Manuscript submitted to
AIMS' Journals
Volume **X**, Number **0X**, XX **200X**

doi:10.3934/xx.xx.xx.xx

pp. **X–XX**

STABILITY AND ROBUSTNESS ANALYSIS FOR A MULTISPECIES CHEMOSTAT MODEL WITH DELAYS IN THE GROWTH RATES AND UNCERTAINTIES

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(Communicated by X. Han)

Abstract. We study a chemostat model with an arbitrary number of competing species, one substrate, and constant dilution rates. We allow delays in the growth rates and additive uncertainties. Using constant inputs of certain species, we derive bounds on the sizes of the delays that ensure asymptotic stability of an equilibrium when the uncertainties are zero, which can allow persistence of multiple species. Under delays and uncertainties, we provide bounds on the delays and on the uncertainties that ensure input-to-state stability with respect to uncertainties.

1. Introduction.

1.1. **Preliminaries.** This paper continues our work (which we began in [8, 9, 22, 25, 26, 27, 28, 30, 39]) on control and other methods to ensure desired asymptotic behaviors in chemostat models, such as the coexistence of multiple competing species, convergence to equilibria, or input delay compensation. Our work is strongly motivated by the ubiquity of chemostats in biological and engineering settings that are of compelling ongoing interest. The chemostat is a laboratory device and a mathematical model for the continuous culture of microorganisms. It was introduced primarily in the works [34] of Monod and [37] of Novick and Szilard from 1950. In the past few decades, chemostat models have been studied extensively, because

2010 *Mathematics Subject Classification.* Primary: 92D40, 93D09; Secondary: 34D23.
Key words and phrases. Delay, nonlinear, bioreactors, stability.
The third author is supported by NSF grant 1408295. A summary of some of this work that was confined to the case where the delays are zero was presented at the 2017 American Control Conference.

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of their role in biotechnology, ecology, and microbiology as ideal representations for modeling cell or microorganism growth, natural environments such as lakes, and wastewater treatment processes [5]; see [42] for an overview of the chemostat literature.

The classical model of competition in the chemostat is described by the system

$$\left\{\begin{array}{rcl} \dot{s}(t) & = & D[s_{\rm in}-s(t)]-\sum\limits_{i=1}^{n} Y_i^{-1}\mu_i(s(t))x_i(t) \\ \dot{x}_i(t) & = & x_i(t)\mu_i(s(t))-Dx_i(t) \ \text{ for } \ i=1,\ldots,n \end{array}\right. \tag{1}$$

where $n \geq 2$ microbial species (whose concentrations are denoted by $x_1, \ldots, x_n$) are in competition for a nutrient with concentration s [42]. The positive constants $s_{\rm in}$ and D are called the input nutrient concentration and the dilution rate, respectively, and Y_i is a positive yield constant related to the conversion rate of the substrate into new biomass for each i. The continuously differentiable functions μ_i for $i = 1, \ldots, n$ are strictly increasing, satisfy $\mu_i(0) = 0$, and describe the consumption of the nutrient by species i. The model also assumes that the growth of the ith species is proportional to the consumption of the nutrient.

It is well known (e.g., from [12, 42]) that if the preceding conditions hold, and if

$$0 < \mu_n^{-1}(D) < \mu_{n-1}^{-1}(D) < \ldots < \mu_2^{-1}(D) < \mu_1^{-1}(D) < s_{\rm in}, \tag{2}$$

then

$$\begin{array}{l} \lim\limits_{t\to+\infty} s(t) = \mu_n^{-1}(D), \quad \lim\limits_{t\to+\infty} x_n(t) = Y_n[s_{\rm in}-\mu_n^{-1}(D)], \\ \text{and} \quad \lim\limits_{t\to+\infty} x_i(t) = 0 \ \text{ if } \ 1 \leq i \leq n-1, \end{array} \tag{3}$$

which is the *competitive exclusion principle* [12, 15, 33, 35]. The constant $\mu_i^{-1}(D)$ is called the *break-even concentration* for the ith species, namely the minimal nutrient concentration that ensures a positive growth for the ith species. Condition (2) says that the species can be ordered by their competitive ability, which is determined by their break-even concentrations. Condition (3) implies that only the nth species persists, because it only requires the lowest concentration of the nutrient to have positive growth.

However, it is commonly observed in experiments that multiple competing species can persist in chemostats with one limiting substrate. Numerous methods and theories have been developed to generate or explain coexistence in chemostats, such as crowding effects, feedback controls in which the inputs are functions of the state variables instead of being constant (e.g., in [8, 27]), flocculation [11], heterogeneity properties of the medium (as noted in [10, 16, 36, 38]), impulsive use of substrates (as explained in [31, 32, 47]), intra-species competition [22], multiple substrates [10, 20], and deterministic or stochastic time-varying inputs (as explained, e.g., in [2, 3, 7, 14, 19, 29, 30, 41, 45]). In this work, we study another approach, based on an alternative model that we describe next.

1.2. **Description of Our Model.** The work [39] modifies the model described by (1) by introducing microbial inputs of the form

$$\left\{\begin{array}{rcl} \dot{s}(t) & = & D[s_{\rm in}-s(t)]-\sum\limits_{i=1}^{n} Y_i^{-1}\mu_i(s(t))x_i(t) \\ \dot{x}_i(t) & = & x_i(t)\mu_i(s(t))+D[x_i^0-x_i(t)] \ \text{ for } \ i=1,\ldots,n, \end{array}\right. \tag{4}$$

in order to promote the coexistence of all species and provides sufficient conditions on the nonnegative constant species inputs x_i^0 for $i = 1, \ldots, n$ that can ensure the coexistence of multiple species, which puts [39] outside the scope of the previously

cited works. One approach that was used in [39] involved polytopic Lyapunov functions [9], which are related to other types of piecewise continuous or piecewise differentiable Lyapunov functions such as those in [46].

The system (4) can be seen as a limiting dynamics for a chain of interconnected chemostats, by the following argument. If we consider the system (1) with $n = 2$ under condition (2), then the competitive exclusion principle will imply that the concentration of the first species will converge to 0 as $t \to +\infty$. To promote the coexistence of the two species, the first species (which is the less advantaged competitor) is cultivated in a first chemostat, whose dynamics is described by the system

$$\left\{\begin{array}{rcl} \dot{s}_1(t) &=& D[s_{\rm in} - s_1(t)] - Y_i^{-1}\mu_1(s_1(t))x_{11}(t), \\ \dot{x}_{11}(t) &=& x_{11}(t)\mu_1(s_1(t)) - Dx_{11}(t), \end{array}\right. \tag{5}$$

whose asymptotic behavior is described by (3) with $n = 1$, that is

$$\lim_{t\to+\infty} s_1(t) = s^* = \mu_1^{-1}(D), \quad \lim_{t\to+\infty} x_{11}(t) = x_1^* = Y_1[s_{\rm in} - \mu_1^{-1}(D)].$$

If the output of (5) becomes the input of (1) with $n = 2$, then we obtain the coupled system

$$\left\{\begin{array}{rcl} \dot{s}_1(t) &=& D[s_{\rm in} - s_1(t)] - Y_1^{-1}\mu_1(s_1(t))x_{11}(t), \\ \dot{x}_{11}(t) &=& x_{11}(t)\mu_1(s_1(t)) - Dx_{11}(t), \\ \dot{s}_2(t) &=& D[s_1(t) - s_2(t)] - Y_1^{-1}\mu_1(s_2(t))x_{12}(t) - Y_2^{-1}\mu_2(s_2(t))x_{22}(t), \\ \dot{x}_{12}(t) &=& x_{12}(t)\mu_1(s_2(t)) + D[x_{11}(t) - x_{12}(t)], \\ \dot{x}_{22}(t) &=& x_{22}(t)\mu_2(s_2(t)) - Dx_{22}(t), \end{array}\right. \tag{6}$$

where x_{ij} is the concentration of the ith species in the jth chemostat, while s_i is the concentration of the same nutrient in the ith chemostat. The last three equations of (6) can be written as the perturbed system

$$\left\{\begin{array}{rcl} \dot{s}(t) &=& D[s^* - s(t)] - Y_1^{-1}\mu_1(s(t))x_1(t) - Y_2^{-1}\mu_2(s(t))x_2(t) + q_0(t), \\ \dot{x}_1(t) &=& x_1(t)\mu_1(s_2(t)) + D[x_1^* - x_1(t)] + q_1(t), \\ \dot{x}_2(t) &=& x_2(t)\mu_2(s_2(t)) - Dx_2(t), \end{array}\right. \tag{7}$$

where the perturbations $q_0(t) = D[s_1(t) - s^*]$ and $q_1(t) = D[x_{11}(t) - x_1^*]$ converge to zero as $t \to +\infty$, so (7) is asymptotically autonomous to

$$\left\{\begin{array}{rcl} \dot{s}(t) &=& D[s^* - s(t)] - Y_1^{-1}\mu_1(s(t))x_1(t) - Y_2^{-1}\mu_2(s(t))x_2(t), \\ \dot{x}_1(t) &=& x_1(t)\mu_1(s_2(t)) + D[x_1^* - x_1(t)], \\ \dot{x}_2(t) &=& x_2(t)\mu_2(s_2(t)) - Dx_2(t), \end{array}\right. \tag{8}$$

which is a particular case of (4) with $n = 2$, $s_{\rm in} = s^*$, $x_1^0 = x_1^*$ and $x_2^0 = 0$. A generalization for a chain of n chemostats can be done in a recursive way, by considering the competitive abilities described in (2).

In this article, we propose a generalization of the model (4) by taking into in account (i) the presence of additive perturbations and (ii) the effect of delays in the growth responses [31, 46]. Therefore, the system (4) is changed to

$$\left\{\begin{array}{rcl} \dot{s}(t) &=& D[s_{\rm in} - s(t)] - \sum\limits_{i=1}^{n} Y_i^{-1}\mu_i(s(t))x_i(t) + \delta_0(t) \\ \dot{x}_i(t) &=& x_i(t)\mu_i(s(t-\tau_i)) + D[x_i^0 - x_i(t)] + \delta_i(t) \ \text{ for } \ i = 1, \ldots, n. \end{array}\right. \tag{9}$$

The functions $\delta_i : [0, +\infty) \to [\underline{d}_i, \bar{d}_i]$ are measurable and essentially bounded (for $i = 0, 1, \ldots, n$) and have known constant lower and upper bounds $\underline{d}_i$ and $\bar{d}_i$, respectively. The system (7) is a particular case of (9) but the functions δ_i can

describe uncertainties such as unmodeled features (for example, disturbances in the chain of chemostats mentioned above), external perturbations, or uncertainties in the input concentrations which commonly occur in applications. For example, a perturbed biomass input $x_i^0 + \Delta_i(t)$ can be represented by an additive perturbation $\delta_i(t) = D\Delta_i(t)$. Also, a disturbance Δ_D added to the dilution rate can be captured by setting $\delta_0(t) = \Delta_D(t)[s_{\rm in} - s(t)]$ and $\delta_i(t) = \Delta_D(t)[x_i^0 - x_i(t)]$ for $i = 1, 2, \ldots, n$, and uncertainties in the uptake functions μ_i or in $s_{\rm in}$ can be modeled in an analogous way using suitable choices of the δ_i's.

Our assumptions will imply that $\underline{d}_0 > -Ds_{\rm in}$ and $\underline{d}_i \geq -Dx_i^0$ for $i = 1, 2, \ldots, n$; see Section 2 for our assumptions, in which the lower bounds $\underline{d}_i$ are allowed to be negative for each $i \geq 1$ such that $x_i^0 > 0$ (so the disturbances need not be positive valued). Therefore, all solutions of (9) with positive valued initial conditions are in the positive orthant for all positive instants, so (9) has the state space $\mathcal{X} = (0, +\infty)^{n+1}$. A key component of our analysis is that we will prove a uniform persistence condition, where we compute positive lower bounds on the $x_i(t)$ values for all i such that $x_i^0 > 0$ and for sufficiently large t; see Lemma 3.3.

The model (9) assumes the existence of a time interval $[0, \tau_i]$ necessary for the ith microbial species metabolize the nutrient. The delays τ_i have been reported experimentally in several works, including [1, 4, 40]. Other delays can arise in our model but will not be considered in this note (but their effects can be incorporated into our δ_i's). For example, in [13, 17, 23] it is assumed that there is mortality of microbial biomass and a fraction is recycled into nutrient with some time delay. The mortality is also considered in [6, 21, 44], where the growth of biomass term $x_i(t)\mu_i(s(t-\tau_i))$ of (9) is replaced by $e^{-d_i\tau_i}x_i(t-\tau_i)\mu_i(s(t-\tau_i))$. Through a change of coordinates (based on a scaling the x_i's, x_i^0's, and δ_i's for $i \geq 1$), the model (9) becomes

$$\left\{\begin{array}{rcl} \dot{s}(t) & = & D[s_{\rm in} - s(t)] - \displaystyle\sum_{i=1}^{n} \mu_i(s(t))x_i(t) + \delta_0(t) \\ \dot{x}_i(t) & = & x_i(t)\mu_i(s(t-\tau_i)) + D[x_i^0 - x_i(t)] + \delta_i(t) \ \text{ for } \ i = 1, \ldots, n, \end{array}\right. \tag{10}$$

where for simplicity we kept the same notation, and (10) will be the subject of this paper.

1.3. **Structure of Article.** In the next section, we provide our theorem for (10), which we prove in Section 3 and illustrate in an example in Section 4. Our work is novel in its use of the more general model (10) (which we believe had not been studied in the presence of nonzero delays or uncertainties) and our use of a new Lyapunov-Krasovskii functional method that is beyond the scope of our prior Lyapunov function designs (such as those in [24, 39], which were confined to undelayed systems). Also, the equilibrium that we stabilize is in the boundary of the state space $\mathcal{X}$ when at least one of the x_i^0's is 0. Moreover, while our previous work [39] required that the nth species input be $x_n^0 = 0$, here we allow a range of possible x_n^0 values, so we cover a much broader class of equilibria than [39].

2. **Definitions, Assumptions, and Main Result.** Our main result provides sufficient conditions ensuring input-to-state stability (or ISS) properties for the dynamics for the error variable

$$\mathcal{E}(t) = (s(t) - s_*, x(t) - x_*) \tag{11}$$

with respect to the disturbance vector $\delta = (\delta_0, \delta_1, \ldots, \delta_n)$, for a large class of possible equilibrium points $\mathcal{E}_* = (s_*, x_*)$, where $x_* = (x_{1*}, \ldots, x_{n*})$ and $x = (x_1, \ldots, x_n)$. The ISS framework is used extensively across engineering; see [18] for the definition of ISS for undelayed systems without state constraints. To allow delays and state constraints, we use a variant of the usual ISS property. To explain this variant, we first need several definitions. Let $\mathcal{K}_\infty$ be the set of all continuous strictly increasing unbounded functions $\gamma : [0, +\infty) \to [0, +\infty)$ such that $\gamma(0) = 0$. Also, $\mathcal{KL}$ is the set of all continuous functions $\bar{\beta} : [0, +\infty) \times [0, +\infty) \to [0, +\infty)$ such that (i) for each $t \geq 0$, the function $f(s) = \bar{\beta}(s, t)$ is of class $\mathcal{K}_\infty$ and (ii) for each $s \geq 0$, the function $g(t) = \bar{\beta}(s, t)$ is nonincreasing and satisfies $\lim_{t\to+\infty} g(t) = 0$. We also set $q_t(\ell) = q(t+\ell)$ for all $\ell \leq 0$, $t \geq 0$, and functions q for which the equality is defined. By ISS of a delay system of the form $\dot{q}(t) = \mathcal{F}(q_t, \delta(t))$ with respect to a pair $(\mathcal{D}, \mathcal{S})$, we mean that there exist functions $\beta \in \mathcal{KL}$ and $\gamma \in \mathcal{K}_\infty$ such that

$$|q(t)| \leq \beta(|q(0)|, t) + \gamma(|\delta|_{[0,t]}) \tag{12}$$

holds for all $t \geq 0$, all solutions $q(t)$ of the system that have initial states $q(0) \in \mathcal{S}$, and all measurable essentially bounded functions $\delta : [0, +\infty) \to \mathcal{D}$. Here and in the sequel, we assume that the initial conditions of our systems are constant, $|\cdot|$ is the usual Euclidean norm, $|\cdot|_{[0,t]}$ is the essential supremum over $[0, t]$, and $|\cdot|_\infty$ is the essential supremum. Later we specialize the preceding definitions to cases where $q = \mathcal{E}$, and where q is an error vector in a different set of variables that we introduce later. Our first assumption is:

Assumption 1. The constants $s_* > 0$ and $s_{\text{in}} > 0$ are such that

$$\mu_i(s_*) < D \ \text{ for } \ i = 1, 2, \ldots, n, \ \text{ and } \ s_{\text{in}} = s_* + \sum_{i=1}^{n} \frac{\mu_i(s_*) x_i^0}{D - \mu_i(s_*)}, \tag{13}$$

and the constants x_i^0 are all nonnegative. Also, the constant D satisfies $0 < D < \mu_n(s_{\text{in}})$.

Assumption 1 can always be satisfied for all choices of the constant

$$D \in (0, \sup_{s\geq 0} \mu_n(s)),$$

by first fixing s_* such that $\mu_i(s_*) < D$ for all i, and then choosing the x_i^0's such that $D < \mu_n(s_{\text{in}})$ and $s_{\text{in}} > 0$, i.e., we view the x_i^0's and s_{in} as constant controls. Although this differs from the usual treatment of controls where the controls depend on time (i.e., open loop controls) or on the state (as in feedback controls), our use of constant controls is sufficient for our delays and robustness analysis (and is included in the usual framework of open loop or feedback controls, by specializing the usual framework to cases where the controls are constant ones). By the symmetry of the dynamics for the x_i's, we can replace the condition $D < \mu_n(s_{\text{in}})$ by the requirement that $D < \mu_i(s_{\text{in}})$ for some i, by renumbering the species. Assumption 1 implies that when the δ_i's and τ_i's are 0, the system (10) admits the equilibrium $\mathcal{E}_* = (s_*, x_*)$, where

$$x_{i*} = \frac{D x_i^0}{D - \mu_i(s_*)} \ \text{ for } \ i = 1, ..., n. \tag{14}$$

Then $\mathcal{E}_* \in [0, +\infty)^{n+1}$, and when the x_i^0's are all positive, we have $\mathcal{E}_* \in (0, +\infty)^{n+1}$. From Assumption 1, we have $\mu_n(s_*) < \mu_n(s_{\text{in}})$, so since μ_n is strictly increasing, we have $s_* \in (0, s_{\text{in}})$. Our assumption on the measurable essentially bounded uncertainties $\delta_i(t)$ is as follows, where $\mathcal{P} = \{i \in \{1, \ldots, n\} : x_i^0 > 0\}$:

Assumption 2. We have $\delta(t) \in [\underline{d}_0, \bar{d}_0] \times \ldots \times [\underline{d}_n, \bar{d}_n]$ for almost all $t \geq 0$, where the known constants $\underline{d}_i$ and $\bar{d}_i \geq 0$ are such that $Ds_{\rm in} + \underline{d}_0 > 0$, $\bar{d}_0 < 0.5Ds_*$, $Dx_i^0 + \underline{d}_i > 0$ for all $i \in \mathcal{P}$, and $\underline{d}_i = 0$ for all $i \in \{1, 2, \ldots, n\} \setminus \mathcal{P}$.

Assumption 2 allows $\underline{d}_i = \bar{d}_i = 0$ for $i = 0, 1, \ldots, n$ which corresponds to cases where the δ_i's are all zero, but is far more general, e.g., because the $\bar{d}_i$'s for $i \geq 1$ can be as large as we want. Notice that in important cases where the x_i^0's are all positive, there is no systematic positive bias in the disturbance values, since for instance, we can allow δ to be take its values in sets such as $[\underline{d}_0, \bar{d}_0] \times \ldots \times [\underline{d}_n, \bar{d}_n] = [-\min\{0.25Ds_*, 0.5Dx_*^0\}, \min\{0.25Ds_*, 0.5Dx_*^0\}]^{n+1}$ where $x_*^0 = \min\{x_i^0 : 1 \leq i \leq n\}$ that are symmetric hypercubes centered at the origin. To state our assumption on the constant delays τ_i, we assume that the μ_i's have the Monod's form

$$\mu_i(s) = \frac{m_i s}{a_i + s} \tag{15}$$

with $m_i > 0$ and $a_i > 0$ being respectively the maximal growth rate and the half saturation constants for all $i \in \{1, 2, \ldots, n\}$, and we set

$$\bar{s}^\sharp = \bar{s} + \frac{\bar{d}_0}{D}, \tag{16}$$

where the constant $\bar{s} \geq s_{\rm in}$ will be specified later. Finally, we use the positive constants

$$\begin{aligned}
&C = 2\left(s_{\rm in} + \sum_{i=1}^n x_i^0 + \frac{1}{D}\sum_{i=0}^n \bar{d}_i\right), \quad \Gamma_0 = D + \sum_{i=1}^n \frac{a_i m_i x_{i*}}{(a_i + s_*)(a_i + \bar{s}^\sharp)},\\
&\bar{\mathcal{L}}_i = e^{\tau_i(\mu_i(\bar{s}^\sharp) - \mu_i(s_*))},\\
&r_i = \frac{a_i m_i C \bar{\mathcal{L}}_i \mu_i(\bar{s}^\sharp) e^{\tau_i B_i}}{a_i + s_*}, \quad q_i = \frac{(a_i + s_*)\left(D - \mu_i(s_*)\right)}{a_i},\\
&B_i = \max\left\{\mu_i(\bar{s}^\sharp) - \mu_i(s_*), \mu_i(s_*)\right\},\\
&\underline{s}_1 = \min\left\{s_*, \frac{Ds_{\rm in} + \underline{d}_0}{D + C\sum_{i=1}^n \frac{m_i}{a_i} e^{\mu_i(\bar{s}^\sharp)\tau_i}}\right\},\\
&\text{and } \ \underline{\alpha}_i = e^{-\tau_i \mu_i(s_*)} \min\left\{x_{i*}, x_i^0 + \frac{\underline{d}_i}{D}\right\}.
\end{aligned} \tag{17}$$

The motivation for the constant Γ_0 is that it is a lower bound for the function

$$\Gamma(s) = D + \sum_{i=1}^n \frac{a_i m_i x_{i*}}{(a_i + s_*)(a_i + s)} \tag{18}$$

for all $s \in [0, \bar{s}^\sharp]$. The function (18) will play an important role in the proof of our theorem, but is not needed to state our theorem. Our main result is:

Theorem 2.1. *If Assumptions 1-2 hold, and if there exists a constant $\bar{s} \geq s_{\rm in}$ such that each of the constant delays τ_i satisfies*

$$M\tau_i < \Gamma_0 \ \text{ for } \ i = 1, 2, \ldots, n, \tag{19}$$

where M is defined by

$$M = \frac{\bar{s}^\sharp}{2}\left(\frac{1}{\Gamma_0 \underline{s}_1}\max_{1\le i\le n}\frac{2r_i^2\tau_i}{(\underline{s}_1+a_i)(\bar{s}^\sharp+a_i)} + \sum_{i\in\mathcal{P}}\frac{\tau_i\left(De^{\tau_i B_i}x_i^0 m_i\right)^2}{q_i\underline{\alpha}_i(a_i+\underline{s}_1)(\bar{s}^\sharp+a_i)}\right), \tag{20}$$

then for all constants $\underline{x}>0$, the dynamics for the error (11) are ISS with respect to $(\mathcal{D},\mathcal{S})$ with the disturbance set $\mathcal{D}=[\underline{d}_0,\bar{d}_0]\times\ldots\times[\underline{d}_n,\bar{d}_n]$ and $\mathcal{S}=\{\mathcal{E}:\mathcal{E}+\mathcal{E}_*\in(0,\bar{s}]\times(0,+\infty)^{n-1}\times(\underline{x},+\infty)\}$.

Our proof of Theorem 2.1 will show how the constants $\underline{s}_1$ and $\underline{\alpha}_i$ described in (17) are related to the lower bounds of the solutions of (10) for arbitrarily large values of t. Note also that M depends on the τ_i's for all $i=1,\ldots,n$ and is equal to zero when these delays are 0, which implies that there are positive values $\bar{\tau}_i$ such that (19) is satisfied when the delays τ_i all satisfy $0\le\tau_i\le\bar{\tau}_i$.

Since $\mathcal{E}(t)+\mathcal{E}_*=(s(t),x(t))$ for all $t\ge 0$, our choice of $\mathcal{S}$ in Theorem 2.1 corresponds to the requirement that $(s(0),x(0))\in(0,\bar{s}]\times(0,+\infty)^{n-1}\times(\underline{x},+\infty)$. However, since $\bar{s}\ge s_{\rm in}$ and $\underline{x}>0$ are arbitrary, it follows that when the δ_i's are zero, Theorem 2.1 implies that all solutions $(s(t),x(t))$ of (10) starting in $\mathcal{X}=(0,+\infty)^{n+1}$ remain in $\mathcal{X}$ at all positive times and satisfy $\lim_{t\to+\infty}(s(t),x(t))=(s_*,x_*)$. This ensures uniform persistence of the ith species for all $i\in\mathcal{P}$, i.e., x_i has a positive lower bound (and $\lim_{t\to+\infty}x_i(t)=0$ for all $i\in\{1,\ldots,n\}\setminus\mathcal{P}$). Our results are new, even in the special cases where the delays τ_i or the uncertainties δ_i are all zero, because [39] did not include delays or uncertainties. Since we do not restrict the values of $\bar{d}_i\ge 0$ for $i\ge 1$, we obtain ISS under arbitrarily large upper bounds on the disturbances δ_i in the x subdynamics. The functions $\beta\in\mathcal{KL}$ and $\gamma\in\mathcal{K}_\infty$ in the final ISS estimate will depend on $\bar{s}$, $\underline{x}$, and the disturbance bounds $\bar{d}_i$ and $\underline{d}_i$ from Assumption 2, and our proof of Theorem 2.1 can be used to provide an algorithm for constructing β and γ. Moreover, as noted in Section 1.2, several types of uncertainties (including in the dilution rate or in the concentration of species input) can be captured by our additive uncertainties δ_i, so our ISS results can estimate or measure the effects of these types of uncertainties.

3. Proof of Theorem 2.1.

3.1. Changes of Variables and Preliminary State Bounds.

We set $\bar{\tau}=\max_i\tau_i$. Since (10) is forward complete on $\mathcal{X}=(0,+\infty)^{n+1}$, we can first fix any solution $(s(t),x(t))$ of the system all of whose components are positive for all $t\ge 0$, with $x_n(0)>\underline{x}$. Then Assumption 2 implies that $s(t)\le\bar{s}^\sharp$ for all $t\ge 0$, since we would have $\dot{s}(t)<0$ for all t for which $s(t)>\bar{s}^\sharp$ and $s(0)\le\bar{s}$. We use the new variables

$$\alpha_i(t)=x_i(t)e^{\int_{t-\tau_i}^t[\mu_i(s(\ell))-\mu_i(s_*)]\mathrm{d}\ell}\ \text{ and }\ \Delta_i(t)=\delta_i(t)e^{\int_{t-\tau_i}^t[\mu_i(s(\ell))-\mu_i(s_*)]\mathrm{d}\ell} \tag{21}$$

for all $i\in\{1,2,\ldots,n\}$. Then we obtain the new system

$$\left\{\begin{array}{rcl}\dot{s}(t) &=& D[s_{\rm in}-s(t)]-\displaystyle\sum_{i=1}^n\mu_i(s(t))\alpha_i(t)e^{\int_{t-\tau_i}^t[\mu_i(s_*)-\mu_i(s(\ell))]\mathrm{d}\ell}\\ &&+\Delta_0(t)\\ \dot{\alpha}_i(t) &=& [\mu_i(s(t))-D]\alpha_i(t)+Dx_i^0e^{\int_{t-\tau_i}^t[\mu_i(s(\ell))-\mu_i(s_*)]\mathrm{d}\ell}\\ &&+\Delta_i(t)\ \text{ for }\ i=1,...,n\end{array}\right. \tag{22}$$

in our new variables, where we also set $\Delta_0=\delta_0$ for consistency. We next prove three lemmas which produce three functions $T_i\in\mathcal{K}_\infty$ for $i=1,2,3$, whose class

$\mathcal{K}_\infty$ properties will be used later to build an ISS estimate that is valid for all times $t \geq 0$. Set $(\tilde{s}, \tilde{x}) = (s - s_*, x - x_*)$. Our first lemma is:

Lemma 3.1. *There is a function $T_1 \in \mathcal{K}_\infty$ such that $s(t) \leq s_{\rm in} + \bar{d}_0/D$ for all $t \geq T_1(|\tilde{s}(0)|)$.*

Proof. Assumptions 1-2 imply that for all $t \geq 0$, we have $s(t) > 0$ and $\alpha_i(t) > 0$ for all $i \in \{1, ..., n\}$. If there is a time $t_l \geq 0$ such that $s(t_l) \leq s_{\rm in} + \bar{d}_0/D$, then for all $t > t_l$, we have $s(t) \leq s_{\rm in} + \bar{d}_0/D$, since $\dot{s}(t) < 0$ at all times $t \geq 0$ such that $s(t) \geq s_{\rm in} + \bar{d}_0/D$. Hence, to prove the lemma, it suffices to consider the case where $s(0) > s_{\rm in} + \bar{d}_0/D$ and consequently $\tilde{s}(0) \neq 0$. In this case, it follows that for all $t \geq 0$ such that $s(\ell) > s_{\rm in} + \bar{d}_0/D$ for all $\ell \in [0, t]$, we also have $\dot{s}(\ell) < 0$. Therefore, for any such t, we can use the facts that $D < \mu_n(s_{\rm in})$ and μ_n is nondecreasing, combined with the inequalities $Dx_n^0 + \underline{d}_n \geq 0$ and $s_* < s_{\rm in} \leq s(\ell)$ for all $\ell \in [0, t]$, to deduce that for all $\ell \in [0, t]$, we have $\alpha_n(\ell) \geq \alpha_n(0) \geq \underline{x} e^{-\mu_n(s_*)\tau_n}$ and $D(s_{\rm in} - s(\ell)) + \Delta_0(\ell) \leq 0$, so

$$\begin{aligned} t\mu_n(s_{\rm in})\underline{x}e^{-2\mu_n(\bar{s}^\sharp)\tau_n} &\leq \int_0^t \mu_n(s_{\rm in})\alpha_n(\ell)e^{\int_{\ell-\tau_n}^{\ell}(\mu_n(s_*)-\mu_n(s(p)))\mathrm{d}p}\,\mathrm{d}\ell \\ &\leq \int_0^t \mu_n(s(\ell))x_n(\ell)\mathrm{d}\ell \\ &\leq s(0) - s(t) \ \leq \ s(0) - s_* \ \leq \ |\tilde{s}(0)| \end{aligned} \tag{23}$$

(by integrating $\dot{s}(\ell)$ on $[0, t]$) which implies that $t \leq |\tilde{s}(0)|e^{2\mu_n(\bar{s}^\sharp)\tau_n}/(\mu_n(s_{\rm in})\underline{x})$, where we used the fact that $-\mu_n(s(p)) \geq -\mu_n(\bar{s}^\sharp)$ for all $p \in [0, t]$). Therefore, there is a time

$$t_* \in \left[0, 2|\tilde{s}(0)|e^{2\mu_n(\bar{s}^\sharp)\tau_n}/(\mu_n(s_{\rm in})\underline{x})\right] \tag{24}$$

such that $s(t_*) \leq s_{\rm in} + \bar{d}_0/D$ (since by the preceding argument, the largest possible time t such that $s(t) > s_{\rm in} + \bar{d}_0/D$ is $|\tilde{s}(0)|\exp(2\mu_n(\bar{s}^\sharp)\tau_n)/(\mu_n(s_{\rm in})\underline{x})$, so at any later times t, it must be the case that $s(t) \leq s_{\rm in} + \bar{d}_0/D$), which by the first part of the proof, implies that $s(t) \leq s_{\rm in} + \bar{d}_0/D$ for all $t \geq t_*$. Hence, we can choose $T_1(r) = 2e^{2\mu_n(\bar{s}^\sharp)\tau_n} r/(\mu_n(s_{\rm in})\underline{x})$. □

Consider the operator

$$\begin{aligned} &\sigma(t) = s(t) + \sum_{i=1}^{n} \frac{\alpha_i(t)}{\mathcal{L}_i}, \\ &\text{where } \ \mathcal{L}_i = \sup_{p \geq 0} e^{\int_{p-\tau_i}^{p}(\mu_i(s(\ell))-\mu_i(s_*))\mathrm{d}\ell} \ \text{ for } \ i = 1, 2, \ldots, n \, . \end{aligned} \tag{25}$$

Then the constants $\mathcal{L}_i$ satisfy $\mathcal{L}_i \leq \bar{\mathcal{L}}_i$ for all i, where the constant $\bar{\mathcal{L}}_i$'s were defined in (17); this follows from our assumptions that the initial conditions are constant combined with the facts that μ_i's are nondecreasing and $s(\ell) \leq \bar{s}^\sharp$ for all $\ell \geq 0$, which gives $\mu_i(s(\ell)) \leq \mu_i(\bar{s}^\sharp)$ for all $\ell \geq -\tau_i$ and all i. Pick any constant $\lambda_1 > 1$ such that our delay upper bounds from (19) are satisfied with C replaced by $\lambda_1 C$ in the formulas from (17). Such a λ_1 exists, because of the strictness of the inequalities in (19), by picking $\lambda_1 > 1$ close enough to 1. We next prove:

Lemma 3.2. *If Assumptions 1-2 hold, then there is a $T_2 \in \mathcal{K}_\infty$ such that $\sigma(t) \leq \lambda_1 C$ for all $t \geq T_2(|\mathcal{E}(0)|)$.*

Proof. By (22),

$$\begin{aligned}\dot{\sigma}(t) &= D[s_{\text{in}} - \sigma(t)] - \sum_{i=1}^{n} \mu_i(s(t))\alpha_i(t) e^{\int_{t-\tau_i}^{t} [\mu_i(s_*) - \mu_i(s(\ell))]\mathrm{d}\ell} \\ &+ \sum_{i=1}^{n} \left[\frac{\alpha_i(t)\mu_i(s(t))}{\mathcal{L}_i} + \frac{D x_i^0}{\mathcal{L}_i} e^{\int_{t-\tau_i}^{t} [\mu_i(s(\ell)) - \mu_i(s_*)]\mathrm{d}\ell} \right] + \Delta_0(t) + \sum_{i=1}^{n} \frac{\Delta_i(t)}{\mathcal{L}_i}\end{aligned} \tag{26}$$

for all $t \geq 0$. Next, note that our choices of the $\mathcal{L}_i$'s from (25), combined with (26) and our upper bounds on the δ_i's from Assumption 2 and the nonnegative valuedness of $\mu_i(s(t))\alpha_i(t)$ for all $i \in \{1, 2, \ldots, n\}$ imply that

$$\begin{aligned}\dot{\sigma}(t) &\leq \tfrac{CD}{2} - D\sigma(t) + \sum_{i=1}^{n} \mu_i(s(t))\alpha_i(t) \left[\tfrac{1}{\mathcal{L}_i} - e^{\int_{t-\tau_i}^{t} [\mu_i(s_*) - \mu_i(s(\ell))]\mathrm{d}\ell} \right] \\ &\leq \tfrac{CD}{2} - D\sigma(t)\end{aligned} \tag{27}$$

for all $t \geq 0$. Since $\lambda_1 > 1$, we deduce that $\sigma(t) \leq \lambda_1 C$ for all $t \geq 0$ if $\sigma(0) \in (0, \lambda_1 C]$, and that there exists a function $T_2^\flat \in \mathcal{K}_\infty$ such that $\sigma(t) \leq \lambda_1 C$ for any $t \geq T_2^\flat(\sigma(0))$ when $\sigma(0) > \lambda_1 C$.

Therefore, the lemma will follow once we find a function $T_2 \in \mathcal{K}_\infty$ such that $T_2(|\mathcal{E}(0)|) \geq T_2^\flat(\sigma(0))$ for all solutions of (10) such that $\sigma(0) > \lambda_1 C$. To find T_2, first notice that (25) and our formula for s_{in} in (13) give

$$\begin{aligned}\sigma(0) &\leq s(0) + \sum_{i=1}^{n} x_i(0) = \tilde{s}(0) + \sum_{i=1}^{n} \tilde{x}_i(0) + s_* + \sum_{i=1}^{n} x_{i*} \\ &= \tilde{s}(0) + \sum_{i=1}^{n} \tilde{x}_i(0) + s_* + \sum_{i=1}^{n} \frac{D x_i^0}{D - \mu_i(s_*)} = \tilde{s}(0) + \sum_{i=1}^{n} \tilde{x}_i(0) \\ &\quad + s_{\text{in}} + \sum_{i=1}^{n} x_i^0.\end{aligned} \tag{28}$$

We next consider two cases. Case 1: If $|\mathcal{E}(0)| \leq (s_{\text{in}} + x_1^0 + \ldots + x_n^0)/(n+1)$, then the last equality in (28) gives $\sigma(0) \leq 2(s_{\text{in}} + x_1^0 + \ldots + x_n^0) \leq \lambda_1 C$, so this case does not produce any restriction on the allowable values of T_2. Case 2: If $|\mathcal{E}(0)| > (s_{\text{in}} + x_1^0 + \ldots + x_n^0)/(n+1)$, then we use the fact that the last equality in (28) gives $T_2^\flat((n+1)|\mathcal{E}(0)| + s_{\text{in}} + x_1^0 + \ldots + x_n^0) \geq T_2^\flat(\sigma(0))$. It follows that the function

$$T_2(\ell) = T_1(\ell) + \begin{cases} \frac{(n+1)\ell}{s_{\text{in}} + x_1^0 + \ldots + x_n^0} T_2^\flat\big(2(s_{\text{in}} + x_1^0 + \ldots + x_n^0)\big), & 0 \leq \ell \leq \frac{s_{\text{in}} + x_1^0 + \ldots + x_n^0}{n+1} \\ T_2^\flat\left((n+1)\ell + s_{\text{in}} + x_1^0 + \ldots + x_n^0\right), & \ell > \frac{s_{\text{in}} + x_1^0 + \ldots + x_n^0}{n+1} \end{cases} \tag{29}$$

satisfies our requirements, where the formula for the restriction of T_2 to the interval $[0, (s_{\text{in}} + x_1^0 + \ldots + x_n^0)/(n+1)]$ was chosen to ensure that (29) provides a class $\mathcal{K}_\infty$ function. □

We now fix a constant $\lambda_2 \in (0,1)$ such that our delay bounds from (19) hold with C replaced by $\lambda_1 C$ in (17) and with $\underline{s}_1$ and the $\underline{\alpha}_i$'s replaced by

$$\underline{s}_\lambda = \lambda_2 \min\left\{ s_*, \frac{Ds_{\rm in} + \underline{d}_0}{D + \lambda_1 C \displaystyle\sum_{i=1}^n \frac{m_i}{a_i} e^{\mu_i(\bar{s}^\sharp)\tau_i}} \right\} \text{ and}$$
$$\underline{\alpha}_{i\lambda} = \lambda_2 e^{-\tau_i \mu_i(s_*)} \min\left\{ x_{i*}, x_i^0 + \frac{\underline{d}_i}{D} \right\} \tag{30}$$

respectively for all i in (17). As in the λ_1 case, the existence of such a λ_2 follows from the strictness of the inequalities in our conditions on the delays, by choosing $\lambda_2 \in (0,1)$ and $\lambda_1 > 1$ both to be close enough to 1. The following lemma provides useful positive lower bounds on $s(t)$, and on the $\alpha_i(t)$'s for all $i \in \mathcal{P}$:

Lemma 3.3. *If Assumptions 1-2 hold, then there is a function $T_3 \in \mathcal{K}_\infty$ such that $s(t) \geq \underline{s}_\lambda$ and $\alpha_i \geq \underline{\alpha}_{i\lambda}$ hold for all $t \geq T_3(|\mathcal{E}(0)|) - \bar{\tau}$ and all $i \in \mathcal{P}$.*

Proof. For all $t \geq T_2(|\mathcal{E}(0)|)$, Lemma 3.2 and our choice of σ in (25) give $\alpha_i(t) \leq \lambda_1 \bar{\mathcal{L}}_i C$ for all $i \in \{1, 2, \ldots, n\}$. Hence, for all $t \geq T_2(|\mathcal{E}(0)|)$, the (s, α) dynamics described by (22), and the Monod's description (15) for the growth functions, give

$$\dot{s}(t) \;\geq\; D(s_{\rm in} - s(t)) - \lambda_1 C \sum_{i=1}^n \frac{m_i s(t)}{a_i} e^{\mu_i(s_*)\tau_i} \bar{\mathcal{L}}_i + \underline{d}_0 \text{ and} \tag{31}$$

$$\dot{\alpha}_i(t) \;\geq\; -D\alpha_i(t) + (Dx_i^0 + \underline{d}_i) e^{-\mu_i(s_*)\tau_i} \text{ for all } i \in \mathcal{P}, \tag{32}$$

where we also used the fact that $Dx_i^0 + \underline{d}_i > 0$ for all $i \in \mathcal{P}$ to get (32). The right side of (31) is bounded below by the positive value $(Ds_{\rm in} + \underline{d}_0)(1 - \lambda_2)$ if t is such that $s(t) \leq \underline{s}_\lambda$. Also, for each $i \in \mathcal{P}$, the right side of (32) is bounded below by the positive value $(1 - \lambda_2)(Dx_i^0 + \underline{d}_i) e^{-\mu_i(s_*)\tau_i}$ if t is such that $\alpha_i(t) \leq \underline{\alpha}_{i\lambda}$. Hence, for any $t_0 \geq 0$ such that $s(t_0) \geq \underline{s}_\lambda$, we have $s(t) \geq \underline{s}_\lambda$ for all $t \geq t_0$. Also, for each $i \in \mathcal{P}$, and for any $t_0 \geq 0$ such that $\alpha_i(t_0) \geq \underline{\alpha}_{i\lambda}$, we have $\alpha_i(t) \geq \underline{\alpha}_{i\lambda}$ for all $t \geq t_0$. Hence, to construct T_3, it suffices to choose $T_3 \in \mathcal{K}_\infty$ such that the following conditions hold: (i) If $s(0) < \underline{s}_\lambda$, then $s(t) \geq \underline{s}_\lambda$ for some $t \in (0, T_3(|\mathcal{E}(0)|) - \bar{\tau}]$ (which implies that $s(t) \geq \underline{s}_\lambda$ for all $t \geq T_3(|\mathcal{E}(0)|) - \bar{\tau}$, by the preceding argument) and (ii) for each $i \in \mathcal{P}$ such that $\alpha_i(0) < \underline{\alpha}_{i\lambda}$, we have $\alpha_i(t) \geq \underline{\alpha}_{i\lambda}$ for some $t \in (0, T_3(|\mathcal{E}(0)|) - \bar{\tau}]$ (which implies that $\alpha_i(t) \geq \underline{\alpha}_{i\lambda}$ for all $t \geq T_3(|\mathcal{E}(0)|) - \bar{\tau}$, also by the preceding argument).

To satisfy the preceding conditions (i)-(ii), first note that if we choose any constant $T_L > 0$ such that

$$T_L > \frac{1}{1 - \lambda_2} \max\left\{ \frac{\underline{s}_\lambda}{Ds_{\rm in} + \underline{d}_0}, \max\left\{ \frac{e^{\mu_i(s_*)\tau_i} \underline{\alpha}_{i\lambda}}{Dx_i^0 + \underline{d}_i} : i \in \mathcal{P} \right\} \right\} + \bar{\tau} \tag{33}$$

then it follows from the Fundamental Theorem of Calculus and the positive valuedness of s and the α_i's that: (A) If $s(0) < \underline{s}_\lambda$, then $s(\ell) \geq \underline{s}_\lambda$ for some $\ell \in [0, T_L - \bar{\tau}]$ and (B) if $i \in \mathcal{P}$ is such that $\alpha_i(0) < \underline{\alpha}_{i\lambda}$, then $\alpha_i(\ell) \geq \underline{\alpha}_{i\lambda}$ for some $\ell \in [0, T_L - \bar{\tau}]$. Conditions (A)-(B) follow because $s(\ell) \geq s(0) + \ell(Ds_{\rm in} + \underline{d}_0)(1 - \lambda_2)$ for all ℓ such that $\max_{r \in [0,\ell]} s(r) < \underline{s}_\lambda$, and $\alpha_i(\ell) \geq \alpha_i(0) + \ell(1 - \lambda_2)(Dx_i^0 + \underline{d}_i) e^{-\mu_i(s_*)\tau_i}$ for all ℓ such that $\max_{r \in [0,\ell]} \alpha_i(r) < \underline{\alpha}_{i\lambda}$, so $\ell \leq T_L - \bar{\tau}$. On the other hand, if $|\mathcal{E}(0)| \leq T_M$ where $T_M = (1 - \lambda_2) \min\{s_*, \min\{x_{i*} : i \in \mathcal{P}\}\}$, then $s(0) - s_* \geq (\lambda_2 - 1)s_*$, and for all $i \in \mathcal{P}$, we have $x_i(0) - x_{i*} \geq (\lambda_2 - 1)x_{i*}$, so our definition of the α_i's in (21)

gives $s(0) \geq \lambda_2 s_* \geq \underline{s}_\lambda$ and $\alpha_i(0) \geq x_i(0)e^{-\tau_i \mu_i(s_*)} \geq \lambda_2 x_{i*} e^{-\tau_i \mu_i(s_*)} \geq \underline{\alpha}_{i\lambda}$ for all $i \in \mathcal{P}$, which imply that $s(t) \geq \underline{s}_\lambda$ and $\alpha_i(t) \geq \underline{\alpha}_{i\lambda}$ all hold for all $t \geq 0$ and $i \in \mathcal{P}$. Hence, we can choose

$$T_3(r) = T_2(r) + \begin{cases} (T_L + T_M)\frac{r}{T_M}, & 0 \leq r \leq T_M \\ T_L + r, & r > T_M \end{cases}, \tag{34}$$

where the formula for the restriction of T_3 to $[0, T_M]$ was chosen to ensure that T_3 is of class $\mathcal{K}_\infty$. □

3.2. **Representing the Error Dynamics.** We use the functions

$$\Gamma(s) = D + \sum_{i=1}^{n} \frac{a_i m_i x_{i*}}{(a_i + s_*)(a_i + s)} \quad \text{and} \quad \tilde{\alpha}_i(t) = \alpha_i(t) - x_{i*} \text{ for } i = 1, 2, \ldots, n. \tag{35}$$

Then $\tilde{\alpha}_i = \alpha_i$ for all $i \in \{1, 2, \ldots, n\} \setminus \mathcal{P}$. Recall that $\Gamma(s(t)) \geq \Gamma_0$ for all $t \geq 0$, where the constant Γ_0 was defined in (17). We assume that

$$t \geq T_3(|\mathcal{E}(0)|), \tag{36}$$

which implies that $t \geq \max\{T_1(|\mathcal{E}(0)|), T_2(|\mathcal{E}(0)|)\}$. [By our formulas for s_{in} and the x_{i*}'s from (13) and (14), we have

$$Ds_{\text{in}} = Ds_* + \sum_{i=1}^{n} \mu_i(s_*)x_{i*} \quad \text{and} \quad Dx_{i*} = Dx_i^0 + \mu_i(s_*)x_{i*} \tag{37}$$

for all $i \in \{1, 2, \ldots, n\}$. Hence, using our formula (22) for the dynamics of s and the α_i's, and the formulas for the components x_{i*} of the equilibrium from (14), and reorganizing terms, we obtain:

$$\begin{cases} \dot{\tilde{s}}(t) &= -D\tilde{s}(t) + \sum_{i=1}^{n}[\mu_i(s_*) - \mu_i(s(t))]x_{i*} - \sum_{i=1}^{n} \mu_i(s(t))\tilde{\alpha}_i(t) \\ &\quad + \sum_{i=1}^{n} \mu_i(s(t))\alpha_i(t)\left[1 - e^{\int_{t-\tau_i}^{t}[\mu_i(s_*) - \mu_i(s(\ell))]\mathrm{d}\ell}\right] + \Delta_0(t) \\ \dot{\tilde{\alpha}}_i(t) &= [\mu_i(s(t)) - \mu_i(s_*)]\alpha_i(t) + \tilde{\alpha}_i(t)\mu_i(s_*) - D\tilde{\alpha}_i(t) \\ &\quad + Dx_i^0\left[e^{\int_{t-\tau_i}^{t}[\mu_i(s(\ell)) - \mu_i(s_*)]\mathrm{d}\ell} - 1\right] + \Delta_i(t), \ i = 1, ..., n. \end{cases} \tag{38}$$

For all $s > 0$, we can use Monod's description (15) for the growth functions to obtain

$$\begin{array}{l} \mu_i(s) - \mu_i(s_*) = \frac{m_i s}{a_i + s} - \frac{m_i s_*}{a_i + s_*} = \frac{a_i}{a_i + s_*}\frac{m_i \tilde{s}}{a_i + s} \\ = \frac{a_i}{a_i + s_*}\mu_i(s)\frac{\tilde{s}}{s} = \mu_i(\tilde{s} + s_*) - \mu_i(s_*) \end{array} \tag{39}$$

for all $i \in \{1, 2, \ldots, n\}$. Hence, our formula (35) for the function Γ can be rewritten as

$$\Gamma(s) = D + \sum_{i=1}^{n} \frac{\mu_i(s) - \mu_i(s_*)}{s - s_*} x_{i*} \tag{40}$$

for all $s \neq s_*$. Using the constants $p_i = D - \mu_i(s_*)$ (which are positive for all $i \in \{1, 2, \dots, n\}$, by Assumption 1) and the function Γ, we obtain

$$\left\{\begin{array}{rcl} \dot{\tilde{s}}(t) & = & -\Gamma(s(t))\tilde{s}(t) - \displaystyle\sum_{i=1}^{n} \mu_i(s(t))\tilde{\alpha}_i(t) \\ & & + \displaystyle\sum_{i=1}^{n} \mu_i(s(t))\alpha_i(t)\left[1 - e^{\int_{t-\tau_i}^{t}[\mu_i(s_*)-\mu_i(s(\ell))]\mathrm{d}\ell}\right] + \Delta_0(t) \\ \dot{\tilde{\alpha}}_i(t) & = & -p_i\tilde{\alpha}_i(t) + c_i\alpha_i(t)\mu_i(s(t))\frac{\tilde{s}(t)}{s(t)} \\ & & + Dx_i^0\left(e^{\int_{t-\tau_i}^{t}[\mu_i(s(\ell))-\mu_i(s_*)]\mathrm{d}\ell} - 1\right) + \Delta_i(t),\ i = 1, ..., n\ , \end{array}\right. \tag{41}$$

where $c_i = \frac{a_i}{a_i + s_*}$ for all $i \in \{1, ..., n\}$.

3.3. **Construction of a Lyapunov-Like Functional.** We define the transformed error vector $\hat{\mathcal{E}}(t) = (\tilde{s}(t), \tilde{\alpha}_1(t), ..., \tilde{\alpha}_n(t))$, and we choose the C^1 function

$$V_1(\hat{\mathcal{E}}) = \nu(\tilde{s}) + \sum_{i=1}^{n} \frac{1}{c_i}\Psi_i(\tilde{\alpha}_i), \text{ where } \nu(\tilde{s}) = \tilde{s} - s_* \ln\left(\frac{\tilde{s} + s_*}{s_*}\right) \text{ and}$$
$$\Psi_i(\tilde{\alpha}_i) = \tilde{\alpha}_i - x_{i*}\ln\left(\tfrac{\tilde{\alpha}_i + x_{i*}}{x_{i*}}\right)$$

for all $i \in \mathcal{P}$, and $\Psi_i(\tilde{\alpha}_i) = \alpha_i$ for all $i \in \{1, \dots, n\} \setminus \mathcal{P}$. Since $\nu'(\tilde{s}) = \tilde{s}/s$ and $\Psi_i'(\tilde{\alpha}_i) = \tilde{\alpha}_i/\alpha_i$ hold for all values of $\tilde{s}$, the $\tilde{\alpha}_i$'s, and $i \in \mathcal{P}$, it follows from the chain rule that along all solutions of (41) and for all $i \in \{1, 2, \dots, n\}$, we have

$$\begin{array}{rcl} \dot{\nu}(t) & = & -\Gamma(s(t))\dfrac{\tilde{s}^2(t)}{s(t)} - \displaystyle\sum_{i=1}^{n} \frac{\tilde{s}(t)}{s(t)}\mu_i(s(t))\tilde{\alpha}_i(t) + \left\{\frac{\tilde{s}(t)}{s(t)}\Delta_0(t)\right\} \\ & & + \frac{\tilde{s}(t)}{s(t)}\displaystyle\sum_{i=1}^{n} \mu_i(s(t))\alpha_i(t)\left[1 - e^{\int_{t-\tau_i}^{t}[\mu_i(s_*)-\mu_i(s(\ell))]\mathrm{d}\ell}\right] \\ \dot{\Psi}_i(t) & = & -p_i\dfrac{\tilde{\alpha}_i^2(t)}{\alpha_i(t)} + c_i\mu_i(s(t))\tilde{\alpha}_i(t)\dfrac{\tilde{s}(t)}{s(t)} \\ & & + \dfrac{\tilde{\alpha}_i(t)}{\alpha_i(t)}Dx_i^0\left(e^{\int_{t-\tau_i}^{t}[\mu_i(s(\ell))-\mu_i(s_*)]\mathrm{d}\ell} - 1\right) + \left\{\dfrac{\tilde{\alpha}_i(t)}{\alpha_i(t)}\Delta_i(t)\right\}. \end{array} \tag{42}$$

It follows that for all $t \geq T_3(|\mathcal{E}(0)|)$, the time derivative of V_1 along the solutions of (41) satisfies

$$\begin{array}{rcl} \dot{V}_1(t) & \leq & -\left\{\Gamma(s(t))\dfrac{\tilde{s}^2(t)}{s(t)} + \displaystyle\sum_{i=1}^{n} q_i\frac{\tilde{\alpha}_i^2(t)}{\alpha_i(t)}\right\} \\ & & + \frac{\tilde{s}(t)}{s(t)}\displaystyle\sum_{i=1}^{n} \mu_i(s(t))\alpha_i(t)\left[1 - e^{\int_{t-\tau_i}^{t}[\mu_i(s_*)-\mu_i(\tilde{s}(\ell)+s_*)]\mathrm{d}\ell}\right] \\ & & + \displaystyle\sum_{i=1}^{n} D\frac{x_i^0}{c_i}\frac{\tilde{\alpha}_i(t)}{\alpha_i(t)}\left(e^{\mathcal{G}_i(t)} - 1\right) + \bar{N}|\delta|_{[0,t]}, \end{array} \tag{43}$$

where the positive constants $q_i = p_i/c_i = (D - \mu_i(s_*))/c_i$ are defined in (17), and where the formula

$$\bar{N} = (n+1)\max\left\{\tfrac{\bar{s}^\sharp + s_*}{\underline{s}_\lambda}, \max_{i \notin \mathcal{P}}\tfrac{\bar{\mathcal{L}}_i}{c_i}, \max_{i \in \mathcal{P}}\tfrac{\bar{\mathcal{L}}_i(\lambda_1 C + x_{i*})}{c_i\underline{\alpha}_{i\lambda}}\right\} \tag{44}$$

follows from Lemmas 3.2-3.3 and the relationship between the Δ_i's and the δ_i's in (21), and was used to bound the coefficients of the Δ_i's in the curly braces in (42). Our choice of V_1 is motivated by the fact that if the delays and uncertainties are all 0, then V_1 is a Lyapunov function for the system (41).

By Lemma 3.2, our decay estimate (43) on V_1 gives

$$\begin{aligned}\dot{V}_1(t) \leq & -\mathcal{N}\big(\hat{\mathcal{E}}(t)\big) \\ & +\lambda_1 C \max_{i\in\{1,\dots,n\}} \left\{\mu_i\left(\bar{s}^\sharp\right)\mathcal{L}_i\left|1-e^{\int_{t-\tau_i}^t[\mu_i(s_*)-\mu_i(\tilde{s}(\ell)+s_*)]\mathrm{d}\ell}\right|\right\}\frac{|\tilde{s}(t)|}{s(t)} \\ & +\sum_{i=1}^n \frac{Dx_i^0}{c_i}\frac{\tilde{\alpha}_i(t)}{\alpha_i(t)}\left(e^{\mathcal{G}_i(t)}-1\right)+\bar{N}|\delta|_{[0,t]},\end{aligned} \tag{45}$$

where $\mathcal{N}(\hat{\mathcal{E}}(t))$ is the quantity in curly braces in (43). By using the Mean Value Theorem, we can deduce the inequality

$$|e^X-1|\leq |X|e^{|X|}, \tag{46}$$

for all $X\in\mathbb{R}$. We apply (46) twice, by choosing X to be the integrals in (45). We deduce that when $t\geq T_3(|\mathcal{E}(0)|)$, and if we set

$$\mathcal{G}_i(t)=\int_{t-\tau_i}^t[\mu_i(\tilde{s}(\ell)+s_*)-\mu_i(s_*)]\mathrm{d}\ell,$$

then

$$\begin{aligned}\dot{V}_1(t) \quad \leq \quad & -\mathcal{N}\left(\hat{\mathcal{E}}(t)\right)+\sum_{i=1}^n\frac{Dx_i^0}{c_i}\frac{|\tilde{\alpha}_i(t)|}{\alpha_i(t)}|\mathcal{G}_i(t)|\,e^{|\mathcal{G}_i(t)|} \\ & +\lambda_1 C\max_{i\in\{1,\dots,n\}}\left\{\mathcal{L}_i\mu_i(\bar{s}^\sharp)|\mathcal{G}_i(t)|\,e^{|\mathcal{G}_i(t)|}\right\}\frac{|\tilde{s}(t)|}{s(t)}+\bar{N}|\delta|_{[0,t]}\end{aligned}$$

and therefore also

$$\begin{aligned}\dot{V}_1(t) \quad \leq \quad & -\mathcal{N}\left(\hat{\mathcal{E}}(t)\right)+\lambda_1\max_{i\in\{1,\dots,n\}}\left\{C\bar{\mathcal{L}}_i\mu_i(\bar{s}^\sharp)e^{\tau_i B_i}|\mathcal{G}_i(t)|\right\}\frac{|\tilde{s}(t)|}{s(t)} \\ & +\sum_{i=1}^n e^{\tau_i B_i}\frac{Dx_i^0}{c_i}\frac{|\tilde{\alpha}_i(t)|}{\alpha_i(t)}|\mathcal{G}_i(t)|+\bar{N}|\delta|_{[0,t]}\end{aligned} \tag{47}$$

where the B_i's are defined in (17). Using the second equality in (39), and the fact that the function Γ from (35) satisfies $\Gamma(s)\geq\Gamma_0$ for all $s\in(0,\bar{s}^\sharp]$, it follows that for all $t\geq T_3(|\mathcal{E}(0)|)$, we have

$$\begin{aligned}\dot{V}_1(t) \quad \leq \quad & -\Gamma_0\frac{\tilde{s}^2(t)}{s(t)}-\sum_{i=1}^n q_i\frac{\tilde{\alpha}_i^2(t)}{\alpha_i(t)} \\ & +\left[\lambda_1\max_{i\in\{1,\dots,n\}}\left\{r_i\int_{t-\tau_i}^t\frac{|\tilde{s}(\ell)|}{a_i+s(\ell)}\mathrm{d}\ell\right\}\frac{|\tilde{s}(t)|}{s(t)}\right. \\ & \left.+\sum_{i\in\mathcal{P}}b_i\frac{|\tilde{\alpha}_i(t)|}{\alpha_i(t)}\int_{t-\tau_i}^t\frac{|\tilde{s}(\ell)|}{a_i+s(\ell)}\mathrm{d}\ell\right]+\bar{N}|\delta|_{[0,t]},\end{aligned} \tag{48}$$

where the r_i's are defined in (17) and $b_i=De^{\tau_i B_i}x_i^0 m_i$ (and where we used the formula $\mu_i(s)-\mu_i(s_*)=c_i m_i\tilde{s}/(a_i+s)$). We next use the positive lower bounds $\underline{s}_\lambda$ and $\underline{\alpha}_{i\lambda}$ from Lemma 3.3, to upper bound the nonnegative valued terms contained

between the brackets in (48), and then we will convert (48) into a decay condition on a suitable Lyapunov-like function.

3.4. **Converting (48) into a Decay Estimate.** We can use Jensen's inequality and Lemma 3.3 to check that for all $t \geq T_3(|\mathcal{E}(0)|)$, we have

$$\begin{aligned}
&\lambda_1 r_i \int_{t-\tau_i}^{t} \frac{|\tilde{s}(\ell)|}{a_i + s(\ell)} \mathrm{d}\ell \frac{|\tilde{s}(t)|}{s(t)} \\
&\leq \left\{ \frac{\lambda_1 r_i}{\sqrt{\Gamma_0 \underline{s}_\lambda (a_i + \underline{s}_\lambda)}} \sqrt{s_i^*} \int_{t-\tau_i}^{t} \frac{|\tilde{s}(\ell)|}{\sqrt{s(\ell)}} \mathrm{d}\ell \right\} \left\{ \frac{\sqrt{\Gamma_0}|\tilde{s}(t)|}{\sqrt{s(t)}} \right\} \\
&\leq \frac{\tau_i \lambda_1^2 r_i^2}{2\Gamma_0 \underline{s}_\lambda (a_i + \underline{s}_\lambda)} s_i^* \int_{t-\tau_i}^{t} \frac{\tilde{s}^2(\ell)}{s(\ell)} \mathrm{d}\ell + \frac{\Gamma_0 \tilde{s}^2(t)}{2s(t)} \quad \text{and} \\
&b_i \frac{|\tilde{\alpha}_i(t)|}{\alpha_i(t)} \int_{t-\tau_i}^{t} \frac{|\tilde{s}(\ell)|}{a_i + s(\ell)} \mathrm{d}\ell \\
&\leq \left\{ \frac{b_i}{\sqrt{\lambda_2 q_i \underline{\alpha}_{i\lambda} (a_i + \underline{s}_\lambda)}} \sqrt{s_i^*} \int_{t-\tau_i}^{t} \frac{|\tilde{s}(\ell)|}{\sqrt{s(\ell)}} \mathrm{d}\ell \right\} \left\{ \frac{\sqrt{\lambda_2 q_i}|\tilde{\alpha}_i(t)|}{\sqrt{\alpha_i(t)}} \right\} \\
&\leq \frac{\tau_i b_i^2}{4\lambda_2 q_i \underline{\alpha}_{i\lambda} (a_i + \underline{s}_\lambda)} s_i^* \int_{t-\tau_i}^{t} \frac{\tilde{s}^2(\ell)}{s(\ell)} \mathrm{d}\ell + \frac{\lambda_2 q_i \tilde{\alpha}_i^2(t)}{\alpha_i(t)}
\end{aligned} \tag{49}$$

for all $i \in \mathcal{P}$, where

$$s_i^* = \frac{\bar{s}^\sharp}{\bar{s}^\sharp + a_i} \tag{50}$$

and where we also applied the inequality $c_1 c_2 \leq \frac{1}{2}c_1^2 + \frac{1}{2}c_2^2$ and then Young's inequality $c_1 c_2 \leq \frac{1}{4}c_1^2 + c_2^2$, with c_1 and c_2 being the corresponding terms in curly braces in (49) in both applications, and we used the fact that $s(\ell) \leq \bar{s}^\sharp$ for all $\ell \geq 0$ to get

$$\frac{1}{a_i + s(\ell)} \leq \frac{1}{\sqrt{a_i + \underline{s}_\lambda}} \sqrt{\frac{s(\ell)}{a_i + s(\ell)}} \frac{1}{\sqrt{s(\ell)}} \quad \text{and} \quad \sqrt{\frac{s(\ell)}{s(\ell) + a_i}} \leq \sqrt{s_i^*}$$

for all i and all $\ell \geq T_3(|\mathcal{E}(0)|) - \bar{\tau}$.

Using (49) to upper bound the terms in brackets in (48) gives the decay estimate

$$\begin{aligned}
&\dot{V}_1(t) \leq -\frac{\Gamma_0 \tilde{s}^2(t)}{2s(t)} - \sum_{i=1}^{n} \frac{q_i(1-\lambda_2)\tilde{\alpha}_i^2(t)}{\alpha_i(t)} + \mathcal{M}_\lambda(\tau) \int_{t-\bar{\tau}}^{t} \frac{\tilde{s}^2(\ell)}{s(\ell)} \mathrm{d}\ell + \bar{N}|\delta|_{[0,t]}, \\
&\text{where } \mathcal{M}_\lambda(\tau) \\
&= \frac{\bar{s}^\sharp}{4} \left(\frac{1}{\Gamma_0 \underline{s}_\lambda} \max_{1 \leq i \leq n} \frac{2\tau_i \lambda_1^2 r_i^2}{(\underline{s}_\lambda + a_i)(\bar{s}^\sharp + a_i)} + \sum_{i \in \mathcal{P}} \frac{\tau_i \left(D e^{\tau_i B_i} x_i^0 m_i \right)^2}{\lambda_2 q_i \underline{\alpha}_{i\lambda} (a_i + \underline{s}_\lambda)(\bar{s}^\sharp + a_i)} \right).
\end{aligned} \tag{51}$$

Our bound (19) from Theorem 2.1 and our choices of the λ_i's imply that $\bar{\tau}\mathcal{M}_\lambda(\tau)\lambda_1 < \Gamma_0/2$, by choosing $\lambda_2 \in (0,1)$ and $\lambda_1 > 1$ close enough to 1. Therefore, there is a constant v_0 such that along all solutions of (35) in our state space $\mathcal{X} = (0,\infty)^{n+1}$ and for all times $t \geq T_3(|\mathcal{E}(0)|)$, the time derivative of the function

$$V_2(\tilde{s}_t, \tilde{\alpha}_t) = V_1(\tilde{s}(t), \tilde{\alpha}(t)) + \lambda_1 \mathcal{M}_\lambda(\tau) \int_{t-\bar{\tau}}^{t} \int_{\ell}^{t} \frac{\tilde{s}^2(r)}{s(r)} \mathrm{d}r \, \mathrm{d}\ell \tag{52}$$

satisfies

$$\dot{V}_2(\tilde{s}_t,\tilde{\alpha}_t) \leq -v_0\left(\frac{\tilde{s}^2(t)}{s(t)}+\sum_{i=1}^{n}\frac{\tilde{\alpha}_i^2(t)}{\alpha_i(t)}+\int_{t-\bar{\tau}}^{t}\int_{\ell}^{t}\frac{\tilde{s}^2(r)}{s(r)}\mathrm{d}r\,\mathrm{d}\ell\right)+\bar{N}|\delta|_{[0,t]}, \tag{53}$$

where we used the relations

$$\begin{array}{l}\frac{d}{dt}\int_{t-\bar{\tau}}^{t}\int_{\ell}^{t}\frac{\tilde{s}^2(r)}{s(r)}\mathrm{d}r\,\mathrm{d}\ell=\bar{\tau}\frac{\tilde{s}^2(t)}{s(t)}-\int_{t-\bar{\tau}}^{t}\frac{\tilde{s}^2(\ell)}{s(\ell)}\mathrm{d}\ell \text{ and}\\ \int_{t-\bar{\tau}}^{t}\int_{\ell}^{t}\frac{\tilde{s}^2(r)}{s(r)}\mathrm{d}r\,\mathrm{d}\ell\leq\bar{\tau}\int_{t-\bar{\tau}}^{t}\frac{\tilde{s}^2(\ell)}{s(\ell)}\mathrm{d}\ell\end{array} \tag{54}$$

to find v_0. The remainder of the proof consists of converting (53) into an ISS estimate in the transformed error variable $\hat{\mathcal{E}}(t)=(\tilde{s}(t),\tilde{\alpha}_1(t),...,\tilde{\alpha}_n(t))$ that is valid for all $t\geq 0$, which we then convert into an ISS estimate in the original error variable $\mathcal{E}=(s,x)-\mathcal{E}_*$; for details for the completion of the proof, see the appendix below.

4. **Illustration.** Consider the system (10) with $n=2$, $D=0.4$, $s_*=0.5$, $x_1^0=1$, and $x_2^0=0.55$ and the growth functions

$$\mu_1(s)=\frac{s}{5+s} \quad \text{and} \quad \mu_2(s)=\frac{s}{2+s}. \tag{55}$$

We apply our theorem with the choice $\bar{s}=s_{\text{in}}$. Then Assumption 1 is satisfied with $s_{\text{in}}=1.34412$, and the corresponding equilibria (14) are $x_{1*}=1.29412$ and $x_{2*}=1.1$. In this illustration, we will use the vectors $\delta(t)$ to model uncertainties in applying the constant input concentrations (which may occur in applications, because it may be difficult to maintain the inputs x_i^0 at constant levels), so we can set $\delta_0(t)=0$ and therefore choose $\underline{d}_0=\bar{d}_0=0$. To isolate the effects of delays in one of the species, we assume that τ_1 is positive but that $\tau_2=0$ (but analogous results can be obtained if the delay is in the dynamics for the second species, or in the dynamics for both species). Then Assumption 2 is satisfied with $\bar{d}_1=-\underline{d}_1=\bar{d}_2=-\underline{d}_2=0.1$, and our requirements (19) on the delays τ_i are satisfied with the choice $\bar{s}=s_{\text{in}}$ for all values $\tau_1\in[0,0.145)$.

We simulated the dynamics (10) using the command `NDSolve` in Mathematica [43], with the preceding choices of the parameters, the delays $\tau_1=0.14$ and $\tau_2=0$, and the disturbance vector $\delta(t)=(\delta_0(t),\delta_1(t),\delta_2(t))=(0,-0.1\sin(t),0.1\cos(t))$, to isolate the effects of uncertainties in applying the constant input concentrations x_i^0 in the x subdynamics. We report our results in the figures below, with the initial state $(s(0),x_1(0),x_2(0))=(0.2,0.1,1)$, and then with the initial state $(s(0),x_1(0),x_2(0))=(1.3,0.2,0.1)$. The figures show rapid convergence towards an oscillatory steady state, with a deviation from the equilibrium point $(s_*,x_{1*},x_{2*})=(0.5,1.29412,1.1)$ that can be explained by the presence of the uncertainties δ_1 and δ_2, and therefore help illustrate our theory.

5. **Boundedness of Solutions of (10) for All Delays τ_i.** Theorem 2.1 leaves open the question of whether all solutions of (10) are bounded when our Assumptions 1-2 are satisfied. Therefore, we prove the following result on boundedness of solutions of (10):

Proposition 1. *Let Assumptions 1-2 hold and the growth functions μ_i satisfy $\mu_i(0)=0$ and be C^1 and strictly increasing for all $i\in\{1,2,\dots,n\}$. Assume that $D<\sup_{s\geq 0}\mu_i(s)$ for all $i\in\{1,2,\dots,n\}$. Then for all constant delays $\tau_i\geq 0$, all solutions of (10) starting in $(0,+\infty)^{n+1}$ are bounded.*

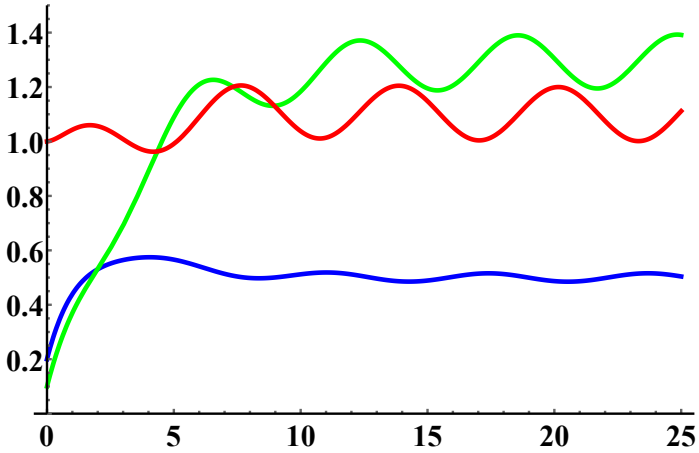

FIGURE 1. Solution Components of (10) Plotted on Time Interval $[0, 25]$. Species $x_1(t)$ and $x_2(t)$ and Substrate $s(t)$. Initial State: $(s(0), x_1(0), x_2(0)) = (0.2, 0.1, 1)$.

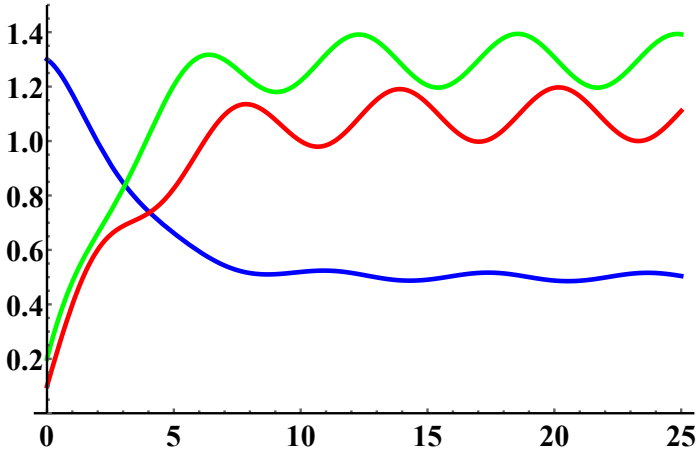

FIGURE 2. Solution Components of (10) Plotted on Time Interval $[0, 25]$. Species $x_1(t)$ and $x_2(t)$ and Substrate $s(t)$. Initial State: $(s(0), x_1(0), x_2(0)) = (1.3, 0.2, 0.1)$.

Proof. Choose any constant $s_d \geq s_{\text{in}} + (\bar{d}_0/D)$ such that $\mu_i(s_d) > D$ for all $i \in \{1, 2, \ldots, n\}$, and fix any solution $(s(t), x(t))$ of (10) whose initial value is componentwise positive. Then Lemma 3.1 provides a constant $t_a \geq 0$ such that $s(t) \leq s_d$ for all $t \geq t_a$, and our assumptions ensure that all components of $(s(t), x(t))$ are nonnegative valued for all $t \geq 0$. Hence, $s(t)$ is bounded. Set $D_* = Ds_{\text{in}} + \bar{d}_0$. Then our assumptions give $\dot{s}(t) \leq D_*$ for all $t \geq 0$, which gives

$$s(m_2) \leq s(m_1) + (m_2 - m_1)D_* \tag{56}$$

for all values $m_1 \geq 0$ and $m_2 \geq m_1$. Also, for each $i \in \{1, 2, \ldots, n\}$ and all $t \geq t_a + \tau$, we have $\dot{x}_i(t) \leq x_i(t)[\mu_i(s_d) - D] + Dx_i^0 + \bar{d}_i$ for all $t \geq 0$, which we can integrate to obtain

$$x_i(a_2) \leq e^{(a_2 - a_1)(\mu_i(s_d) - D)} \left[x(a_1) + \frac{Dx_i^0 + \bar{d}_i}{\mu_i(s_d) - D} \right] \tag{57}$$

for all values $a_1 \geq 0$ and $a_2 \geq 0$ such that $t_a + \tau \leq a_1 \leq a_2$. Since $s(t)$ is bounded, it remains to show that $x_i(t)$ is a bounded function of t for all $i \in \{1, 2, \ldots, n\}$, which we prove by contradiction.

Suppose that there were a $j \in \{1, ..., n\}$ such that x_j is unbounded. For later use, we define the constant $s_0 > 0$ by $\mu_j(s_0) = D/2$. Since $x_j(t)$ is unbounded, there is a sequence of values $t_k \geq t_a + 2\tau + (s_0/(2D_*)$ such that $t_{k+1} \geq t_k + 2\tau + s_0/(2D_*)$ for all $k \geq 1$, and such that the following four conditions hold: (i) $x(t_k)$ is increasing, (ii) $\lim_{k\to\infty} x_j(t_k) = +\infty$, (iii) $\dot{x}_j(t_k) \geq 0$ for all $k \geq 1$, and (iv) the inequality

$$x_j(t_k) \geq 2 \sum_{i=1}^{n} \left(x_i^0 + \frac{\bar{d}_j}{D} \right) \tag{58}$$

holds for all $k \geq 1$. We can satisfy the preceding conditions (i)-(iv) by first choosing the t_k's such that (i)-(ii) and (iv) are all satisfied, then replacing t_2 by a value $t_{2*} \in [t_1, t_2]$ such that $\dot{x}_j(t_{2*}) \geq 0$ (in case $\dot{x}_j(t_2) < 0$, by setting $t_{2*} = \inf\{t \in [t_1, t_2] : \dot{x}_j(r) < 0 \text{ for all } r \in (t, t_2]\}$, and such a t_{2*} exists because $x_j(t_1) \leq x_j(t_2)$), then replacing t_3 by a value t_i such that $i > 3$ and $x_j(t_i) > x_j(t_{2*})$ and deleting $t_2, \ldots, t_{i-1}$ from the sequence, then repeating the preceding process with t_1 replaced by t_i, and then reasoning inductively. Since $\dot{x}_j(t_k) \geq 0$ for all $k \geq 1$, it follows that $x_j(t_k)\mu_j(s(t_k - \tau)) + D[x_j^0 - x_j(t_k)] + \delta_j(t_k) \geq 0$, which we can rearrange to obtain

$$\mu_j(s(t_k - \tau)) \geq D - \frac{D(x_j^0 + (\bar{d}_j/D))}{x_j(t_k)} \tag{59}$$

for all $k \geq 1$. Then condition (iv) gives $\mu_j(s(t_k - \tau)) \geq \frac{D}{2} = \mu_j(s_0)$, and therefore also $s(t_k - \tau) \geq s_0$ for all $k \geq 1$.

Consider the intervals

$$I_k = \left[t_k - \tau - \tfrac{s_0}{2D_*}, t_k - \tau \right]. \tag{60}$$

Then $m \geq t_a + \tau$ for all $m \in I_k$ and $k \geq 1$. We deduce from (56) (with the choices $m_1 = \ell$ and $m_2 = t_k - \tau$) that for all $\ell \in I_k$, we have

$$s(t_k - \tau) + (-t_k + \tau + \ell)D_* \leq s(\ell)\ . \tag{61}$$

Also, we deduce from (61) (with the choice $\ell = t_k - \tau - \frac{s_0}{2D_*}$) that

$$\tfrac{s_0}{2} \leq s(t_k - \tau) - \tfrac{s_0}{2} = s(t_k - \tau) - \tfrac{s_0}{2D_*} D_* \leq s(\ell) \tag{62}$$

for all $\ell \in I_k$, where the first inequality used the fact that $s(t_k - \tau) \geq s_0$. As an immediate consequence of (10) and (62), we deduce that $\dot{s}(t) \leq D_* - \mu_j(s_0/2)x_j(t)$ for all $t \in I_k$, which we can integrate over I_k to obtain

$$s(t_k - \tau) \leq s_d + \frac{s_0}{2} - \int_{t_k - \tau - \frac{s_0}{2D_*}}^{t_k - \tau} \mu_j\left(\frac{s_0}{2}\right) x_j(m)\mathrm{d}m, \tag{63}$$

by using the lower bound on the t_k's and our choice of s_d, and noting that the lower limit of integration in (63) satisfies $t_k - \tau - (s_0/(2D_*)) \geq t_a$ to obtain $s(t_k - \tau - (s_0/(2D_*))) \leq s_d$.

We can also use (57) to conclude that for all $m \in I_k$, we have

$$x_j(t_k) \leq e^{(t_k - m)(\mu_j(s_d) - D)} \left[x_j(m) + \tfrac{Dx_j^0 + \bar{d}_j}{\mu_j(s_d) - D} \right]\ . \tag{64}$$

Since $\mu_j(s_d) - D \geq 0$, we deduce that for all $m \in I_k$, we also have $t_k - m \leq \tau + s_0/(2D_*)$ and so also

$$e^{\left(\tau + \frac{s_0}{2D_*}\right)(D - \mu_j(s_d))} x_j(t_k) - \tfrac{Dx_j^0 + \bar{d}_j}{\mu_j(s_d) - D} \leq x_j(m)\ . \tag{65}$$

Since $\lim_{k\to\infty} x_j(t_k) = +\infty$, it follows from (65) that there is $k_p > 0$ such that for all $k \geq k_p$, we have

$$\frac{1}{2} e^{\left(\tau + \frac{s_0}{2D_*}\right)(D - \mu_j(s_d))} x_j(t_k) \leq x_j(m) \tag{66}$$

for all $m \in I_k$. Combining (66) with (63), we obtain

$$\begin{array}{rcl} s(t_k - \tau) & \leq & s_d + \frac{s_0}{2} - \mu_j\left(\frac{s_0}{2}\right) \int_{t_k - \tau - \frac{s_0}{2D_*}}^{t_k - \tau} \frac{1}{2} e^{\left(\tau + \frac{s_0}{2D_*}\right)(D - \mu_j(s_d))} x_j(t_k) \mathrm{d}m \\ & = & s_d + \frac{s_0}{2} - \mu_j\left(\frac{s_0}{2}\right) \frac{s_0}{4D_*} e^{\left(\tau + \frac{s_0}{2D_*}\right)(D - \mu_j(s_d))} x_j(t_k) \ . \end{array} \tag{67}$$

Since $\lim_{k\to\infty} x_j(t_k) = +\infty$, it follows that there is a $k \geq k_p$ such that $s(t_k - \tau) < 0$. This yields a contradiction with the fact that $s(t) \geq 0$ for all $t \geq 0$. □

6. **Conclusions.** We solved an input-to-state stabilization problem for a chemostat model with one limiting substrate, an arbitrary number of competing species, a constant dilution rate, delays in the uptake functions, and uncertainties. We used the constant species inputs and the input nutrient concentration as constant controls, and these controls can be chosen to input-to-state stabilize a large class of possible equilibria. In the special case where all of the constant inputs x_i^0 are positive and the disturbances are zero, we first proved (in Lemma 3.3) that all solutions whose initial states are in the positive orthant are uniformly persistent, meaning, there is a positive lower bound on the species levels. Then by using a Lyapunov functional, we proved that the solutions asymptotically converge towards a positive equilibrium, which generalizes [39]. We use the x_i^0's and the input nutrient concentration s_{in} as constant controls.

To cope with delays in uptake functions or uncertainties, we used a new Lyapunov functional approach. The decay estimate for our Lyapunov-like function made it possible to prove robustness to uncertainties. We hope to generalize our work to larger classes of models with multiple species and multiple limiting substrates. Our choices of the uptake functions (15) made it possible to obtain lower and upper bounds in several intermediate steps of the construction of the Lyapunov functional. The Michaelis-Menten growth functions that we used provide a wide range of generality for our results, since the growth rates of many species are described by such functions. A more general result is still unsolved for more general uptake functions, due to the technical difficulties induced by the lack of monotonicity and more complex nonlinearities.

Appendix: Completing the Proof of Theorem 2.1. We complete the proof of Theorem 2.1, by converting the decay estimate (53) into an ISS estimate in the transformed error variable $\hat{\mathcal{E}}(t) = (\tilde{s}(t), \tilde{\alpha}_1(t), ..., \tilde{\alpha}_n(t))$ that is valid for all $t \geq 0$, which we then convert into an ISS estimate in the original error variable $\mathcal{E}$ from the statement of the theorem. To this end, first note that we can use our three lemmas to find a function $\underline{\gamma} \in \mathcal{K}_\infty$ such that

$$v_0\left(\frac{\tilde{s}^2(t)}{s(t)} + \sum_{i=1}^{n} \frac{\tilde{\alpha}_i^2(t)}{\alpha_i(t)} + \int_{t-\bar{\tau}}^{t} \int_{\ell}^{t} \frac{\tilde{s}^2(r)}{s(r)} \mathrm{d}r \, \mathrm{d}\ell\right) \ \geq \ \underline{\gamma}\left(V_2\left(\hat{\mathcal{E}}_t\right)\right) \tag{A.1}$$

and therefore also $\dot{V}_2(\hat{\mathcal{E}}_t) \leq -\underline{\gamma}(V_2(\hat{\mathcal{E}}_t)) + \bar{N}|\delta|_{[0,t]}$ along all trajectories of the $\mathcal{E}$ dynamics starting in our set $\mathcal{S}$ of initial states from the statement of our theorem, and for all $t \geq T_3(|\mathcal{E}(0)|)$ (by using the known positive upper and lower bounds for

$s(t)$ and the $\alpha_i(t)$'s for $i \in \mathcal{P}$ that are valid for all $t \geq T_3(|\mathcal{E}(0)|)$. One method for finding $\underline{\gamma}$ is as follows. First, pick a function $\underline{\gamma}_0 \in \mathcal{K}_\infty$ such that

$$(n+1)\nu(\tilde{s}) \leq \underline{\gamma}_0(|\tilde{s}|) \text{ and } (n+1)\Psi_i(\tilde{\alpha}_i)/c_i \leq \underline{\gamma}_0(|\tilde{\alpha}_i|) \tag{A.2}$$

for all $i \in \{1, \ldots, n\}$ and all $\hat{\mathcal{E}} = (\tilde{s}, \tilde{\alpha}_1, \ldots \tilde{\alpha}_n)$ such that the following conditions hold: $\tilde{s} \in [\underline{s}_\lambda - s_*, \lambda_1 C - s_*]$, $\tilde{\alpha}_i \in [\underline{\alpha}_{i\lambda} - x_{i*}, \lambda_1 C\bar{\mathcal{L}}_i - x_{i*}]$ for all $i \in \mathcal{P}$, and $\tilde{\alpha}_i \in (0, \lambda_1 C\bar{\mathcal{L}}_i]$ for all $i \in \{1, \ldots, n\} \setminus \mathcal{P}$. Then $V_1(\hat{\mathcal{E}}(t)) \leq \underline{\gamma}_0(|\hat{\mathcal{E}}(t)|)$ for all $t \geq T_3(|\mathcal{E}(0)|)$. Hence, Lemma 3.2 gives

$$\left(\underline{\gamma}_0^{-1}(V_1(\hat{\mathcal{E}}(t)))\right)^2 \leq |\hat{\mathcal{E}}(t)|^2 \leq \lambda_1 C\left(\frac{\tilde{s}^2(t)}{s(t)} + \max_i \bar{\mathcal{L}}_i \sum_{i=1}^n \frac{\tilde{\alpha}_i^2(t)}{\alpha_i(t)}\right), \tag{A.3}$$

since $\max\{s(t), \max\{\alpha_i(t)/\bar{\mathcal{L}}_i : 1 \leq i \leq n\}\} \leq \lambda_1 C$ for all $t \geq T_3(|\mathcal{E}(0)|)$. Therefore, the function

$$\Theta(r) = \min\left\{\left(\underline{\gamma}_0^{-1}\left(\frac{r}{2}\right)\right)^2, \frac{r}{2\lambda_1(\mathcal{M}_\lambda(\tau)+1)}\right\} \tag{A.4}$$

satisfies

$$\begin{aligned}
&\Theta(V_2(\hat{\mathcal{E}}_t)) \leq \Theta(2V_1(\hat{\mathcal{E}}(t))) + \Theta(2\lambda_1\mathcal{M}_\lambda(\tau)\mathcal{D}_I(t)) \\
&\leq \left(\underline{\gamma}_0^{-1}(V_1(\hat{\mathcal{E}}(t)))\right)^2 + \mathcal{D}_I(t) \leq \lambda_1 C \max_i \bar{\mathcal{L}}_i \left(\frac{\tilde{s}^2(t)}{s(t)} + \sum_{i=1}^n \frac{\tilde{\alpha}_i^2(t)}{\alpha_i(t)}\right) \\
&+\mathcal{D}_I(t),
\end{aligned} \tag{A.5}$$

where $\mathcal{D}_I(t)$ is the double integral in (A.1), and where the first inequality in (A.5) used the fact that $\Theta(a+b) \leq \Theta(2a) + \Theta(2b)$ where a and b are the two terms in our formula (52) for V_2, and where the last inequality in (A.5) used the fact that $\max_i \bar{\mathcal{L}}_i \geq 1$. Therefore, we can choose $\underline{\gamma} = \Theta v_0/v_a$, where $v_a = \max\{\lambda_1 C \max_i \bar{\mathcal{L}}_i, 1\}$. Hence, standard ISS arguments (e.g., from [18]) provide functions $\beta_0 \in \mathcal{KL}$ and $\gamma_0 \in \mathcal{K}_\infty$ such that

$$V_2\left(\hat{\mathcal{E}}_t\right) \leq \beta_0\left(V_2\left(\hat{\mathcal{E}}_{T_3(|\mathcal{E}(0)|)}\right), t\right) + \gamma_0(|\delta|_{[0,t]}) \tag{A.6}$$

for all $t \geq T_3(|\mathcal{E}(0)|)$. Then the structure of V_2 provides functions $\beta_1 \in \mathcal{KL}$ and $\gamma_1 \in \mathcal{K}_\infty$ such that

$$|\hat{\mathcal{E}}(t)| \leq \beta_1\big(|\hat{\mathcal{E}}_{T_3(|\mathcal{E}(0)|)}|_{[-\bar{\tau},0]}, t\big) + \gamma_1\big(|\delta|_\infty\big) \tag{A.7}$$

for all $t \geq T_3(|\mathcal{E}(0)|)$.

To extend (A.7) to obtain an ISS estimate that is valid for all $t \geq 0$, first note that the structure (38) of the $\hat{\mathcal{E}}$ dynamics and the Mean Value Theorem estimate (46), combined with our bounds on the μ_i's, $s(t)$, and Γ and the global Lipschitzness of the μ_i's, provide a constant $\bar{L}$ (that is independent of the choice of the solution) such that

$$\left|\frac{d}{d\ell}\hat{\mathcal{E}}(\ell)\right| \leq \bar{L}\left(\max\{|\hat{\mathcal{E}}_\ell(r)| : r \in [-\bar{\tau}, 0]\} + |\delta|_{[0,\ell]}\right) \tag{A.8}$$

for all $\ell \in [0, T_3(|\mathcal{E}(0)|)]$; this can be done by rewriting both occurrences of $\alpha_i(t)$ in the dynamics (38) for $\hat{\mathcal{E}}$ in the form $\tilde{\alpha}_i(t) + x_{i*}$, and $\hat{\mathcal{E}}_\ell$ is defined over the entire interval $[-\bar{\tau}, 0]$ for all choices of $\ell \in [0, T_3(|\mathcal{E}(0)|)]$ because of our assumption that the initial functions are constant, which allows us to extend their domains to include

all negative real values). Integrating (A.8) over $[0,t]$ for any $t \in [0, T_3(|\mathcal{E}(0)|)]$ and applying the Fundamental Theorem of Calculus to $\hat{\mathcal{E}}$ gives

$$\mathcal{F}(t) \leq \mathcal{F}(0) + \bar{L}\int_0^t \mathcal{F}(\ell)\mathrm{d}\ell + \bar{L}T_3(|\mathcal{E}(0)|)|\delta|_\infty, \tag{A.9}$$

where $\mathcal{F}(\ell) = |\hat{\mathcal{E}}|_{[\ell-\bar{\tau},\ell]}$.

We now apply Gronwall's inequality to $\mathcal{F}$ and use the constantness of the initial functions to get

$$\begin{aligned} \left|\hat{\mathcal{E}}(t)\right| \ \leq \ \mathcal{F}(t) \ &\leq \ \left(\mathcal{F}(0) + \bar{L}T_3(|\mathcal{E}(0)|)|\delta|_\infty\right) e^{\bar{L}T_3(|\mathcal{E}(0)|)} \\ &= \ |\hat{\mathcal{E}}(0)|e^{\bar{L}T_3(|\mathcal{E}(0)|)} + \left\{\bar{L}T_3(|\mathcal{E}(0)|)e^{\bar{L}T_3(|\mathcal{E}(0)|)}\right\}\{|\delta|_\infty\} \\ &\leq \ e^{T_3(|\mathcal{E}(0)|)-t}\left[\left|\hat{\mathcal{E}}(0)\right| e^{\bar{L}T_3(|\mathcal{E}(0)|)}\right. \\ &\quad \left. + \tfrac{1}{2}\bar{L}^2T_3^2(|\mathcal{E}(0)|)e^{2\bar{L}T_3(|\mathcal{E}(0)|)}\right] + \tfrac{1}{2}|\delta|_\infty^2 \end{aligned} \tag{A.10}$$

for all $t \in [0, T_3(|\mathcal{E}(0)|)]$, by applying the triangle inequality to the terms in curly braces in (A.10). The final ISS estimate in the original error variable $\mathcal{E} = (s-s_*, x-x_*)$ now follows from adding (A.7) and (A.10) (using (A.10) to upper bound the $|\hat{\mathcal{E}}_{T_3(|\mathcal{E}(0)|)}|_{[-\bar{\tau},0]}$ in the right side of (A.7), and the fact that $\hat{\mathcal{E}}(t)$ only depends on values of $\delta(r)$ for times $r \leq t$, which allows us to replace $|\delta|_\infty$ by $|\delta|_{[0,t]}$ throughout (A.7) and (A.10), to get an ISS estimate in the variable $\hat{\mathcal{E}}$ that is valid for all $t \geq 0$), and using the fact that $T_3 \in \mathcal{K}_\infty$ and the fact that there are constants $c_* > 0$ and $c_{**} > 0$ such that for all solutions of that $\mathcal{E}$ dynamics with initial states in $\mathcal{S}$, we have

$$|\mathcal{E}(t)| \leq c_{**}|\hat{\mathcal{E}}|_{[t-\bar{\tau},t]} \ \text{ for all } \ t \geq 0 \ \text{ and } \ |\hat{\mathcal{E}}(0)| \leq c_*|\mathcal{E}(0)| \, . \tag{A.11}$$

To find values for c_* and c_{**}, first note that for each $i \in \{1,2,\ldots,n\}$ and $t \geq 0$ and any global Lipschitz constant L_i for μ_i, the Mean Value Theorem estimate (46) and the constantness of the initial functions give

$$\begin{aligned} |\tilde{x}_i(t)| \ &= \ \left|\alpha_i(t)e^{\int_{t-\tau_i}^t(\mu_i(s_*)-\mu_i(s(\ell)))\mathrm{d}\ell} - x_{i*}\right| \\ &= \ \left|(\tilde{\alpha}_i(t)+x_{i*})e^{\int_{t-\tau_i}^t(\mu_i(s_*)-\mu_i(s(\ell)))\mathrm{d}\ell} - x_{i*}\right| \\ &\leq \ |\tilde{\alpha}_i(t)|e^{2\tau_i\mu_i(\bar{s}^\sharp)} + x_{i*}\left|e^{\int_{t-\tau_i}^t(\mu_i(s_*)-\mu_i(\ell))\mathrm{d}\ell} - 1\right| \\ &\leq \ |\tilde{\alpha}_i(t)|e^{2\tau_i\mu_i(\bar{s}^\sharp)} + x_{i*}L_ie^{2\mu_i(\bar{s}^\sharp)\bar{\tau}}\tau_i|\tilde{s}|_{[t-\tau_i,t]} \end{aligned} \tag{A.12}$$

and

$$\begin{aligned} |\tilde{\alpha}_i(0)| \ &= \ \left|x_i(0)e^{\tau_i(\mu_i(s(0))-\mu_i(s_*))} - x_{i*}\right| \\ &= \ \left|\tilde{x}_i(0)e^{\tau_i(\mu_i(s(0))-\mu_i(s_*))} + x_{i*}\left(e^{\tau_i(\mu_i(s(0))-\mu_i(s_*))} - 1\right)\right| \\ &\leq \ e^{2\mu_i(\bar{s}^\sharp)\tau_i}\left(|\tilde{x}_i(0)| + x_{i*}L_i\tau_i|\tilde{s}(0)|\right). \end{aligned} \tag{A.13}$$

Then we can check that we can choose

$$\begin{aligned} c_{**} &= 1 + ne^{2\bar{\tau}\max_i \mu_i(\bar{s}^\sharp)} + n\bar{\tau}\max_i\left\{L_ix_{i*}e^{2\tau_i\mu_i(\bar{s}^\sharp)}\right\} \ \text{ and} \\ c_* &= 1 + n\max_i\left\{e^{2\tau_i\mu_i(\bar{s}^\sharp)}x_{i*}L_i\tau_i\right\} + ne^{2\bar{\tau}\max_i \mu_i(\bar{s}^\sharp)}, \end{aligned} \tag{A.14}$$

where the maxima are over all $i \in \{1,2,\ldots,n\}$; this can be checked by comparing the formulas for the components of $\mathcal{E}$ and $\hat{\mathcal{E}}$. This proves the theorem.

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Received xxxx 20xx; revised xxxx 20xx.

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