lemma 3.3, for any $\varepsilon > 0$, we find a sequence $\{t_m\} \uparrow \infty$ such that $\lim_{m\to\infty} V(t_m) = \beta$, $V'(t_m) = 0$, $x_1(t_m) \geq \delta_1 - \varepsilon$. The first equation of (4.12) then gives

$$\begin{aligned} S^0D &= D\,V(t_m) + (D_1 - D)\,x_1(t_m) + \varepsilon_1(t_m) \\ &\geq D\,V(t_m) + (D_1 - D)\,(\delta_1 - \varepsilon) + \varepsilon_1(t_m). \end{aligned}$$

Letting $m \to \infty$ and $\varepsilon \to 0$, we obtain

$$D\,\beta + (D_1 - D)\,\delta_1 \leq S^0D. \tag{4.16}$$

Similarly, by Lemma 3.3 and using a sequence $\{s_m\} \uparrow \infty$, we can show that

$$S^0D \leq D\,\alpha + (D_1 - D)\,\gamma_1. \tag{4.17}$$

Now (4.16) in conjunction with (4.17) yields

$$\beta - \alpha \leq \frac{D_1 - D}{D}\,(\gamma_1 - \delta_1). \tag{4.18}$$

From (4.13) and (4.18), it follows that

$$\beta - \alpha \leq \frac{D_1 - D}{D}\,(\beta - \alpha).$$

Note that $\beta - \alpha \neq 0$. The above inequality leads to $D \leq D_1 - D$, i.e., $2D \leq D_1$, a contradiction.

Case 2. $0 < D_1 \leq D$. In this case, we can also apply Lemma 3.3 in a similar way to obtain

$$\begin{aligned} D\,\beta &\leq (D - D_1)\,\gamma_1 + S^0D, \\ D\,\alpha &\geq (D - D_1)\,\delta_1 + S^0D. \end{aligned}$$

With (4.13) in mind, we then obtain

$$\beta - \alpha \leq \frac{D - D_1}{D}\,(\beta - \alpha).$$

This leads to $D \leq D - D_1$, a contradiction.

Therefore, we must have $\delta_1 = \gamma_1$ and $\alpha = \beta$. Equation (4.11) then can be obtained by applying Lemma 2.1 and taking the limit ($t \to \infty$) on two sides of each equation in (4.12). This establishes the lemma. □

We now obtain the following result, which generalizes Theorem 3.1.

THEOREM 4.4. *Let* (4.7) *and* (4.8) *hold. If* $D_1 < 2D$, *then every positive solution* $\pi(\varphi;t) = \big(S(t), N_1(t), \dots, N_n(t)\big)$ *of* (4.1) *satisfies*

$$\lim_{t\to\infty} \pi(\varphi;t) = \left(\lambda_1, \frac{\alpha_1\,(S^0-\lambda_1)\,D}{D_1}, 0, \dots, 0\right). \tag{4.19}$$

Proof. This is a direct consequence of Lemmas 4.2 and 4.3. ∎

Similarly, we can extend Theorem 3.9 to model (4.1). By repeatedly using (4.5) and (4.10), the proof of Theorem 3.9 obviously carries over to the differential removal rates model (4.1). Before stating the theorem we set up the relevant notation.

Fix any $\tau \geq 0$. We define

$$\tilde{\gamma} = \sum_{j=2}^{n} \alpha_j\, p_j(S^0)\, \left(\frac{S^0 D}{D_{\min}} - \lambda_j\right) \big|\tau_j - \tau\big|$$

and $\tilde{\ell}_j = \frac{S^0 D}{D_{\min}} - \tilde{x}_j^*$, where $\tilde{x}_j^*$ is the unique solution of the equation

$$\alpha_j\, p_j \left(\frac{S^0 D}{D_{\min}} - x\right) = \frac{\tilde{D}_{\min}\, x}{\tilde{\gamma} + x}, \quad j \geq 2,\ x \in \left(0, \frac{S^0 D}{D_{\min}}\right),$$

and $\tilde{D}_{\min} = \min\,(D_2, D_3, \dots, D_n)$.

THEOREM 4.5. *Assume that* $D_1 < 2D$ *and for all* $j = 2, 3, \dots, n$

$$\lambda_1 < \tilde{\ell}_j < S^0 \quad \textit{and} \quad \left(\frac{S^0 D}{D_{\min}} - \frac{S^0 D}{D_{\max}}\right) < \tilde{\ell}_j - \lambda_1. \tag{4.20}$$

Then every positive solution $\pi(\varphi;t)$ *of* (4.1) *satisfies* (4.19).

If all τ_i's are zero, model (4.1) reduces to the ODE model considered in [45]. In this particular case, we can remove the assumption $D_1 < 2D$ and thus have the following slightly stronger result.

COROLLARY 4.6. *Assume that* (4.20) *holds. Then every solution of*

$$\begin{aligned} S'(t) &= \big(S^0 - S(t)\big)\, D - \sum_{i=1}^{n} N_i(t)\, p_i\big(S(t)\big), \\ N_i'(t) &= N_i(t)\, \big[-D_i + p_i\big(S(t)\big)\big],\ \ i = 1, 2, \dots, n, \end{aligned} \tag{4.21}$$

with positive initial conditions satisfies

$$\lim_{t\to\infty} \big(S(t), N_1(t), \dots, N_n(t)\big) = \left(\lambda_1, \frac{(S^0-\lambda_1)\,D}{D_1}, 0, \dots, 0\right). \tag{4.22}$$

Proof. First, as in Theorem 4.5, we can show that under assumption (4.20), $\liminf_{t\to\infty} N_1(t) > 0$ and $\lim_{t\to\infty} N_j(t) = 0$ for all $j \geq 2$. Therefore, the omega limit set, ω, of the bounded solution $\big(S(t), N_1(t), \dots, N_n(t)\big)$ must be a compact, invariant set on the $S - N_1$ coordinate plane, and it is uniformly bounded away from the S-axis. It now suffices to show that $\omega = \{(\lambda_1, N_1^*, 0, \dots, 0)\}$, a singleton, where $N_1^* = \frac{(S^0-\lambda_1)D}{D_1}$.

Let P denote the projection $P : R^{n+1} \to R^2$ defined by $P(x_0, x_1, x_2, \dots, x_n) = (x_0, x_1)$, where $(x_0, x_1, x_2, \dots, x_n) \in R^{n+1}$. We have seen that

$$\omega = \{(S, N_1, 0, \dots, 0) :\ (S, N_1) \in P(\omega)\}.$$

In what follows, we show that $P(\omega) = \{(\lambda_1, N_1^*)\}$. To see this, we first note that the $S - N_1$ plane is invariant under the flow defined by (4.21), and hence $P(\omega)$ is an invariant set of the restricted flow generated by the two-dimensional system

$$\begin{aligned} S'(t) &= \big(S^0 - S(t)\big)\, D - N_1(t)\, p_1\big(S(t)\big), \\ N_1'(t) &= N_1(t)\, \big[\, -D_1 + p_1\big(S(t)\big)\, \big]. \end{aligned} \tag{4.23}$$

Observe that the first quadrant $R^+_{SN_1}$ of the $S-N_1$ plane is positively invariant under (4.23) and the flow is transverse to the N_1-axis. It follows that $P(\omega)$ must lie in the interior of $R^+_{SN_1}$. Now, by using a Liapunov function of the form

$$\int_{\lambda_1}^{S} \frac{p_1(\xi) - D_1}{p_1(\xi)}\, d\,\xi + N_1 - N_1^* \,\ln\, N_1$$

and the LaSalle extension theorem as mentioned in Wolkowicz, Ballyk, and Lu [46], we see that the positive equilibrium (λ_1, N_1^*) of (4.23) is globally asymptotically stable with respect to the interior of $R^+_{SN_1}$. This implies that (λ_1, N_1^*) is the only invariant set of (4.23) in the interior of $R^+_{SN_1}$. Therefore, $P(\omega) = \{(\lambda_1, N_1^*)\}$ and, consequently, $\omega = \{(\lambda_1, N_1^*, 0, \ldots, 0)\}$. This shows (4.22) and completes the proof. □

We finally remark that the sufficient condition (4.20) for the global attractivity of the equilibrium $(\lambda_1, \frac{(S^0-\lambda_1)\,D}{D_1}, 0, \ldots, 0)$ of (4.21) is different from that obtained by Wolkowicz and Lu [45], who use a Liapunov function. This condition is new and can be applied to model (4.21) with any monotone response functions p_i provided that all D_i's are relatively close to the washout rate D. For example, if $n = 2$ and $D \le D_i,\ i = 1, 2$, then $\tilde{\ell}_2 = \lambda_2$ and criterion (4.20) reduces to $\lambda_1 < \lambda_2 < S^0$ and $S^0 - \frac{S^0 D}{D_{\max}} < \lambda_2 - \lambda_1$. Thus, Corollary 4.6 provides justification for neglecting differences in the death rates in the model when they are relatively small compared to the dilution rate D. On the other hand, the condition given in [45] can be applied to model (4.21) with any differential removal rates but the p_i's have to satisfy a technical condition.

5. Discussion. In this paper we considered a time delay model of purely exploitative competition of n species in a chemostat for a single growth-limiting resource. Sufficient conditions are determined in the general case for the survival of only one species, and the results are extended to the differential removal rates model. In particular, we showed that when only two species are engaged in competition, the species with the smaller $\lambda_i < S^0$ will displace the other species, independent of initial conditions, and chaotic coexistence, as questioned in Ellermeyer [8], cannot occur. When the contributions to the removal rate of each species from factors other than the washout rate are relatively small, our results demonstrate that these other factors can be neglected without altering the prediction of the outcome of the competition. This result is new even for the ODE model in which delay is also neglected, and complements the results in Wolkowicz and Lu [45], who used the Liapunov function method to determine the outcome of competition for the corresponding ODE model in the differential death rate case. When delays are relatively small, our predictions are also identical to the predictions given by the corresponding ODE model. This is typical of the effects of delay as discussed by MacDonald [27, 28] and supports the argument of Ellermeyer [8] that model (1.1) is more reasonable than the previous ones considered by Bush and Cook [2] and Freedman, So, and Waltman [11].

However, other new effects of delay on the outcome of competition are found. Model (1.1) may give predictions that are different from those given by the corresponding ODE model if the delays are large, and so neglecting delays in the model can lead to incorrect predictions. To see this, we take, for simplicity, the two-species competition case as an example. If $\lambda_1(0) < \lambda_2(0) < S^0$, the results of Hsu, Hubbell, and Waltman [20] and Butler and Wolkowicz [3] predict that species N_1 will win the competition, while N_2 tends toward extinction. Suppose now that for population N_1 there is a time delay $\tau_1 > 0$ in conversion of nutrient to its viable biomass as in model (1.1) and τ_1 is so significant that $S^0 > \lambda_1(\tau_1) > \lambda_2(\tau_2)$. Then our theory predicts that it is population N_2, not N_1, that will win the competition, contrary to the prediction of [3, 20]. Note also, that it need not be the case that $\tau_1 \geq \tau_2$ for this reversal to occur. This effect of delay thus suggests further theoretical as well as experimental investigations. In particular, the J-criterion for competitive ability in continuous culture, as formulated by Hansen and Hubbell [15] and Tilman [41], requires further experimental verification.

It has been well known that environmental changes affect the growth rate of species and thus the outcome of microbial interaction. In the elaborate reviews of Jannasch and Mateles [22] and Veldkamp [42], competitive reversals depending on the dilution rate D and the input nutrient concentration S^0 are reported. These reversals, as pointed out by Hansen and Hubbell [15], do not result from competition but from a high flow rate that washes out the inadequate competitor. However, with the general response functions satisfying (1.2), it seems more feasible to test outcome reversals due to competition. We find that competitive reversals are also possible by changing the time delay. As mentioned earlier, our results indicate that an otherwise dominant species can lose the competition and reversal of the outcome can occur due to an increase in the delay. It seems very unlikely to have the time delay depend on the dilution rate or nutrient concentration, yet it is plausible that the delay may vary when other environmental parameters (such as temperature) change. Tilman [41] has performed a series of elegant experiments showing the dependence of the outcome of competition on temperature. Halbach [14] has even noticed that in laboratory populations, the length of the time delay in growth response is a function of the controlled temperature. See also Herbert [16] for a discussion of the effect of temperature on substrate uptake of microorganisms.

We suggest a different approach to measuring the species specific time delay in growth response, the one discussed by Ellermeyer [8]. Assume that the functional response p_i is known and that the delay is incorporated as in model (1.1). Let us hold the dilution rate D and the nutrient input concentration S^0 constant and culture the species i alone in the chemostat. If $D_i < p_i(S^0)$ and a steady-state equilibrium is reached in the culture, measure the yield constant and the concentrations of the species and the nutrient at the equilibrium and read as, say, $y_e > 0$, $N_e > 0$, and $S_e > 0$. Then the time delay would be (approximately)

$$\tau_i = \frac{1}{D_i} \ln \left(\frac{y_e(S^0 - S_e)D}{N_e D_i} \right)$$

if $y_e(S^0 - S_e)D \geq N_e D_i$, as our theory indicates. If $y_e(S^0 - S_e)D < N_e D_i$, then a discrepancy occurs between the theory and the experimental data and further modifications of model (1.1) are suggested. (For example, incorporating a distributed delay in (1.1) may be more reasonable. See Caperon [4] and Wolkowicz, Xia, and Ruan [47].) However, we should remark that even if we have $y_e(S^0 - S_e)D < N_e D_i$, the

theory may still qualitatively, if not quantitatively, fit biological data. We refer to Waltman [43] and Waltman, Hubbell, and Hsu [44] for a similar discussion on the experimental results of Hansen and Hubbell [15], who test the theory of Hsu, Hubbell, and Waltman [20].

On the other hand, the results in this paper also suggest that it should still be possible to predict the outcome of competition of n competitors in a chemostat without even knowing the form of the response functions, the species specific death rates, and the time delays involved in the conversion from nutrient to biomass, since the critical parameter λ_i for each population can still be determined by culturing each population alone in the chemostat using the appropriate feed concentration S^0 and dilution rate D. In each case, only the equilibrium concentration of $S(t)$ need be measured, since this concentration is the break-even concentration λ_i for that population, whether or not there are differential death rates and/or time delays.

A few comments on some of the existing results are also in order. In [12], Freedman, So, and Waltman considered the single-species culture model and discussed the delay effect on the ultimate fate of the species. Their conclusion is similar to ours, although we have studied competition in the chemostat. In two-species competition, Ellermeyer [8] showed that competitive exclusion occurs when $\lambda_j < S^0 \leq \lambda_i,\ i \neq j,\ i, j \in \{1, 2\}$. However, as our Theorem 2.3 indicates, when $\lambda_j < S^0 \leq \lambda_i$, the extinction of N_i is predicted, not because of competition but because the species N_i (the inadequate competitor) is washed out at the higher flow rate, independent of the competition, whereas the species N_j is not. The result of Hsu, Waltman, and Ellermeyer [21] is interesting. It deals with the case where each competitor can survive in the absence of the other and competition is then really the agent of elimination.

We finally remark that although we have shown the global attractivity of (1.1) under certain conditions, whether the transient behavior involves damped oscillations was not investigated. It was shown in [20] that the solutions of the generalized Monod model approach the steady-state monotonically, and this is also the case for Droop's model [36]. The question as to whether the solutions of (1.1) have certain (damped) oscillatory behavior, as some biological data indicate, is of much interest and is left for a future investigation.

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