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# A mathematical model of anaerobic digestion with syntrophic relationship, substrate inhibition and distinct removal rates \*

Radhouane Fekih-Salem<sup>†,‡</sup>, Yessmine Daoud<sup>‡</sup>, Nahla Abdellatif<sup>‡,§</sup>, and Tewfik Sari<sup>¶</sup>

**Abstract.** Understanding and exploiting the syntrophic relationship between microbial species is a major challenge in the mathematical theory of the anaerobic digestion process. In this work, we focus on the acetogenesis and hydrogenotrophic methanogenesis phases and we include distinct removal rates for the species. Our study gives a quite comprehensive analysis of a syntrophic model by analyzing the joined effects of syntrophy relationship, mortality, substrate inhibition and input concentrations that were neglected in previous studies. The mathematical analysis of the model involving the mortality is a difficult problem since the model is not reduced to a planar system as in the case where the dilution rates of the substrates and the removal rates of microbial species are equal. Using general nonmonotonic growth rates, the necessary and sufficient conditions of existence and local stability of all steady states of the four-dimensional system are determined, according to the operating parameters. This general model exhibits a rich behavior with the coexistence of two microbial species, the bistability, the multiplicity of coexistence steady states, and the existence of two steady states of extinction of the first species. The operating diagram shows how the model behaves by varying the control parameters and illustrates the effect of the substrate inhibition and the new input substrate concentration (hydrogen) on the appearance or the disappearance of coexistence and bistability regions. Similarly to the classical chemostat model, including the substrate inhibition can destabilize a two-tiered microbial ‘food chain’, where the asymptotic behavior of the system depends on the initial condition.

**Key words.** Anaerobic digestion, chemostat, syntrophy, inhibition, bistability, operating diagram

**AMS subject classifications.** 34A34, 34D20, 37N25, 92B05

**1. Introduction.** Anaerobic Digestion (AD) is a process used for the biological treatment of municipal, agricultural and industrial wastes with the additional benefit of producing energy in the form of biogas. During this process, the waste is first partially transformed into volatile fatty acids and then converted into methane and carbon dioxide, which can be used as a carbon source for microalgae [30]. AD process is too complex with difficulty to collect informative experimental data which complicates the model validation and the parameter identification [15]. The generic AD Model No.1 (ADM1) of the IWA Task Group for Mathematical Modeling of AD Processes is characterized by its extreme complexity with 32 dynamic concentration state variables and a large number of parameters [3].

Many mathematical models describing the whole process or some key steps have been considered in the last three decades; see [5, 7, 10, 17, 21, 25, 40, 41, 42, 49, 51, 52, 53]. A synthetic and unified vision of many models involving two or three cross-feeding species and various types of inhibition has been proposed in [14]. Using specific growth functions, the numerical simulations reveal the reduction in both productivity and stability due to inhibitions with the occurrence of stable periodic orbits owing to the presence of negative and positive feedback loops. In [25], a mathematical analysis of the protein-rich Microalgae AD model (the so-called MAD) shows the process behavior according to the control parameters where the operating diagram illustrates the ideal conditions to optimize biogas yield and ammonia toxicity. In fact, the MAD model has been proposed in [28] and was validated from experimental data of an AD process of *Chlorella vulgaris* microalgae involving four substrates and three microbial species with three reactions and two steps (hydrolysis-acetogenesis and methanogenesis).

Recently, a complete mathematical analysis was provided in [31] of a two-step model (acidogenesis and methanogenesis) introduced in [9] where a fifth state variable (ammonia) is included. The decay and the inhibition caused by ammonia were taken into account by considering a general class of response functions. In [52, 53], an eight-dimensional mathematical model describing three of the

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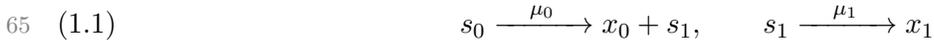
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46 four main stages of AD (acidogenesis, acetogenesis, and methanogenesis) was analyzed by considering  
 47 syntrophy and substrate inhibition effects. Following [51] and using general functional responses, a  
 48 three-tiered microbial food-web model was studied in [41] discovering the emergence of the coexistence  
 49 region in the operating diagram where a stable limit cycle is born via the Hopf bifurcation, which has  
 50 not been reported by [51]. The work of [41] has been recently extended in [34, 35] by considering the  
 51 effects of the phenol and hydrogen input concentrations, together with the effects of maintenance (or  
 52 decay) terms.

53 Using a step by step parameter identification procedure, Bernard et al. [7] have proposed and have  
 54 validated a reduced two-step model (the so-called AM2) from experimental data of the AD process.  
 55 This model has a cascade structure and has been widely applied for control and optimization of AD  
 56 process [21, 42, 43, 44]. Using a maximum likelihood principal component analysis [27] and generated  
 57 data built from ADM1 model, the appropriate number of reactions is determined by a systematic  
 58 data driven-approach followed by a parameter identification procedure [22]. The resulting low-order  
 59 model is the two-tiered microbial ‘food chain’ leading to perfectible direct and cross-validation results.  
 60 The AM2 model was mathematically studied in [5, 38] and was extended in [4, 6], where a fifth state  
 61 variable (SMP: Soluble Microbial Products), important for fouling of membranes, is included. For  
 62 a review of mathematical modeling of anaerobic digestion with respect to theory, applications and  
 63 technologies, the reader is referred to [50].

64 The two-tiered microbial model we consider here describes the next two biological reactions:



66 where a substrate  $s_0$  (Volatile Fatty Acid) is consumed by a biomass  $x_0$  (acetogenic bacteria) to produce  
 67 a product  $s_1$  (hydrogen). The substrate  $s_1$  is consumed in the second reaction by another biomass  
 68  $x_1$  (hydrogenotrophic methanogenic bacteria).  $\mu_0$  and  $\mu_1$  are the bacterial growth rates, depending  
 69 eventually on one or both substrates. The substrates  $s_0$  and  $s_1$  are introduced in the reactor with the  
 70 inflowing concentrations  $s_0^{in}$  and  $s_1^{in}$ , respectively, and a dilution rate  $D$ . These reactions are described  
 71 by the following system of differential equations

$$72 \quad (1.2) \quad \begin{cases} \dot{s}_0 &= D(s_0^{in} - s_0) - \mu_0(\cdot)x_0, \\ \dot{x}_0 &= (\mu_0(\cdot) - D_0)x_0, \\ \dot{s}_1 &= D(s_1^{in} - s_1) + \mu_0(\cdot)x_0 - \mu_1(\cdot)x_1, \\ \dot{x}_1 &= (\mu_1(\cdot) - D_1)x_1, \end{cases}$$

73 where  $D_0$  and  $D_1$  represent, respectively, the disappearance rates of acetogenic and methanogenic  
 74 bacteria. In this study, the two-tiered model (1.2) is analyzed where  $D_i$  can be modeled as in [29, 45]  
 75 by

$$76 \quad (1.3) \quad D_i = \alpha_i D + a_i, \quad i = 0, 1,$$

77 where the nonnegative death (or decay) rate parameters  $a_0$  and  $a_1$  are taken into consideration with  
 78 units of the dilution rate ( $D$  has units 1/d). These decay terms included in model (1.2) are related  
 79 to consumption of energy, other than growth; see for instance [23] or [33]. The coefficients  $\alpha_0$  and  $\alpha_1$   
 80 belong to  $[0, 1]$  and represent, respectively, the first and the second biomass proportion that leaves the  
 81 reactor. For example, in [7] these coefficients are proposed to model a biomass reactor attached to the  
 82 support or to decouple the residence time of solids and the hydraulic residence time ( $1/D$ ). Thus, the  
 83 study will not be restricted to the case  $\alpha_i = 1$ ,  $i = 0, 1$ , as in most of the studies in the literature (see  
 84 Tables 1 and 2 below), and the case  $0 \leq \alpha_i \leq 1$ , which is of biological interest, will be investigated.

85 If the growth rate  $\mu_0$  depends only on substrate  $s_0$  and  $\mu_1$  depends only on  $s_1$ , that is,

$$86 \quad (1.4) \quad \mu_0(\cdot) = \mu_0(s_0), \quad \mu_1(\cdot) = \mu_1(s_1),$$

87 then system (1.2) has a cascade structure and describes a commensalistic relationship where the  
 88 commensal species  $x_1$  needs the first species  $x_0$  to grow, while  $x_0$  can grow without  $x_1$  and it is not

89 affected by the growth of the commensal species  $x_1$ . If  $\mu_0$  depends on both substrates  $s_0$  and  $s_1$ , and  
 90  $\mu_1$  depends on substrate  $s_1$ , that is,

$$91 \quad (1.5) \quad \mu_0(\cdot) = \mu_0(s_0, s_1), \quad \mu_1(\cdot) = \mu_1(s_1),$$

92 then system (1.2) describes a syntrophic relationship where two microbial species depend on each  
 93 other for survival by the production of a required substrate  $s_1$ . In this case, each species benefits from  
 94 the presence of the other species. Tables 1 and 2 summarize the modeling assumptions made in the  
 95 literature on two-tiered model (1.2) describing the commensalistic and the syntrophic relationships,  
 96 respectively, according to the input concentration  $s_1^{in}$ , the removal rates  $D_i$ , and the choice of the  
 growth functions.

**Table 1**

*Literature examples of the commensalistic relationship of two-tiered model (1.2), the modeling assumptions and the description of the growth rates (1.4).*

References	$s_1^{in}$	$D_i$	$\mu_0(s_0)$	$\mu_1(s_1)$
Reilly [37],	0	$D$	Monod	Monod
Simeonov and Stoyanov [47]	0	$D + a_i$	Monod	Monod
Stephanopoulos [48]	0	$D$	Monotonic	Monotonic or Nonmonotonic
Bernard et al. [7]	$\geq 0$	$\alpha D$	Monod	Haldane
Simeonov and Diop [46]	0	$D$	Monod or Contois	Haldane
Sbarciog et al. [42]	$\geq 0$	$D$	Monotonic	Nonmonotonic
Benyahia et al. [5]	$\geq 0$	$\alpha D$	Monotonic	Nonmonotonic

**Table 2**

*Literature examples of the syntrophic relationship of two-tiered model (1.2), the modeling assumptions and the description of the growth rates (1.5).*

References	$s_1^{in}$	$D_i$	$\mu_0(s_0, s_1)$	$\mu_1(s_1)$ or $\mu_1(s_0, s_1)$
Kreikenbohm and Bohl [26]	0	$D$	Monod in $s_0$ , decreasing in $s_1$	Monod
Burchard [10], El-Hajji et al. [16]	0	$D$	Increasing in $s_0$ , decreasing in $s_1$	Increasing
Xu et al. [54]	0	$D + a_i$	Increasing in $s_0$ , decreasing in $s_1$	Monod
Sari et al. [39]	$\geq 0$	$D$	Increasing in $s_0$ , decreasing in $s_1$	Decreasing in $s_0$ , increasing in $s_1$
Harvey et al. [24]	0	$D$	Increasing in $s_0$ , decreasing in $s_1$	Nonmonotonic
Sari and Harmand [40]	0	$D + a_i$	Increasing in $s_0$ , decreasing in $s_1$	Increasing
Fekih et al. [18]	0	$D + a_i$	Increasing in $s_0$ , decreasing in $s_1$	Nonmonotonic
Daoud et al. [11]	$\geq 0$	$D + a_i$	Increasing in $s_0$ , decreasing in $s_1$	Increasing

97  
 98 Harvey et al. [24] have studied model (1.2) in the particular case where  $s_1^{in} = 0$ ,  $D_i = D$ , and  
 99 the growth rate  $\mu_0(s_0, s_1) = f(s_0).g(s_1)$  with  $f$  is increasing in  $s_0$  and  $g$  is decreasing in  $s_1$ . Our  
 100 study provides an extension of the results in [24] to the case where  $D_1$  and  $D_2$  are distinct from  
 101  $D$ . Notice that most of the studies in the existing literature (see Table 2) consider the case of equal  
 102 removal rates ( $D_1 = D_2 = D$ ), where the model can be reduced to a two-dimensional system. In  
 103 this paper, we generalize [10, 16, 24, 26], by allowing distinct removal rates. In this case, the study  
 104 of the stability is much more delicate and requires the Liénard-Chipart stability criteria [20] for a  
 105 four-dimensional system. Furthermore, it is reported in the literature [5, 7, 18, 24, 42, 46, 48] that at  
 106 many times the second reaction of (1.1) is inhibited by large values of  $s_1$ , which instigates to consider a  
 107 Haldane-type growth function for  $\mu_1$ . The goal of the present work is to understand the joined effects  
 108 of syntrophy, mortality of two microbial species, substrate inhibition on their growth and inflowing  
 109 substrate concentration of the second species, which have not been studied in the literature. Moreover,  
 110 here, we do not specify kinetics but we consider qualitative properties on the growth functions and we  
 111 assume that the second species is inhibited when the concentration of substrate becomes significant.  
 112 The particular case  $s_1^{in} = 0$  was considered in [18]. The case where  $\mu_1$  does not present inhibition was  
 113 considered in [11, 40, 54].

114 On the other hand, our study provides an important tool for the experimentation which is the  
 115 operating diagram showing the behavior of the syntrophic model (1.2) according to the control param-  
 116 eters  $D$ ,  $s_0^{in}$  and  $s_1^{in}$ , when all biological parameters are fixed. This operating diagram is often studied

numerically or theoretically both in the biological literature [36, 42, 51, 54] and the mathematical literature [1, 2, 11, 12, 13, 18, 19, 23, 25, 32, 38, 40, 41, 52, 53].

This paper is organized as follows: in section 2, we present the assumptions made on the growth functions and give some preliminary results. Section 3 is devoted to the analysis of steady states and their local stability. In section 4, we present the operating diagrams which depict the different outcomes of the model according to control parameters. Finally, some conclusions are drawn in section 5. The definition domains of some auxiliary functions used for the description of the steady states with their conditions of existence and stability are given in Appendix A. The proofs of all results are reported in Appendix B. With specific growth rates satisfying the general assumptions, the maximal number of solutions of an equation which determines some definition domains are given in Appendix C. Finally, some tables are given in Appendix D.

**2. Mathematical model and assumptions.** In what follows, we study model (1.2) where the removal rates  $D_i$  and the growth rates  $\mu_i$ ,  $i = 0, 1$  are given by (1.3) and (1.5), respectively. Thus, the syntrophic model can be written as follows

$$(2.1) \quad \begin{cases} \dot{s}_0 &= D(s_0^{in} - s_0) - \mu_0(s_0, s_1)x_0, \\ \dot{x}_0 &= (\mu_0(s_0, s_1) - D_0)x_0, \\ \dot{s}_1 &= D(s_1^{in} - s_1) + \mu_0(s_0, s_1)x_0 - \mu_1(s_1)x_1, \\ \dot{x}_1 &= (\mu_1(s_1) - D_1)x_1. \end{cases}$$

We first make the following general assumptions on the bacterial growth rates. The functions  $\mu_0$  and  $\mu_1$  belong to  $\mathcal{C}^1(\mathbb{R}^+, \mathbb{R}^+)$  and  $\mathcal{C}^1(\mathbb{R}^+)$ , respectively and verify:

*Hypothesis 2.1.* Growth of species  $x_0$  can take place if and only if the substrate  $s_0$  is present:  $\mu_0(0, s_1) = 0$ ,  $0 < \mu_0(s_0, s_1) < +\infty$ , for all  $s_0 > 0$  and  $s_1 \geq 0$ .

*Hypothesis 2.2.* Growth of species  $x_1$  can take place if and only if the substrate  $s_1$  is present:  $\mu_1(0) = 0$  and  $\mu_1(s_1) > 0$ , for all  $s_1 > 0$ .

*Hypothesis 2.3.* Growth rate of species  $x_0$  is favored by  $s_0$  and is inhibited by the substrate  $s_1$ :  $\frac{\partial \mu_0}{\partial s_0}(s_0, s_1) > 0$  and  $\frac{\partial \mu_0}{\partial s_1}(s_0, s_1) < 0$ , for all  $s_0 > 0$  and  $s_1 > 0$ .

*Hypothesis 2.4.* The nonmonotonic growth function  $\mu_1$  takes into account the growth-limiting for low concentrations of substrate  $s_1$  and the growth-inhibiting for high concentrations:  $\mu_1(s_1)$  reaches a maximum value  $\mu_1^{max} := \mu_1(s_1^{max})$  at  $s_1 = s_1^{max}$  and satisfies  $\mu_1'(s_1) > 0$ , for all  $s_1 \in [0, s_1^{max})$ ,  $\mu_1'(s_1) < 0$ , for all  $(s_1^{max}, +\infty)$  and  $\mu_1(+\infty) = 0$ .

*Hypothesis 2.5.* The maximum growth rate of the species  $x_0$  decreases with the concentration of substrate  $s_1$ : for all  $s_1 > 0$ ,  $\bar{\mu}_0'(s_1) < 0$  where  $\bar{\mu}_0(s_1) := \sup_{s_0 \geq 0} \mu_0(s_0, s_1)$ .

The following result proves that syntrophic model (2.1) preserves the biological significance where all solutions of the system are nonnegative and bounded for any nonnegative initial condition.

**Proposition 2.6.** *For any nonnegative initial condition, the solution of system (2.1) exists for all nonnegative times, remains nonnegative and is positively bounded. In addition, the set*

$$\Omega = \left\{ (s_0, x_0, s_1, x_1) \in \mathbb{R}_+^4 : 2s_0 + x_0 + s_1 + x_1 \leq \frac{D}{D_{\min}} (2s_0^{in} + s_1^{in}) \right\},$$

where  $D_{\min} = \min(D, D_0, D_1)$ , is positively invariant and a global attractor for (2.1).

**3. Analysis of the syntrophic model.** A steady state exists if and only if all its components are nonnegative. Model (2.1) can have at most six steady states, which we denote as follows:

- $SS_0$  ( $x_0 = x_1 = 0$ ): the washout of both species.
- $SS_1$  ( $x_1 = 0, x_0 > 0$ ): species  $x_1$  is extinct while species  $x_0$  survives.
- $SS_2^i$ ,  $i = 1, 2$  ( $x_0 > 0, x_1 > 0$ ): both species are maintained.
- $SS_3^i$ ,  $i = 1, 2$  ( $x_0 = 0, x_1 > 0$ ): species  $x_0$  is extinct while species  $x_1$  survives.

We show below that all steady states are unique, if they exist. However, bifurcations may occur (see Table 8) where two steady states collide, giving rise to a non hyperbolic steady state. First, we

157 introduce in [Table 3](#) the auxiliary functions for determining the existence and stability conditions.  
 158 Some comments and details on their definition domains are given in [Appendix A](#). In the particular  
 159 case of specific growth rates of Monod-type with hydrogen inhibition and of Haldane-type [\(C.1\)](#), the  
 auxiliary functions defined in [Table 3](#) can be calculated analytically and are given in [Table 12](#).

**Table 3**

*Auxiliary functions where  $\text{dom}(F_0)$  and  $I_j$ ,  $j = 1, 2$  are given in [Table 9](#).*

	Definition
$s_0 = M_0(y, s_1)$	Let $s_1 \geq 0$ . $s_0 = M_0(y, s_1)$ is the unique solution of equation $y = \mu_0(s_0, s_1)$ . It is defined for $y \in [0, \bar{\mu}_0(s_1)]$
$s_1 = M_1^1(y)$	$s_1 = M_1^1(y)$ is the unique solution in $[0, s_1^{max}]$ of equation $y = \mu_1(s_1)$ . It is defined for $y \in [0, \mu_1^{max}]$ .
$s_1 = M_1^2(y)$	$s_1 = M_1^2(y)$ is the unique solution in $[s_1^{max}, +\infty)$ of equation $y = \mu_1(s_1)$ . It is defined for $y \in (0, \mu_1^{max}]$ .
$F_0(D, s_1^{in})$	$F_0(D, s_1^{in}) = M_0(\alpha_0 D + a_0, s_1^{in})$ defined for $(D, s_1^{in}) \in \text{dom}(F_0)$
$F_1^j(D)$	$F_1^j(D) = M_0(\alpha_0 D + a_0, M_1^j(\alpha_1 D + a_1))$ , $D \in I_j$
$F_2^j(D)$	$F_2^j(D) = M_1^j(\alpha_1 D + a_1) + F_1^j(D)$ , $D \in I_j$

160  
 161 The following result gives all the steady states of [\(2.1\)](#) and the necessary and sufficient condi-  
 162 tions of their existence and stability. For convenience, we shall use the abbreviation LES for Locally  
 163 Exponentially Stable.

164 **Proposition 3.1.** *Assume that [Hypotheses 2.1](#) to [2.4](#) hold. Then, the six steady states of [\(2.1\)](#) are*  
 165 *given in [Table 4](#). The conditions of their existence and stability are given in [Table 5](#).*

**Table 4**

*Steady states of [\(2.1\)](#). All functions are defined in [Table 3](#).*

	$s_0, s_1$ components	$x_0, x_1$ components
SS <sub>0</sub>	$s_0 = s_0^{in}, s_1 = s_1^{in}$	$x_0 = 0, x_1 = 0$
SS <sub>1</sub>	$s_0$ is a solution of equation $\mu_0(s_0, s_0^{in} + s_1^{in} - s_0) = D_0$ $s_1 = s_0^{in} + s_1^{in} - s_0$	$x_0 = \frac{D}{D_0} (s_0^{in} - s_0)$ $x_1 = 0$
SS <sub>2</sub> <sup>j</sup>	$s_0 = F_1^j(D)$ $s_1 = M_1^j(D_1)$	$x_0 = \frac{D}{D_0} (s_0^{in} - s_0)$ $x_1 = \frac{D}{D_1} (s_0^{in} + s_1^{in} - s_0 - s_1)$
SS <sub>3</sub> <sup>j</sup>	$s_0 = s_0^{in}$ $s_1 = M_1^j(D_1)$	$x_0 = 0$ $x_1 = \frac{D}{D_1} (s_1^{in} - M_1^j(D_1))$

**Table 5**

*Necessary and sufficient conditions of existence and local stability of steady states of model [\(2.1\)](#).*

	Existence condition	Stability condition
SS <sub>0</sub>	always exists	$s_0^{in} < F_0(D, s_1^{in})$ and $(s_1^{in} < M_1^1(D_1)$ or $s_1^{in} > M_1^2(D_1))$
SS <sub>1</sub>	$s_0^{in} > F_0(D, s_1^{in})$	$s_0^{in} + s_1^{in} < F_2^1(D)$ or $s_0^{in} + s_1^{in} > F_2^2(D)$
SS <sub>2</sub> <sup>1</sup>	$s_0^{in} > \max(F_1^1(D), F_2^1(D) - s_1^{in})$	LES whenever it exists
SS <sub>2</sub> <sup>2</sup>	$s_0^{in} > \max(F_1^2(D), F_2^2(D) - s_1^{in})$	Always unstable
SS <sub>3</sub> <sup>1</sup>	$s_1^{in} > M_1^1(D_1)$ ,	$s_0^{in} < F_1^1(D)$
SS <sub>3</sub> <sup>2</sup>	$s_1^{in} > M_1^2(D_1)$ ,	Always unstable

166 **Remark 3.2.** Since the function  $F_0(D, s_1^{in})$  is defined for  $(D, s_1^{in}) \in \text{dom}(F_0)$  (see [Proposition A.1](#)),  
 167 the condition  $s_0^{in} > F_0(D, s_1^{in})$  means that  $(D, s_1^{in}) \in \text{dom}(F_0)$  and the inequality is satisfied. Con-  
 168 versely, if  $(D, s_1^{in}) \notin \text{dom}(F_0)$ , we let  $F_0(D, s_1^{in}) = +\infty$ . Thus, the condition  $s_0^{in} < F_0(D, s_1^{in})$  means  
 169 that  $(D, s_1^{in}) \notin \text{dom}(F_0)$  or the inequality is satisfied and  $(D, s_1^{in}) \in \text{dom}(F_0)$ . Similarly, the condi-  
 170 tion  $s_1^{in} > M_1^j(D_1)$  means that  $D \in \bar{I}_j$ ,  $j = 1, 2$  and the inequality is satisfied, while the condition  
 171  $s_1^{in} < M_1^j(D_1)$  means  $D \notin \bar{I}_j$  or the inequality is satisfied and  $D \in \bar{I}_j$ . The other conditions involving  
 172 functions  $F_i^j(D)$ ,  $i, j = 1, 2$ , follow similarly.

173 As we will see in [Proposition 4.5](#), the limit case  $D = \bar{D}_1$  corresponds to saddle-node bifurcations  
 174 of SS<sub>2</sub><sup>1</sup> with SS<sub>2</sub><sup>2</sup> and SS<sub>3</sub><sup>1</sup> with SS<sub>3</sub><sup>2</sup> where these steady states are non hyperbolic. In the particular case

175  $s_1^{in} = 0$ , we obtain the same result as in [18, 40] where  $SS_3^1$  and  $SS_3^2$  do not exist since the conditions  
 176 of their existence in Table 5 are not satisfied. Compared to [40], a main change in the existence of  
 177 steady states of our model (2.1) is the appearance of the second positive steady state  $SS_2^2$  and two  
 178 steady states  $SS_3^1$  and  $SS_3^2$ .

179 **4. Operating diagrams.** The operating diagram is a very useful tool to determine the asymptotic  
 180 behavior of the process with respect to the control parameters  $D$ ,  $s_0^{in}$  and  $s_1^{in}$  which are the most easily  
 181 parameters to manipulate in a chemostat. All other parameters are fixed since they have biological  
 182 meaning and cannot be easily manipulated by the biologist. The biological parameter values used in  
 183 all figures are provided in Table 13. To construct the operating diagram, we first define in Table 6 the  
 184 set of surfaces  $\Gamma = \{\gamma_0, \gamma_i^j, \gamma_4, i = 1, 2, 3, j = 1, 2\}$  which are the boundaries of different regions of the  
 185  $(D, s_0^{in}, s_1^{in})$ -space. We define also in Table 6 the curve  $\mathcal{C}_j$  of the function  $y = M_1^j(D_1) - s_1^{in}$ ,  $j = 1, 2$   
 186 to determine its sign according to  $s_1^{in}$  and  $D$ . As we will see in Propositions 4.2 to 4.4, if  $D$  is fixed  
 187 in  $\bar{I}_j$ , then  $s_1^{in} = s_{1j}^{in*} = M_1^j(\alpha_1 D + a_1)$  and if  $s_1^{in}$  is fixed, the equation  $M_1^j(\alpha_1 D + a_1) = s_1^{in}$  can have  
 188 a unique solution  $D = D_j^*$  with  $j = 1, 2$ . As stated in the following result, the surfaces in the set  $\Gamma$   
 189 separate the operating space  $(D, s_0^{in}, s_1^{in})$  into twelve regions, denoted  $\mathcal{J}_k$ ,  $k = 1, \dots, 12$ , and defined  
 in Table 7.

Table 6

The set of surfaces  $\Gamma$ , the curves  $\mathcal{C}_1$  and  $\mathcal{C}_2$ , and the corresponding colors in Figures 1 and 3 to 6.

$\Gamma$ , $\mathcal{C}_1$ and $\mathcal{C}_2$	Color
$\gamma_0 = \{(D, s_0^{in}, s_1^{in}) : s_0^{in} = F_0(D, s_1^{in}), (D, s_1^{in}) \in \text{dom}(F_0)\}$	Black
$\gamma_1^1 = \{(D, s_0^{in}, s_1^{in}) : s_0^{in} = F_1^1(D), D \in I_1\}$	Cyan
$\gamma_1^2 = \{(D, s_0^{in}, s_1^{in}) : s_0^{in} = F_1^2(D), D \in I_2\}$	Green
$\gamma_2^1 = \{(D, s_0^{in}, s_1^{in}) : s_0^{in} = F_2^1(D) - s_1^{in}, D \in I_1\}$	Red
$\gamma_2^2 = \{(D, s_0^{in}, s_1^{in}) : s_0^{in} = F_2^2(D) - s_1^{in}, D \in I_2\}$	Blue
$\gamma_3^1 = \{(D, s_0^{in}, s_1^{in}) : s_1^{in} = M_1^1(D_1), D \in \bar{I}_1\}$	Pink
$= \{(D, s_0^{in}, s_1^{in}) : D = D_1^*\} = \{(D, s_0^{in}, s_1^{in}) : s_1^{in} = s_{11}^{in*}, D \in \bar{I}_1\}$	
$\gamma_3^2 = \{(D, s_0^{in}, s_1^{in}) : s_1^{in} = M_1^2(D_1), D \in \bar{I}_2\}$	Violet
$= \{(D, s_0^{in}, s_1^{in}) : D = D_2^*\} = \{(D, s_0^{in}, s_1^{in}) : s_1^{in} = s_{12}^{in*}, D \in \bar{I}_2\}$	
$\gamma_4 = \{(D, s_0^{in}, s_1^{in}) : D = \bar{D}_1\}$	Coral
$\mathcal{C}_1$ : curve of the function $y = M_1^1(D_1) - s_1^{in}$ , $D \in \bar{I}_1$	Magenta
$\mathcal{C}_2$ : curve of the function $y = M_1^2(D_1) - s_1^{in}$ , $D \in \bar{I}_2$	Brown

190

191 **Proposition 4.1.** Assume that Hypotheses 2.1 to 2.5 hold. The existence and the stability of the  
 192 steady states of (2.1) in the twelve regions  $\mathcal{J}_k$ ,  $k = 1, \dots, 12$  of the operating diagram are determined  
 193 in Table 7.

Table 7

Existence and stability of steady states in the regions of the operating diagram. The letter S (resp. U) means that the corresponding steady state is LES (resp. unstable). No letter means that the steady state does not exist.

Condition 1	Condition 2	Region	Color	SS <sub>0</sub>	SS <sub>1</sub>	SS <sub>2</sub> <sup>1</sup>	SS <sub>2</sub> <sup>2</sup>	SS <sub>3</sub> <sup>1</sup>	SS <sub>3</sub> <sup>2</sup>
$s_1^{in} < M_1^1(D_1)$	$s_0^{in} < F_0(D, s_1^{in})$	$\mathcal{J}_1$	Cyan	S					
	$F_0(D, s_1^{in}) < s_0^{in} < F_2^1(D) - s_1^{in}$	$\mathcal{J}_2$	Green	U	S				
	$F_2^1(D) - s_1^{in} < s_0^{in} < F_2^2(D) - s_1^{in}$	$\mathcal{J}_3$	Red	U	U	S			
	$s_0^{in} > F_2^2(D) - s_1^{in}$	$\mathcal{J}_4$	Yellow	U	S	S	U		
$M_1^1(D_1) < s_1^{in} < M_1^2(D_1)$	$s_0^{in} > F_2^2(D) - s_1^{in}$	$\mathcal{J}_5$	Yellow	U	S	S	U	U	
	$F_0(D, s_1^{in}) < s_0^{in} < F_2^2(D) - s_1^{in}$	$\mathcal{J}_6$	Red	U	U	S		U	
	$F_1^1(D) < s_0^{in} < F_0(D, s_1^{in})$	$\mathcal{J}_7$	Red	U		S		U	
	$s_0^{in} < F_1^1(D)$	$\mathcal{J}_8$	Blue	U				S	
$M_1^2(D_1) < s_1^{in}$	$s_0^{in} < F_1^1(D)$	$\mathcal{J}_9$	Deep pink	S				S	U
	$F_1^1(D) < s_0^{in} < F_1^2(D)$	$\mathcal{J}_{10}$	Gray	S		S		U	U
	$F_1^2(D) < s_0^{in} < F_0(D, s_1^{in})$	$\mathcal{J}_{11}$	Gray	S		S	U	U	U
	$s_0^{in} > F_0(D, s_1^{in})$	$\mathcal{J}_{12}$	Yellow	U	S	S	U	U	U

194

Since the definition domain of the function  $F_i^j$  is  $I_j$  where  $D \leq \bar{D}_1$  with  $\Phi_j(D) > 0$  (see Appen-

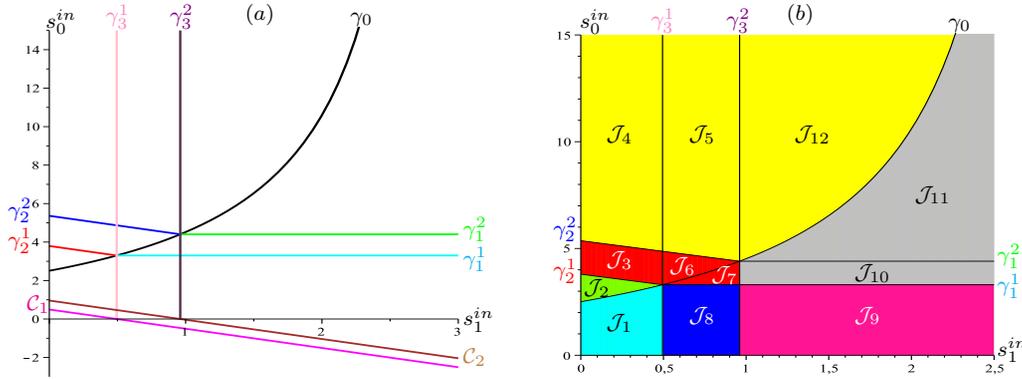
195 dix A), it's necessary to distinguish the following two cases according to the sign of  $\Phi_j(\bar{D}_1)$ :

196 (4.1) case 1:  $\Phi_j(\bar{D}_1) > 0$ , case 2:  $\Phi_j(\bar{D}_1) \leq 0$ .

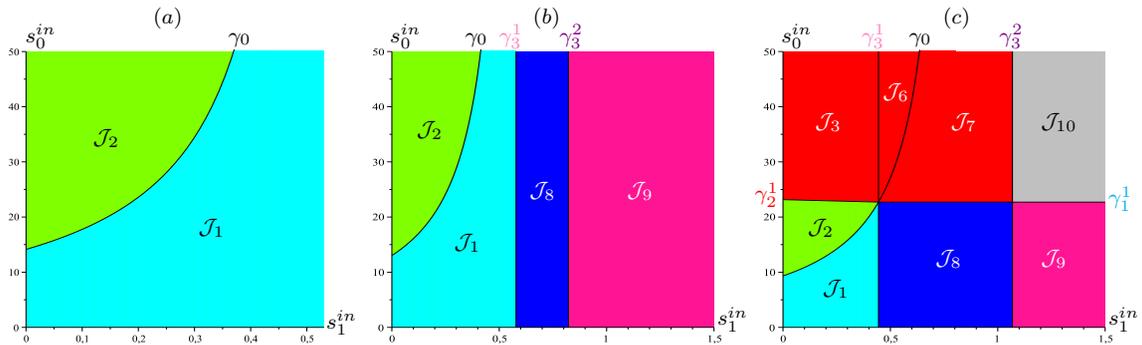
197 Note that, the condition of case 1 is equivalent to  $(\bar{\mu}_0(s_1^{max}) - a_0)/\alpha_0 > \bar{D}_1$  while the opposite  
198 inequality holds in case 2.

199 Since it is very difficult to observe the twelve regions of the operating diagram in three-dimensional  
200 space, it would be much better to illustrate cuts along two-dimensional planes by fixing one of the  
201 three operating parameters in order to have a better vision and understanding. In subsection 4.1, we  
202 study the operating diagrams in the  $(s_1^{in}, s_0^{in})$  plane where  $D$  is fixed. In subsection 4.2, we determine  
203 the operating diagrams in the  $(D, s_0^{in})$  plane where  $s_1^{in}$  is kept constant.

204 **4.1. Operating diagrams in the  $(s_1^{in}, s_0^{in})$  plane when  $D$  fixed.** The intersection of the surface  
205  $\gamma_0$  with the  $(s_1^{in}, s_0^{in})$  plane where  $D$  is kept constant is a curve of a function of  $s_1^{in}$ . However, the  
206 intersections of the surfaces  $\gamma_i^j$ ,  $i = 1, 2, 3$ ,  $j = 1, 2$  with this plane are straight lines (see Table 10).  
207 The various regions of the operating diagram are then very clear to visualize it. To study the operating  
208 diagram when  $D$  is fixed, we need the following result which determines the relative positions of the  
curve  $\gamma_0$  with the straight lines  $\gamma_i^j$ ,  $i, j = 1, 2$  according to the values of  $s_1^{in}$  and  $s_{1j}^{in*}$ .



**Figure 1.** (a) The curves  $C_1$ ,  $C_2$  and those of  $\Gamma$  in the case  $D \in I_2 = [0, \bar{D}_1 \simeq 1.165)$  where  $D = 1.1 < \min(\bar{D}_1, \bar{D}_0(0) \simeq 2.556)$ ,  $s_1^{in} = s_{11}^{in*} \simeq 0.495$  and  $s_1^{in} = s_{12}^{in*} \simeq 0.961$  and Case 1 of (4.1) holds. (b) The corresponding operating diagram in the  $(s_1^{in}, s_0^{in})$  plane.



**Figure 2.** Operating diagrams in the  $(s_1^{in}, s_0^{in})$  plane with  $D$  constant where case 2 of (4.1) holds: (a)  $\bar{D}_1 \simeq 1.856 < D = 1.857 < \bar{D}_0(0) \simeq 2.21$ , (b)  $\hat{D}_1 \simeq 1.829 < D = 1.83 < \bar{D}_1$ , (c)  $\bar{D}_1 \simeq 1.285 < D = 1.7 < \hat{D}_1$ .

209  
210 **Proposition 4.2.** Let  $D \in \bar{I}_j$ . We have  $s_{1j}^{in*} := M_1^j(D_1) \geq 0$ ,  $j = 1, 2$  such that  $s_{11}^{in*} < s_{12}^{in*}$ . For all  
211  $D \in I_1$ , the three curves  $\gamma_0$ ,  $\gamma_1^1$  and  $\gamma_2^1$  intersect at the same point  $s_1^{in} = s_{11}^{in*}$  (see Figures 1 and 2(c))  
212 such that  $s_{11}^{in*} < \bar{s}_1^{in}$  where  $\bar{s}_1^{in}$  is the unique solution of  $\bar{D}_0(s_1^{in}) = D$ . For all  $s_1^{in} \in [0, s_{11}^{in*})$ ,

213 (4.2) 
$$F_0(D, s_1^{in}) < F_1^1(D) < F_2^1(D) - s_1^{in}.$$

214 and for all  $s_1^{in} \in (s_{11}^{in*}, \bar{s}_1^{in})$ ,

215 (4.3) 
$$F_0(D, s_1^{in}) > F_1^1(D) > F_2^1(D) - s_1^{in}.$$

216 For all  $D \in I_2$ , the three curves  $\gamma_0$ ,  $\gamma_1^2$  and  $\gamma_2^2$  intersect at the same point  $s_1^{in} = s_{12}^{in*}$  (see [Figure 1](#))  
 217 such that  $s_{12}^{in*} < \bar{s}_1^{in}$ . For all  $s_1^{in} \in [0, s_{12}^{in*})$ ,

$$218 \quad (4.4) \quad F_0(D, s_1^{in}) < F_1^2(D) < F_2^2(D) - s_1^{in},$$

219 and for all  $s_1^{in} \in (s_{12}^{in*}, \bar{s}_1^{in})$ ,

$$220 \quad (4.5) \quad F_0(D, s_1^{in}) > F_1^2(D) > F_2^2(D) - s_1^{in}.$$

221 According to the position of  $D$  relatively to the critical values  $\tilde{D}_i$ ,  $\hat{D}_1$ ,  $\bar{D}_1$  and  $\bar{D}_0(0)$  which are  
 222 defined in [Table 9](#), the regions of the operating diagram in the  $(s_1^{in}, s_0^{in})$  plane where  $D$  is kept constant  
 223 are cataloged as follows:

- 224 1. if  $D \in I_2$ , then the twelve regions exist (see [Figure 1](#));
- 225 2. if  $D \in I_1 \setminus I_2$ , then eight regions exist where the four regions  $\mathcal{J}_4$ ,  $\mathcal{J}_5$ ,  $\mathcal{J}_{11}$  and  $\mathcal{J}_{12}$  are empty  
 226 (see [Figure 2\(c\)](#));
- 227 3. if  $D \in I_0 \cap \bar{I}_1 \setminus I_1$ , or if  $\hat{D}_1 < D < \min(\bar{D}_1, \bar{D}_0(0))$ , then only the regions  $\mathcal{J}_1$ ,  $\mathcal{J}_2$ ,  $\mathcal{J}_8$  and  $\mathcal{J}_9$   
 228 exist (see [Figure 2\(b\)](#));
- 229 4. if  $D \in \bar{I}_1 \setminus \{I_1 \cup I_0\}$ , or if  $\bar{D}_0(0) < D < \bar{D}_1$ , then only the regions  $\mathcal{J}_1$ ,  $\mathcal{J}_8$  and  $\mathcal{J}_9$  exist (see  
 230 [Figure 2\(b\)](#) where  $\mathcal{J}_2$  is empty);
- 231 5. if  $D \in I_0 \setminus \bar{I}_1$ , or if  $\bar{D}_1 < D < \bar{D}_0(0)$ , then only the regions  $\mathcal{J}_1$  and  $\mathcal{J}_2$  exist (see [Figure 2\(a\)](#));
- 232 6. if  $D \notin I_0 \cup \bar{I}_1$ , or if  $D > \max(\bar{D}_1, \bar{D}_0(0))$ , then only the region  $\mathcal{J}_1$  exists (see [Figure 2\(a\)](#) where  
 233  $\mathcal{J}_2$  is empty).

234 **4.2. Operating diagrams in the  $(D, s_0^{in})$  plane when  $s_1^{in}$  fixed.** The intersection of the surfaces  
 235  $\gamma_0$  and  $\gamma_i^j$ ,  $i, j = 1, 2$  with the  $(D, s_0^{in})$  plane where  $s_1^{in}$  is kept constant is a curve of a function of  $D$ .  
 236 However, the intersections of the surfaces  $\gamma_3^j$ ,  $j = 1, 2$  with this plane are straight lines (see [Table 11](#)).  
 237 To determine the operating diagram when  $s_1^{in}$  is fixed, we show the following result which determines  
 238 the relative positions of the curves  $\gamma_0$  and  $\gamma_i^j$ ,  $i, j = 1, 2$  according to the values of  $D$  and  $D_1^*$ . We  
 239 begin by considering the case  $s_1^{in} \leq s_1^{max}$ .

**Proposition 4.3.** Let  $s_1^{in} \leq s_1^{max}$ . For all  $D \in I_2$ ,

$$F_0(D, s_1^{in}) \leq F_1^2(D) \leq F_2^2(D) - s_1^{in}.$$

240 There exists a solution  $D = D_1^* \in \bar{I}_1$  of equation  $s_1^{in} = M_1^1(\alpha_1 D + a_1)$  if and only if

$$241 \quad (4.6) \quad s_1^{in} \geq M_1^1(a_1).$$

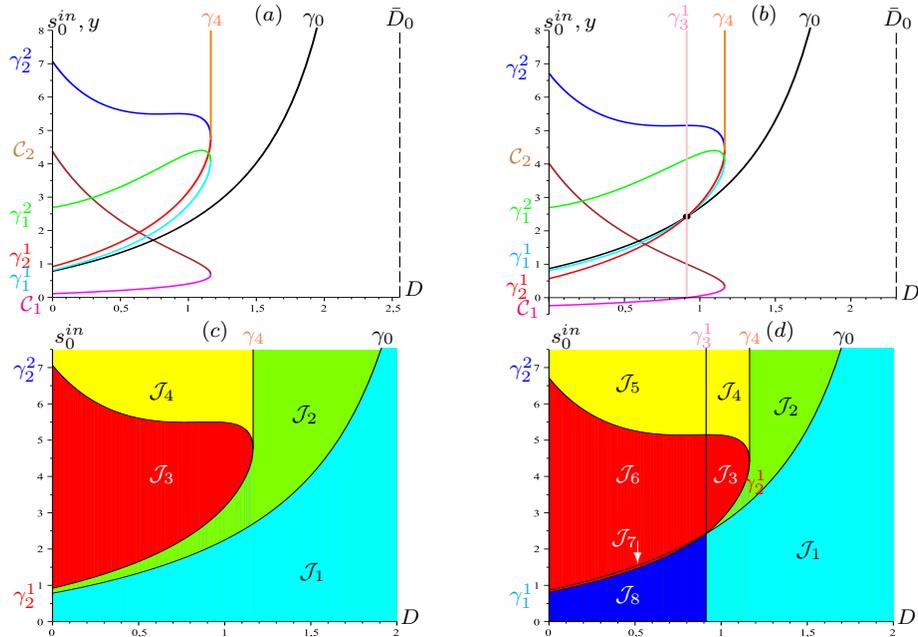
242 It is unique if it exists. If  $D_1^* \in I_1$ , the three curves  $\gamma_0$ ,  $\gamma_1^1$  and  $\gamma_2^1$  intersect at the same point  $D = D_1^*$   
 243 (see [Figures 3](#) and [4\(b\)](#)) such that for all  $D \in [0, D_1^*)$ , [\(4.3\)](#) holds and for all  $D \in (D_1^*, \bar{D}_1) \cap I_0 \cap I_1$ ,  
 244 [\(4.2\)](#) holds. The curves  $\gamma_0$ ,  $\gamma_1^1$  and  $\gamma_2^1$  do not intersect if  $D_1^* \in \bar{I}_1 \setminus I_1$ , where for all  $D \in I_0$ , [\(4.3\)](#) holds  
 245 (see [Figure 4\(c\)](#)) or if  $D_1^*$  does not exist, where for all  $D \in I_1$ , [\(4.2\)](#) holds (see [Figures 3](#) and [4\(a\)](#)).

246 According to the position of  $s_1^{in}$  relatively to  $M_1^1(a_1)$  and the two cases of [\(4.1\)](#) where  $s_1^{in} \in [0, s_1^{max}]$   
 247 and is kept constant, the regions of the operating diagram in the  $(D, s_0^{in})$  plane are cataloged as follows:

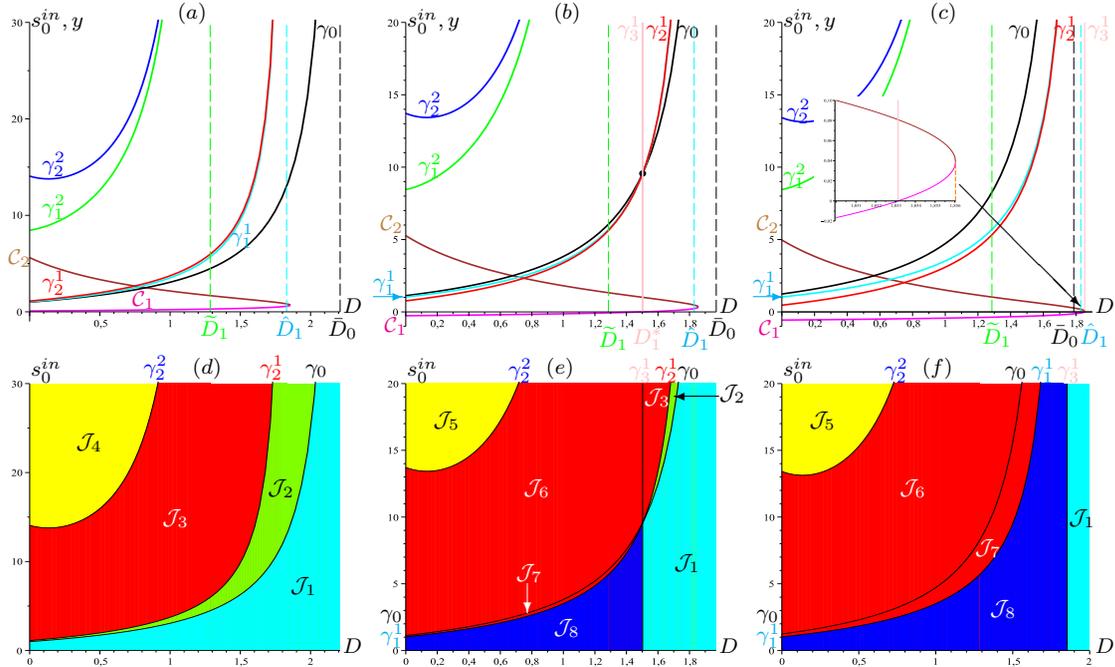
- 248 1. If  $s_1^{in} < M_1^1(a_1)$ , there exist at most four regions  $\mathcal{J}_1$  to  $\mathcal{J}_4$  (see [Figure 3\(a,c\)](#) in case 1 of [\(4.1\)](#)  
 249 and [Figure 4\(a,d\)](#) in case 2).
- 250 2. Let  $s_1^{in} \geq M_1^1(a_1)$ . If  $D_1^* \in I_1$ , there exist at most eight regions  $\mathcal{J}_1$  to  $\mathcal{J}_8$  (see [Figure 3\(b,d\)](#) in  
 251 case 1 and [Figure 4\(b,e\)](#) in case 2). If case 2 holds and  $D_1^* \in \bar{I}_1 \setminus I_1$ , there exist at most five  
 252 regions  $\mathcal{J}_1$  and  $\mathcal{J}_5$  to  $\mathcal{J}_8$  (see [Figure 4\(c,f\)](#)).

253 The operating diagram of [Figure 4\(b,e\)](#) shows the existence of seven regions  $\mathcal{J}_1$  to  $\mathcal{J}_8$  where the region  
 254  $\mathcal{J}_4$  is empty in the case 2 of [\(4.1\)](#) with  $M_1^1(a_1) < s_1^{in} \leq s_1^{max}$  and  $D_1^* \in I_1$ . However, this region  $\mathcal{J}_4$   
 255 can be not empty for another set of parameters such that  $D_1^* < \tilde{D}_1$ .

256 By similar arguments to that in the proof of [Proposition 4.3](#), we can prove the following result  
 257 which determines the relative positions of the curves  $\gamma_0$  and  $\gamma_i^j$ ,  $i, j = 1, 2$  according to the values of  
 258  $D$  and  $D_2^*$  in the case  $s_1^{in} > s_1^{max}$ .



**Figure 3.** The curves  $C_1, C_2$  and those of  $\Gamma$  in case 1 of (4.1) with  $s_1^{in} < s_1^{max} \simeq 0.689$ : (a)  $s_1^{in} = 0 < M_1^1(a_1) \simeq 0.109$ , (b)  $M_1^1(a_1) < s_1^{in} = 0.35$ . (c)-(d) The respective corresponding operating diagrams.



**Figure 4.** The curves  $C_j, j = 1, 2$  and those of  $\Gamma$  in case 2 of (4.1) with  $s_1^{in} < s_1^{max} \simeq 0.689$ : (a)  $s_1^{in} = 0 < M_1^1(a_1) \simeq 0.109$ , (b)  $M_1^1(a_1) < s_1^{in} = 0.35$ ;  $D_1^* \simeq 1.503 \in I_1, \bar{D}_1 \simeq 1.829$  (c)  $M_1^1(a_1) < s_1^{in} = 0.65$ ;  $D_1^* \simeq 1.853 \notin I_1$ , and a magnification of  $C_j$  when  $D \in [1.85, \bar{D}_1], \bar{D}_1 \simeq 1.856$ . (d)-(e)-(f) The respective corresponding operating diagrams.

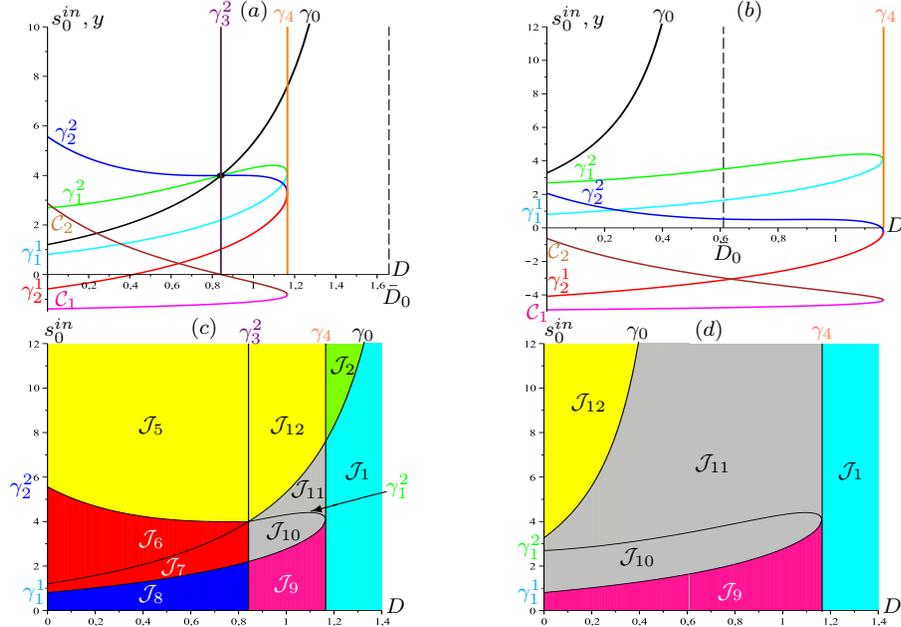
**Proposition 4.4.** Let  $s_1^{in} > s_1^{max}$ . For all  $D \in I_0 \cap I_1$ , we have

$$F_2^1(D) - s_1^{in} < F_1^1(D) < F_0(D, s_1^{in}).$$

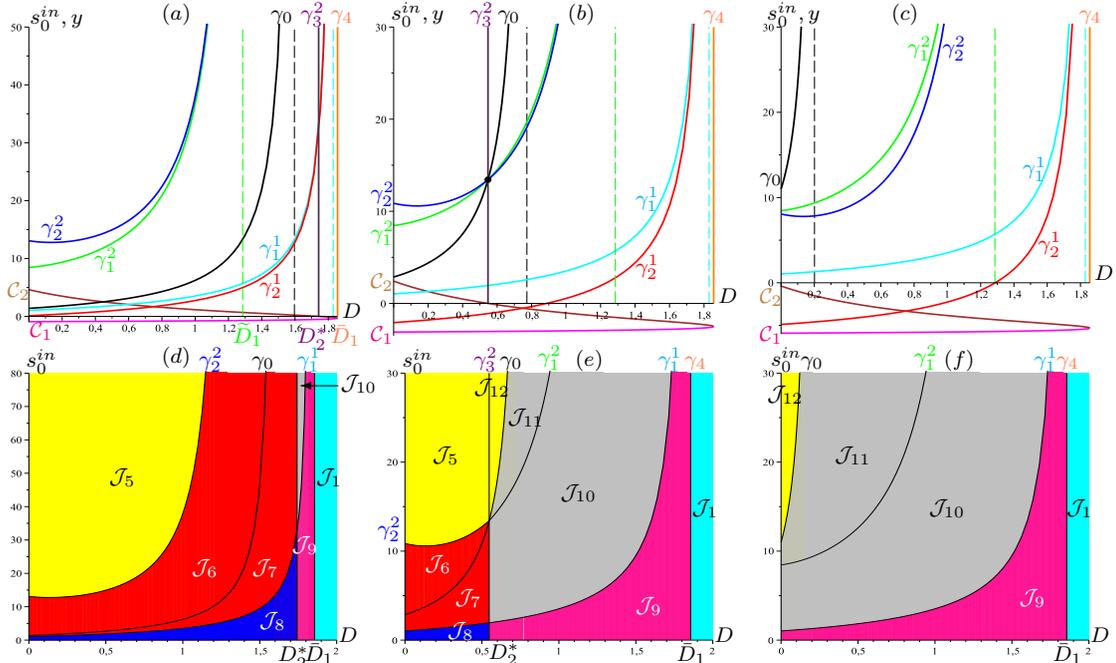
259 There exists a solution  $D = D_2^* \in \bar{I}_2$  of equation  $s_1^{in} = M_1^2(\alpha_1 D + a_1)$  if and only if

260 (4.7) 
$$s_1^{in} \leq M_1^2(a_1).$$

261 It is unique if it exists. If  $D_2^* \in I_2$ , the three curves  $\gamma_0, \gamma_1^1$  and  $\gamma_2^2$  intersect at the same point  
 262  $D = D_2^*$  (see Figure 5(a) and Figure 6(b)) such that for all  $D \in [0, D_2^*) \cap I_2$ , (4.4) holds and for all  
 263  $D \in (D_2^*, \bar{D}_2) \cap I_0 \cap I_2$ , (4.5) holds. The curves  $\gamma_0, \gamma_1^1$  and  $\gamma_2^2$  do not intersect if  $D_2^* \in \bar{I}_2 \setminus I_2$ , where  
 264 for all  $D \in I_2$ , (4.4) holds (see Figure 6(a)) or if  $D_2^*$  does not exist, where for all  $D \in I_2$ , (4.5) holds  
 265 (see Figure 5(b) and Figure 6(c)).



**Figure 5.** The curves  $C_1$ ,  $C_2$  and those of  $\Gamma$  in case 1 of (4.1) with  $s_1^{in} > s_1^{max} \simeq 0.689$ : (a)  $s_1^{in} = 1.5 < M_1^2(a_1) \simeq 4.37$ , (b)  $s_1^{in} = 5 > \max(s_1^{max}, M_1^2(a_1))$ . (c)-(d) The respective corresponding operating diagrams.



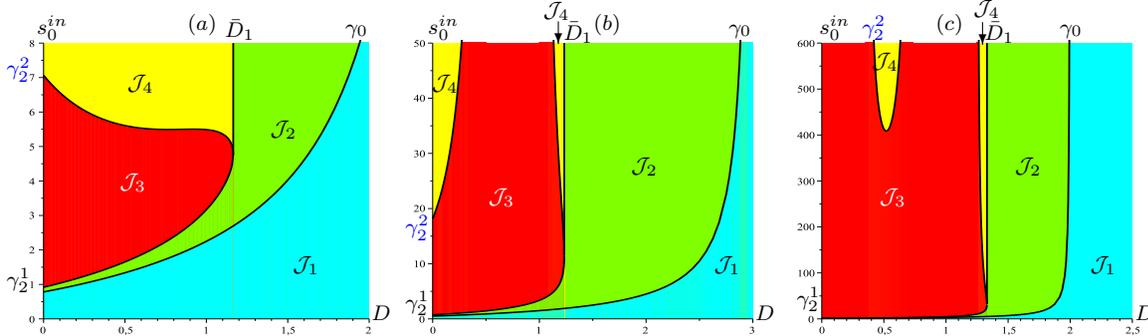
**Figure 6.** The curves  $C_1$ ,  $C_2$  and those of  $\Gamma$  in case 2 of (4.1) with  $s_1^{in} > s_1^{max} \simeq 0.689$ : (a)  $s_1^{in} = 1 < M_1^2(a_1) \simeq 5.615$ ;  $D_2^* \simeq 1.742 \notin I_2 = [0, 1.285]$ , (b)  $s_1^{in} = 3.2 < M_1^2(a_1)$ ;  $D_2^* \in I_2$ , (c)  $s_1^{in} = 6 > M_1^2(a_1)$ . (d)-(e)-(f) The respective corresponding operating diagrams.

266 According to the position of  $s_1^{in}$  relatively to  $M_1^2(a_1)$  and the two cases of (4.1) where  $s_1^{in} > s_1^{max}$   
 267 and is kept constant, the regions of the operating diagram in the  $(D, s_0^{in})$  plane are cataloged as  
 268 follows:

- 269 1. Let  $s_1^{in} \leq M_1^2(a_1)$ . If  $D_2^* \in I_2$ , in case 1 of (4.1),  $\mathcal{J}_3$  and  $\mathcal{J}_4$  are empty and the other ten  
 270 regions can exist (see Figure 5(a,c)), while in case 2,  $\mathcal{J}_2$  to  $\mathcal{J}_4$  are empty and we can have  
 271 up to nine regions in the operating diagram (see Figure 6(b,e) in case 2). If case 2 holds and  
 272  $D_2^* \in \bar{I}_2 \setminus I_2$ , there exist at most seven regions  $\mathcal{J}_1$  and  $\mathcal{J}_5$  to  $\mathcal{J}_{10}$  (see Figure 6(a,d)).  
 273 2. If  $s_1^{in} > M_1^2(a_1)$ , at most the five regions  $\mathcal{J}_1$  and  $\mathcal{J}_9$  to  $\mathcal{J}_{12}$  can exist (see Figure 5(b,d) in case  
 274 1 and Figure 6(c,f) in case 2).

275 With the same set of parameters of the operating diagram of Figure 3(a) that we redraw in Figure 7(a),  
 276 the equation  $\Phi_2(D) = 0$  has no solution. In Appendix C, with the specific growth rates defined in (C.1),

277 we show that this equation has at most three solutions  $\tilde{D}_j$ ,  $j = 1, 2, 3$  such that  $\lim_{D \rightarrow \tilde{D}_j^-} F_i^2(D) = +\infty$ ,  
 278  $i = 1, 2$  (see [Proposition A.4](#)). The operating diagrams of [Figure 7\(b-c\)](#) show that in the case of two  
 279 or three solutions of the equation  $\Phi_2(D) = 0$ , we have the same number of regions but there is a  
 280 change in the shape and the connectivity of the regions. This property is the same for the various  
 281 cases studied above even when the equation  $\Phi_2(D) = 0$  has several roots with general growth rates  
 satisfying [Hypotheses 2.1 to 2.4](#).



**Figure 7.** Operating diagrams of (2.1) when  $s_1^{in} = 0$  and case 1 of (4.1) holds: equation  $\Phi_2(D) = 0$  has no  
 solution, (b) has two solutions (c) has three solutions. The operating diagram (a) is the same in [Figure 3\(c\)](#).

282  
 283 The following result determines the nature of bifurcations of system (2.1) that might happen by  
 284 crossing the various regions of the operating parameters space  $(D, s_0^{in}, s_1^{in})$  through the surfaces of  $\Gamma$   
 285 where the steady states coalesce and can change stability.

286 **Proposition 4.5.** *The bifurcation analysis of the steady states of (2.1) by crossing the surfaces of  $\Gamma$*   
 287 *according to the operating parameters  $D$ ,  $s_0^{in}$  and  $s_1^{in}$  is summarized in [Table 8](#).*

**Table 8**

*Bifurcations according to surfaces of  $\Gamma$ . The letter TB (resp. SNB) means a transcritical bifurcation (resp. saddle-node bifurcation). Note that  $k = 2, 3$ .*

$\Gamma$	Conditions	Transition	Bifurcation
$\gamma_0$	$s_1^{in} < M_1^1(D_1)$	$\mathcal{J}_1$ to $\mathcal{J}_2$	
	$M_1^1(D_1) < s_1^{in} < M_1^2(D_1)$	$\mathcal{J}_6$ to $\mathcal{J}_7$	TB: $SS_0 = SS_1$
	$M_1^2(D_1) > s_1^{in}$	$\mathcal{J}_{11}$ to $\mathcal{J}_{12}$	
$\gamma_1^1$	$M_1^1(D_1) < s_1^{in} < M_1^2(D_1)$	$\mathcal{J}_7$ to $\mathcal{J}_8$	TB: $SS_2^1 = SS_3^1$
	$s_1^{in} > M_1^2(D_1)$	$\mathcal{J}_9$ to $\mathcal{J}_{10}$	
$\gamma_1^2$	$s_1^{in} > M_1^2(D_1)$	$\mathcal{J}_{10}$ to $\mathcal{J}_{11}$	TB: $SS_2^2 = SS_3^2$
$\gamma_2^1$	$s_1^{in} < M_1^1(D_1)$	$\mathcal{J}_2$ to $\mathcal{J}_3$	TB: $SS_1 = SS_2^1$
$\gamma_2^2$	$s_1^{in} < M_1^1(D_1)$	$\mathcal{J}_3$ to $\mathcal{J}_4$	
	$M_1^1(D_1) < s_1^{in} < M_1^2(D_1)$	$\mathcal{J}_5$ to $\mathcal{J}_6$	TB: $SS_1 = SS_2^2$
$\gamma_3^1$	$s_0^{in} > F_2^2 - s_1^{in}$	$\mathcal{J}_4$ to $\mathcal{J}_5$	
	$F_2^1 - s_1^{in} < s_0^{in} < F_2^2 - s_1^{in}$ if $D < D_1^*$ , if not $F_0 < s_0^{in} < F_2^2 - s_1^{in}$	$\mathcal{J}_3$ to $\mathcal{J}_6$	TB: $SS_0 = SS_3^1$
	$s_0^{in} < F_0$ if $D < D_1^*$ , if not $s_0^{in} < F_1^1$	$\mathcal{J}_1$ to $\mathcal{J}_8$	
$\gamma_3^2$	$s_0^{in} > F_2^2 - s_1^{in}$ if $D < D_2^*$ , if not $s_0^{in} > F_0$	$\mathcal{J}_5$ to $\mathcal{J}_{12}$	
	$F_1^1 < s_0^{in} < F_0$ if $D < D_2^*$ , if not $F_1^1 < s_0^{in} < F_1^2$	$\mathcal{J}_7$ to $\mathcal{J}_{10}$	TB: $SS_0 = SS_3^2$
$\gamma_4$	$s_0^{in} < F_1^1$	$\mathcal{J}_8$ to $\mathcal{J}_9$	
	$s_1^{in} < s_1^{max}$	$\mathcal{J}_2$ to $\mathcal{J}_4$	SNB: $SS_2^1 = SS_2^2$
$\gamma_4$	$s_1^{in} > s_1^{max}$	$\mathcal{J}_2$ to $\mathcal{J}_{12}$	SNB: $SS_k^1 = SS_k^2$
		$\mathcal{J}_1$ to $\mathcal{J}_{11}$	SNB: $SS_3^1 = SS_3^2$
		$\mathcal{J}_1$ to $\mathcal{J}_9$	SNB: $SS_3^1 = SS_3^2$

288 We have only studied the bifurcations that occur by transitions through surfaces in two-dimensional  
 289 planes and not through the points given by the intersections of curves and lines. However, the study  
 290 of such bifurcations can be determined in the same way.

291 **5. Discussion and conclusion.** In this paper, we have generalized the mathematical analysis of  
 292 the simplified model (2.1) of anaerobic digestion in the form of a two-tiered microbial food chain  
 293 describing a syntrophic relationship between two microbial species in a chemostat. To this end, we  
 294 allow a large class of growth functions with distinct disappearance rates. The main contribution of this

study is to bring out the mutual effects of the syntrophy relationship, the decay of the two microbial species, the substrate inhibition on the growth of the second species and a new inflowing concentration (hydrogen) which are not studied together in the existing literature. First, we have determined the necessary and sufficient conditions of existence and local stability of all steady states of syntrophic model (2.1) according to the operating parameters  $D$ ,  $s_0^{in}$  and  $s_1^{in}$ . Second, we have analyzed the operating diagrams to determine the behavior of the system according to the control parameters and to choose the appropriate inputs and the initial states to achieve a good operation of the process. The operating diagrams show that the system can have a unique stable steady state: either of coexistence ( $\mathcal{J}_i, i = 3, 6, 7$ ) or washout ( $\mathcal{J}_1$ ) or exclusion of one of two microbial species ( $\mathcal{J}_i, i = 2, 8$ ). It can also exhibit a bistability between coexistence and washout ( $\mathcal{J}_i, i = 10, 11$ ) or exclusion of the second species ( $\mathcal{J}_i, i = 4, 5, 12$ ) or between washout and exclusion of the first species ( $\mathcal{J}_9$ ). If required, to ensure (or to avoid) the coexistence of two microbial species in the process, the operating parameter values can be chosen in (out) the regions  $\mathcal{J}_i, i = 3, 6, 7$ , where there exists a unique stable steady state of coexistence and the other steady states are unstable. The study of the nature of bifurcations of the steady states shows that all the coalesces and the change of stability can be either by a transcritical or a saddle-node bifurcation by crossing the boundary of the regions of the operating parameters space.

In [40], where  $s_1^{in} = 0$  and  $\mu_1$  is increasing, the analysis of the operating diagram of (2.1) shows the existence only of the three regions  $\mathcal{J}_1$  to  $\mathcal{J}_3$  where the bistability cannot occur and the two steady states of extinction of the first species  $SS_3^1$  and  $SS_3^2$  do not exist. In [18], where only  $s_1^{in} = 0$ , that is,  $\mu_1$  is nonmonotonic,  $SS_3^1$  and  $SS_3^2$  do not exist and the operating diagram has at most four regions  $\mathcal{J}_1$  to  $\mathcal{J}_4$  where the system can exhibit a bistability between the steady state  $SS_1$  of exclusion of the second species and the coexistence steady state  $SS_2^1$ . It is shown, when the substrate inhibition increases, that there is an emergence of the bistability region  $\mathcal{J}_4$  first and then its disappearance with the coexistence region  $\mathcal{J}_3$  for a sufficiently large substrate inhibition rate.

Conversely in [11], where  $s_1^{in} \geq 0$  and  $\mu_1$  is increasing, it is shown that the steady states of coexistence  $SS_2$  and of extinction of the first species  $SS_3$  are unique. Moreover, the bistability cannot occur where at most six regions exist such that all bistability regions  $\mathcal{J}_4, \mathcal{J}_5$  and  $\mathcal{J}_9$  to  $\mathcal{J}_{12}$  do not exist. Thus, our mathematical study of the operating diagrams of model (2.1) shows the significant impact of substrate inhibition on the behavior of the process and the emergence of the bistability regions which are empty when the growth rate  $\mu_1$  is increasing [11, 40]. Our findings on the destabilization of a two-tiered microbial ‘food chain’ by substrate inhibition are similar to those in [18, 24] where the behavior of system depends on the initial condition. Furthermore, a low, as well as a high concentration of input substrate, can cause destabilization by the extinction of the highest trophic level of a tri-trophic food chain model in the chemostat [8].

Recently in [38], an extension of the study of the two-tiered model (1.2) in [5] with a commensalistic relationship ( $\mu_0(\cdot) = \mu_0(s_0)$ ) provides a complete analysis of the operating diagram. It is shown that our six steady states exist and at most nine regions exist where only the regions  $\mathcal{J}_7, \mathcal{J}_{10}$  and  $\mathcal{J}_{11}$  are empty. Hence, the main change of the behavior of the process by considering the effect of syntrophic relationship compared to [38] is that the system can exhibit a bistability between the washout  $SS_0$  and the coexistence  $SS_2^1$ .

These theoretical messages explain the joined effect of syntrophy, mortality, substrate inhibition, and input substrates on the maintenance of coexistence and the protection of microbial ecosystems. Finally, the results in this contribution may also serve for optimal experimental design by studying the biogas production and the process performance with respect to operating parameters. This is an important question that deserves further attention and will be the object of future work.

**Appendix A. Definition domains and properties of auxiliary functions.** First, we introduce in Table 9 some notations and the definition domains of the auxiliary functions defined in Table 3 that we will show in this section. The following proposition determines the domain and some properties of the function  $F_0(D, s_1^{in})$ .

**Proposition A.1.** *The function  $F_0(D, s_1^{in})$  is defined for  $(D, s_1^{in}) \in \text{dom}(F_0)$ . Moreover, one has*

Table 9

Notations and intervals of auxiliary functions.

	Definition
$\bar{D}_0(s_1^{in})$	$\bar{D}_0(s_1^{in}) = (\bar{\mu}_0(s_1^{in}) - a_0) / \alpha_0$
$\bar{D}_1$	$\bar{D}_1 = (\mu_1^{max} - a_1) / \alpha_1$
$\Phi_j(D)$	$\Phi_j(D) = \bar{\mu}_0(M_1^j(D_1)) - D_0$ , for $D \in \bar{I}_j$ , $j = 1, 2$
$\hat{D}_1$	$\hat{D}_1$ is the solution of $\Phi_1(D) = 0$
$\tilde{D}_i$	$\tilde{D}_i$ are the solutions of $\Phi_2(D) = 0$ , $i = 1, \dots, n$
$I_0$	Let $s_1^{in} \geq 0$ . $I_0 = [0, \bar{D}_0(s_1^{in})]$ if $\alpha_0 \in (0, 1]$ $I_0 = [0, +\infty)$ if $\alpha_0 = 0$ and $a_0 < \bar{\mu}_0(s_1^{in})$ , otherwise $I_0 = \emptyset$ .
$J_0$	Let $D \geq 0$ . $J_0 = [0, \bar{s}_1^{in}]$ , if $\bar{D}_0(+\infty) < D < \bar{D}_0(0)$ , where $\bar{s}_1^{in}$ is the unique solution of $\bar{D}_0(s_1^{in}) = D$ . $J_0 = [0, +\infty)$ , if $D \leq \bar{D}_0(+\infty)$ and $J_0 = \emptyset$ if $D \geq \bar{D}_0(0)$ .
$dom(F_0)$	$dom(F_0) = \{(D, s_1^{in}) : (D \in I_0 \text{ and } s_1^{in} \geq 0) \text{ or } (s_1^{in} \in J_0 \text{ and } D \geq 0)\}$
$\bar{I}_1$	$\bar{I}_1 = [0, \bar{D}_1]$ if $\alpha_1 \in (0, 1]$ $\bar{I}_1 = [0, +\infty)$ if $\alpha_1 = 0$ and $a_1 \leq \mu_1^{max}$ , otherwise $\bar{I}_1 = \emptyset$ .
$\bar{I}_2$	$\bar{I}_2 = \bar{I}_1$ if $a_1 > 0$ and $\bar{I}_2 = \bar{I}_1 \setminus \{0\}$ if $a_1 = 0$
$I_j$ ,	$I_j = \{D \in \bar{I}_j / \Phi_j(D) > 0\}$ , $j = 1, 2$

345  $\bar{D}_1 < \bar{D}_0(0)$  in case 1 of (4.1),  $\hat{D}_1 < \bar{D}_0(0)$  in case 2 of (4.1) and

346 
$$\lim_{s_1^{in} \rightarrow \bar{s}_1^{in}-} F_0(D, s_1^{in}) = +\infty.$$

347 *Proof.* Let  $s_1^{in}$  be fixed. From Table 3, the function  $F_0(D, s_1^{in})$  is defined if and only if

348 (A.1) 
$$D_0 < \bar{\mu}_0(s_1^{in}) \iff D < \bar{D}_0(s_1^{in}) = \frac{\bar{\mu}_0(s_1^{in}) - a_0}{\alpha_0},$$

where  $\bar{D}_0(s_1^{in})$  is defined and positive if and only if  $\alpha_0 \neq 0$  and  $\bar{\mu}_0(s_1^{in}) > a_0$ . In the particular case  $\alpha_0 = 0$ , the condition  $D_0 < \bar{\mu}_0(s_1^{in})$  is equivalent to  $a_0 < \bar{\mu}_0(s_1^{in})$ . Thus, the function  $F_0(\cdot, s_1^{in})$  is defined on  $I_0$ . Let  $D$  be fixed. From Hypothesis 2.5, the function  $s_1^{in} \mapsto \bar{D}_0(s_1^{in})$  is decreasing from  $\bar{D}_0(0)$  to  $\bar{D}_0(+\infty)$ . If  $D \leq \bar{D}_0(+\infty)$ , then (A.1) holds for all  $s_1^{in} \geq 0$ . If  $\bar{D}_0(+\infty) < D < \bar{D}_0(0)$ , then there exists a unique solution  $\bar{s}_1^{in}$  of equation  $D = \bar{D}_0(s_1^{in})$  such that (A.1) holds for all  $s_1^{in} \in [0, \bar{s}_1^{in}]$ . If  $D \geq \bar{D}_0(0)$ , (A.1) does not hold for all  $s_1^{in} \geq 0$ . Hence, the function  $F_0(D, \cdot)$  is defined on  $J_0$ . Consequently,  $F_0(D, s_1^{in})$  is defined for  $(D, s_1^{in}) \in dom(F_0)$ . Since  $\bar{s}_1^{in}$  satisfies  $D_0 = \mu_0(+\infty, \bar{s}_1^{in})$ , it follows that

$$F_0(D, \bar{s}_1^{in}) = M_0(\mu_0(+\infty, \bar{s}_1^{in}), \bar{s}_1^{in}) = +\infty.$$

When case 1 of (4.1) holds, we have

$$\alpha_0 \bar{D}_1 + a_0 < \bar{\mu}_0(M_1^1(\alpha_1 \bar{D}_1 + a_1)) < \bar{\mu}_0(0),$$

349 because the function  $\bar{\mu}_0(\cdot)$  is decreasing (see Hypothesis 2.5). Thus,  $\bar{D}_1 < \bar{D}_0(0)$ . Moreover, when  
350 case 2 of (4.1) holds, we conclude that  $\hat{D}_1 < \bar{D}_0(0)$  where  $\hat{D}_1$  is a solution of  $\Phi_1(D) = 0$  because

351 
$$\alpha_0 \hat{D}_1 + a_0 = \bar{\mu}_0(M_1^1(\alpha_1 \hat{D}_1 + a_1)) < \bar{\mu}_0(0).$$

352 The following result determines the definition domain  $I_1$  of the function  $F_i^1(\cdot)$ ,  $i = 1, 2$ , according to  
353 the coefficients  $\alpha_0$  and  $\alpha_1$ .

354 **Proposition A.2.** Let  $s_1^{in} \geq 0$  be fixed. The function  $F_i^1(D)$ ,  $i = 1, 2$ , is defined on

355 (A.2) 
$$I_1 = \begin{cases} [0, +\infty), & \text{if } \alpha_0 = \alpha_1 = 0, a_1 < \mu_1^{max}, \bar{\mu}_0(M_1^1(a_1)) > a_0 \\ \emptyset, & \text{if } \alpha_0 = \alpha_1 = 0 \text{ and } a_1 \geq \mu_1^{max} \text{ or } \bar{\mu}_0(M_1^1(a_1)) \leq a_0 \\ [0, (\bar{\mu}_0(M_1^1(a_1)) - a_0) / \alpha_0), & \text{if } \alpha_0 > 0, \alpha_1 = 0, a_1 < \mu_1^{max}, \bar{\mu}_0(M_1^1(a_1)) > a_0 \\ [0, \bar{D}_1], & \text{if } \alpha_0 \geq 0, \alpha_1 > 0, \text{ and case 1 of (4.1) holds} \\ [0, \hat{D}_1], & \text{if } \alpha_0 \geq 0, \alpha_1 > 0, \text{ and case 2 of (4.1) holds.} \end{cases}$$

356 *Proof.* The function  $F_i^1$ ,  $i = 1, 2$ , is defined if and only if

$$357 \quad (\text{A.3}) \quad D_1 < \mu_1^{max} \quad \text{and} \quad D_0 < \bar{\mu}_0 (M_1^1(D_1)).$$

358 If  $\alpha_0 = \alpha_1 = 0$ , (A.3) is equivalent to  $a_1 < \mu_1^{max}$  and  $a_0 < \bar{\mu}_0 (M_1^1(a_1))$ . Thus,  $I_1 = [0, +\infty)$  if  
 359 this last condition holds, else  $I_1 = \emptyset$ . If  $\alpha_0 > 0$  and  $\alpha_1 = 0$ , (A.3) is equivalent to  $a_1 < \mu_1^{max}$   
 360 and  $\alpha_0 D + a_0 < \bar{\mu}_0 (M_1^1(a_1))$ , that is,  $I_1 = [0, (\bar{\mu}_0 (M_1^1(a_1)) - a_0) / \alpha_0)$ . If  $\alpha_0 \geq 0$  and  $\alpha_1 > 0$ ,  
 361 straightforward calculation shows that

$$362 \quad (\text{A.4}) \quad \Phi_j'(D) = \alpha_1 \bar{\mu}_0' (M_1^j(D_1)) M_1^{j'}(D_1) - \alpha_0.$$

363 Recall that the function  $M_1^1$  is increasing. From Hypothesis 2.5, one has  $\Phi_1'(D) < 0$  for all  $D \in \bar{I}_1$ .  
 364 Therefore,  $\Phi_1(D) > 0$  for all  $D \in [0, \bar{D}_1]$  since  $\Phi_1(\bar{D}_1) > 0$  when case 1 of (4.1) holds and  $\Phi_1(D) > 0$   
 365 for all  $D \in [0, \hat{D}_1)$  since  $\Phi_1(\bar{D}_1) \leq 0$  when case 2 of (4.1) holds (see Figures 8 and 9). ■

366 When the growth functions are given by (C.1) (as we will show in Proposition C.1), the equation  
 367  $\Phi_2(D) = 0$  has at most three solutions in the case 1 of (4.1) and two solutions in the case 2 of (4.1).  
 368 For simplicity, we determine in this particular case the definition domain  $I_2$  of the function  $F_i^2$ ,  $i = 1, 2$ .  
 369 The general case can be treated similarly, without added difficulty.

370 **Proposition A.3.** *The function  $F_i^2$  is defined on*

$$371 \quad (\text{A.5}) \quad I_2 = \begin{cases} [0, +\infty), & \text{if } \alpha_0 = 0, \alpha_1 = 0, \bar{\mu}_0 (M_1^2(a_1)) > a_0, \\ [0, (\bar{\mu}_0 (M_1^2(a_1)) - a_0) / \alpha_0), & \text{if } \alpha_0 > 0, \alpha_1 = 0, \bar{\mu}_0 (M_1^2(a_1)) > a_0, \\ [0, \bar{D}_1], & \text{if } \alpha_0 = 0, \alpha_1 > 0, \Phi_2(\bar{D}_1) > 0, \bar{\mu}_0 (M_1^2(a_1)) > a_0, \\ (\tilde{D}_1, \bar{D}_1], & \text{if } \alpha_0 = 0, \alpha_1 > 0, \Phi_2(\bar{D}_1) > 0, \bar{\mu}_0 (M_1^2(a_1)) \leq a_0, \end{cases}$$

372 *otherwise, when  $\alpha_0 > 0$  and  $\alpha_1 > 0$ ,*

$$373 \quad (\text{A.6}) \quad I_2 = \begin{cases} [0, \bar{D}_1], & \text{if case 1 of (4.1) holds and } n = 0, \\ (\tilde{D}_1, \bar{D}_1], & \text{if case 1 of (4.1) holds and } n = 1, \\ [0, \bar{D}_2) \cup (\tilde{D}_1, \bar{D}_1], & \text{if case 1 of (4.1) holds and } n = 2, \\ (\tilde{D}_3, \bar{D}_2) \cup (\tilde{D}_1, \bar{D}_1], & \text{if case 1 of (4.1) holds and } n = 3, \\ [0, \tilde{D}_1), & \text{if case 2 of (4.1) holds and } n = 1, \\ (\tilde{D}_2, \tilde{D}_1) & \text{if case 2 of (4.1) holds and } n = 2, \end{cases}$$

374 *where  $\tilde{D}_i$ ,  $i = 1, \dots, n$ , are the solutions of the equation  $\Phi_2(D) = 0$  and  $n$  denotes the number of*  
 375 *solutions such that  $\bar{D}_i > \tilde{D}_j$ , for all  $i < j$ . Note that the function  $F_i^2$  is not defined for  $D = 0$  in the*  
 376 *particular case  $a_1 = 0$ .*

377 *Proof.* The function  $F_i^2$ ,  $i = 1, 2$ , is defined if and only if

$$378 \quad (\text{A.7}) \quad 0 < D_1 < \mu_1^{max} \quad \text{and} \quad \Phi_2(D) > 0.$$

379 If  $\alpha_1 = 0$ , similar arguments as the proof of  $I_1$  imply that of  $I_2$ . If  $\alpha_0 = 0$  and  $\alpha_1 > 0$ , then  $\Phi_2'(D)$   
 380 is positive for all  $D \in \bar{I}_2$ , using (A.4), Hypothesis 2.5 and the function  $M_1^2$  is decreasing. Hence,  
 381  $\Phi_2(D) > 0$  is positive if and only if  $\Phi_2(\bar{D}_1) > 0$ . In this case,  $\Phi_2(D) > 0$  for all  $D \in [0, \bar{D}_1]$  if  
 382  $\Phi_2(0) > 0$ , that is,  $\bar{\mu}_0 (M_1^2(a_1)) > a_0$ . Otherwise,  $\Phi_2(D) > 0$  for all  $D \in (\tilde{D}_1, \bar{D}_1]$  where  $\tilde{D}_1$  is the  
 383 unique solution of  $\Phi_2(D) = 0$ .

384 Let  $\alpha_0 > 0$  and  $\alpha_1 > 0$ . From (A.4), the sign of  $\Phi_2'(D)$  can change at  $D \in \bar{I}_2$ , that is, the  
 385 function  $\Phi_2$  can be nonmonotonic on  $\bar{I}_2$  (see Figures 8 and 9(b-d)). When case 1 holds and  $n = 0$ ,  
 386 we have  $\Phi_2(\bar{D}_1) > 0$  and the equation  $\Phi_2(D) = 0$  has no solution. Consequently,  $\Phi_2(D) > 0$  for  
 387 all  $D \in [0, \bar{D}_1]$ . Hence, the function  $F_i^2$  is defined on  $I_2 = \bar{I}_2$  where  $\bar{I}_2 = [0, \bar{D}_1]$  when  $a_1 > 0$  and  
 388  $\bar{I}_2 = (0, \bar{D}_1]$  when  $a_1 = 0$ . When case 1 holds and  $n = 1$ , the equation  $\Phi_2(D) = 0$  has a unique solution  
 389  $\tilde{D}_1 \in [0, \bar{D}_1]$ . Thus, the function  $F_i^2$  is defined on  $(\tilde{D}_1, \bar{D}_1]$  since  $\Phi_2(D) > 0$  for all  $D \in (\tilde{D}_1, \bar{D}_1]$ .  
 390 The other cases can be treated similarly (see Figure 8(b-d)). ■

391 The following result describes the properties of the functions  $F_0$  and  $F_i^j$ ,  $i, j = 1, 2$ , when  $s_1^{in}$  is fixed.

**Proposition A.4.** *Let  $s_1^{in} \geq 0$ . We have  $I_2 \subset I_1$ ,  $F_i^1(D) \leq F_i^2(D)$ ,  $i = 1, 2$ , for all  $D \in I_2$  and*

$$\lim_{D \rightarrow \bar{D}_0^-} F_0(D, s_1^{in}) = \lim_{D \rightarrow \bar{D}_1^-} F_i^1(D) = \lim_{D \rightarrow \bar{D}_j^-} F_i^2(D) = +\infty, \quad j = 1, \dots, n.$$

392 When case 1 of (4.1) holds, we have  $F_i^1(\bar{D}_1) = F_i^2(\bar{D}_1)$ ,  $i = 1, 2$ .

393 *Proof.* Using Hypothesis 2.5, given that  $M_1^1(D_1) \leq M_1^2(D_1)$ , for all  $D \in \bar{I}_2$ , we can write

$$394 \quad (\text{A.8}) \quad \Phi_1(D) = \bar{\mu}_0(M_1^1(D_1)) - D_0 \geq \bar{\mu}_0(M_1^2(D_1)) - D_0 = \Phi_2(D).$$

395 If  $D \in I_2$ , that is,  $D \in \bar{I}_2$  such that  $\Phi_2(D) > 0$ , then  $D \in \bar{I}_1$  and  $\Phi_1(D) \geq \Phi_2(D) > 0$ , that is,  $D \in I_1$ .  
396 Thus,  $I_2 \subset I_1$ . Under Hypothesis 2.3 and the definition of  $M_0$  in Table 3, we have for all  $y \in [0, \bar{\mu}_0(s_1)]$   
397 and  $s_1 \geq 0$ ,

$$398 \quad (\text{A.9}) \quad \frac{\partial M_0}{\partial s_1}(y, s_1) = - \left[ \frac{\partial \mu_0}{\partial s_1}(M_0(y, s_1), s_1) \right] \left[ \frac{\partial \mu_0}{\partial s_0}(M_0(y, s_1), s_1) \right]^{-1} > 0.$$

From the definition of  $F_1^j$  in Table 3, it follows that

$$F_1^1(D) = M_0(D_0, M_1^1(D_1)) \leq M_0(D_0, M_1^2(D_1)) = F_1^2(D), \text{ for all } D \in I_2.$$

Similarly,  $F_2^1(D) \leq F_2^2(D)$ , for all  $D \in I_2$ . From the definitions of  $F_0$  and  $\bar{D}_0(s_1^{in})$  in Tables 3 and 9, we then obtain

$$F_0(\bar{D}_0(s_1^{in}), s_1^{in}) = M_0(\alpha_0 \bar{D}_0(s_1^{in}) + a_0, s_1^{in}) = M_0(\bar{\mu}_0(s_1^{in}), s_1^{in}) = +\infty.$$

399 When case 1 of (4.1) holds, the function  $F_i^j$ ,  $i, j = 1, 2$ , is defined for  $D = \bar{D}_1$ . Using Hypothesis 2.4  
400 and the definition of  $\bar{D}_1$  in Table 9, it follows that

$$401 \quad (\text{A.10}) \quad M_1^1(\alpha_1 \bar{D}_1 + a_1) = M_1^1(\mu_1^{max}) = M_1^2(\mu_1^{max}) = s_1^{max}.$$

Consequently,

$$F_1^1(\bar{D}_1) = M_0(\alpha_0 \bar{D}_1 + a_0, s_1^{max}) = F_1^2(\bar{D}_1), \quad F_2^1(\bar{D}_1) = M_0(\alpha_0 \bar{D}_1 + a_0, s_1^{max}) + s_1^{max} = F_2^2(\bar{D}_1).$$

402 From the definitions  $\Phi_1$  and  $\hat{D}_1$  in Table 9, we have  $\bar{\mu}_0(M_1^1(\alpha_1 \hat{D}_1 + a_1)) = \alpha_0 \hat{D}_1 + a_0$ . Therefore,

$$403 \quad F_1^1(\hat{D}_1) = M_0(\bar{\mu}_0(M_1^1(\alpha_1 \hat{D}_1 + a_1)), M_1^1(\alpha_1 \hat{D}_1 + a_1)) = +\infty,$$

$$404 \quad F_2^1(\hat{D}_1) = F_1^1(\hat{D}_1) + M_1^1(\alpha_1 \hat{D}_1 + a_1) = +\infty.$$

405 The last limit follows similarly. ■

## 406 Appendix B. Proofs.

**Proof of Proposition 2.6.** Since the vector field defined by system (2.1) is  $\mathcal{C}^1$ , the uniqueness of solution to initial value problems holds. From (2.1),  $x_i(t_0) = 0$ , for any  $t_0 \geq 0$  implies  $\dot{x}_i(t_0) = 0$ ,  $i = 0, 1$ . If  $x_i(0) = 0$ , then  $x_i(t) = 0$  for all  $t$  as the boundary face  $x_i \equiv 0$  is invariant in the vector field  $\mathcal{C}^1$  by (2.1). If  $x_i(0) > 0$ , then  $x_i(t) > 0$  for all  $t$  as  $x_i \equiv 0$  cannot be reached in finite time by trajectories for which  $x_i(0) > 0$  by the uniqueness of solutions. On the other hand, we have

$$s_0(t_0) = 0 \text{ for any } t_0 \geq 0 \quad \Rightarrow \quad \dot{s}_0(t_0) = Ds_0^{in}.$$

If  $\dot{s}_0(t_0) = 0$ , then  $s_0(t) \geq 0$  for all  $t$ , using arguments similar to case  $x_i$ . However, if  $\dot{s}_0(t_0) > 0$ , then  $s_0(t) \geq 0$  for all  $t$ . In fact, assume that  $s_0(0) \geq 0$  and that it exists  $t_0 > 0$ , such that  $s_0(t_0) = 0$  and  $s_0(t) > 0$ , for  $t \in (0, t_0)$ . Then  $\dot{s}_0(t_0) \leq 0$  which contradicts  $\dot{s}_0(t_0) > 0$ . Finally, we have

$$s_1(t_0) = 0 \text{ for any } t_0 \geq 0 \quad \Rightarrow \quad \dot{s}_1(t_0) = Ds_1^{in} + \mu_0(s_0(t_0), 0)x_0(t_0).$$

Similarly to case  $s_0$ , no trajectory can leave the positive octant  $\mathbb{R}_+^4$  by crossing the boundary face  $s_1 = 0$  since  $s_0 \geq 0$  and  $x_0 \geq 0$ . Therefore, all solutions of (2.1) remain nonnegative. Let  $z = 2s_0 + x_0 + s_1 + x_1$ . From (2.1), it follows that

$$\dot{z} = D(2s_0^{in} + s_1^{in} - 2s_0 - s_1) - D_0x_0 - D_1x_1 \leq D_{\min} \left( \frac{D}{D_{\min}} (2s_0^{in} + s_1^{in}) - z \right).$$

407 By applying Gronwall's lemma, we obtain

$$408 \quad (\text{B.1}) \quad z(t) \leq \frac{D}{D_{\min}} (2s_0^{in} + s_1^{in}) + \left( z(0) - \frac{D}{D_{\min}} (2s_0^{in} + s_1^{in}) \right) e^{-D_{\min}t}, \quad \text{for all } t \geq 0.$$

We deduce that

$$z(t) \leq \max \left( z(0), \frac{D}{D_{\min}} (2s_0^{in} + s_1^{in}) \right), \quad \text{for all } t \geq 0.$$

409 Consequently, the solutions of (2.1) are bounded for all  $t \geq 0$ . Inequality (B.1) implies that the set  $\Omega$   
410 is positively invariant and is a global attractor for (2.1).  $\blacksquare$

411 **Proof of Proposition 3.1.** The steady states of (2.1) are the solutions of the following set of  
412 equation

$$413 \quad (\text{B.2}) \quad D(s_0^{in} - s_0) - \mu_0(s_0, s_1)x_0 = 0$$

$$414 \quad (\text{B.3}) \quad (\mu_0(s_0, s_1) - D_0)x_0 = 0$$

$$415 \quad (\text{B.4}) \quad D(s_1^{in} - s_1) + \mu_0(s_0, s_1)x_0 - \mu_1(s_1)x_1 = 0$$

$$416 \quad (\text{B.5}) \quad (\mu_1(s_1) - D_1)x_1 = 0.$$

418 Using (B.2)+(B.3) and (B.4)-(B.3)+(B.5), we obtain the set of equations

$$419 \quad (\text{B.6}) \quad \begin{cases} D(s_0^{in} - s_0) - D_0x_0 = 0 \\ D(s_1^{in} - s_1) + D_0x_0 - D_1x_1 = 0. \end{cases}$$

420 By solving (B.6), we obtain  $x_0$  and  $x_1$  with respect to  $s_0$  and  $s_1$ :

$$421 \quad (\text{B.7}) \quad x_0 = \frac{D}{D_0} (s_0^{in} - s_0),$$

$$422 \quad (\text{B.8}) \quad x_1 = \frac{D}{D_1} (s_0^{in} - s_0 + s_1^{in} - s_1).$$

424 We can also solve (B.6) and obtain  $s_0$  and  $s_1$  with respect to  $x_0$  and  $x_1$ :

$$425 \quad (\text{B.9}) \quad s_0 = s_0^{in} - \frac{D_0}{D}x_0,$$

$$426 \quad (\text{B.10}) \quad s_1 = s_1^{in} + \frac{D_0}{D}x_0 - \frac{D_1}{D}x_1.$$

428 For  $\text{SS}_0$ , one has  $x_0 = x_1 = 0$ . Hence, (B.9) and (B.10) result in  $s_0 = s_0^{in}$  and  $s_1 = s_1^{in}$ . Thus,  $\text{SS}_0$   
429 always exists.

For  $\text{SS}_1$ , one has  $x_0 > 0$ ,  $x_1 = 0$ . Hence, (B.7) results in

$$x_0 = \frac{D}{D_0} (s_0^{in} - s_0).$$

Using (B.8) and  $x_1 = 0$ , it follows that

$$s_1 = s_1^{in} + s_0^{in} - s_0.$$

430 Since  $x_0 > 0$ , (B.3) results in

$$431 \quad (\text{B.11}) \quad \psi(s_0) := \mu_0(s_0, s_1^{in} + s_0^{in} - s_0) = D_0.$$

432 Thus,  $\text{SS}_1$  exists if and only if equation (B.11) has a nonnegative solution and the  $s_1$  and  $x_0$ -components  
433 are positive. This condition is equivalent to say that  $0 \leq s_0 < s_0^{in}$ . From Hypotheses 2.1 and 2.3, we

434 see that the function  $s_0 \mapsto \psi(s_0)$  is strictly increasing from 0 for  $s_0 = 0$  to  $\mu_0(s_0^{in}, s_1^{in})$  for  $s_0 = s_0^{in}$ .  
 435 Therefore, there exists a solution of equation (B.11) in  $[0, s_0^{in}]$  if and only if

436 (B.12) 
$$\mu_0(s_0^{in}, s_1^{in}) > D_0.$$

437 If such a solution exists, then it is unique. Under Hypothesis 2.3 and the definition of  $M_0$  in Table 3,  
 438 we have for all  $y \in [0, \bar{\mu}_0(s_1))$  and  $s_1 \geq 0$ ,

439 (B.13) 
$$\frac{\partial M_0}{\partial y}(y, s_1) = \left[ \frac{\partial \mu_0}{\partial s_0}(M_0(y, s_1), s_1) \right]^{-1} > 0.$$

440 Using (B.13), condition (B.12) is equivalent to the existence condition of  $SS_1$  in Table 5.

For  $SS_2^j$ ,  $j = 1, 2$ , one has  $x_0 > 0$  and  $x_1 > 0$ . Hence, (B.7) and (B.8) result in

$$x_0 = \frac{D}{D_0}(s_0^{in} - s_0), \quad x_1 = \frac{D}{D_1}(s_0^{in} + s_1^{in} - s_0 - s_1).$$

Moreover, (B.3) and (B.5) result in  $\mu_0(s_0, s_1) = D_0$  and  $\mu_1(s_1) = D_1$ . Using the definitions of  $M_0$  and  $M_1^j$  in Table 3, we obtain

$$s_0 = M_0(D_0, s_1), \quad s_1 = M_1^j(D_1),$$

where the function  $M_1^j(D_1)$  is defined for all  $D \in \bar{I}_j$ . From Hypotheses 2.1, 2.3, and 2.5, the function  $s_0 \mapsto \mu_0(s_0, M_1^j(D_1))$  is strictly increasing from 0 for  $s_0 = 0$  to  $\bar{\mu}_0(M_1^j(D_1))$  when  $s_0$  tends towards infinity. Using the definitions of  $\Phi_j(D)$  and  $I_j$  in Table 9, equation  $\mu_0(s_0, M_1^j(D_1)) = D_0$  has a solution  $s_0 \geq 0$  if and only if

$$\Phi_j(D) := \bar{\mu}_0(M_1^j(D_1)) - D_0 > 0, \quad \text{with } D \in \bar{I}_j,$$

441 or equivalently  $D \in I_j$ . Thus,  $SS_2^j$  exists if and only if  $s_0^{in} + s_1^{in} > s_0 + s_1$  and  $s_0^{in} > s_0$ , that is, the  
 442 existence condition in Table 5 is satisfied with  $D \in I_j$ .

For  $SS_3^j$ ,  $j = 1, 2$ , one has  $x_0 = 0$  and  $x_1 > 0$ . Hence, (B.8) and (B.9) result in

$$s_0 = s_0^{in}, \quad x_1 = \frac{D}{D_1}(s_1^{in} - s_1).$$

Since  $x_1 > 0$ , (B.5) results in  $\mu_1(s_1) = D_1$ . Using the definitions of  $M_1^j$  in Table 3, we obtain

$$s_1 = M_1^j(D_1), \quad \text{where } D \in \bar{I}_j.$$

443 Thus, we conclude that  $SS_3^j$  exists if and only if  $s_1^{in} > M_1^j(D_1)$ .

444 In what follows, we determine the local asymptotic stability of each steady state of (2.1). Let  $J$   
 445 be the Jacobian matrix of (2.1) at a steady state  $(s_0, x_0, s_1, x_1)$ , that is given by

446 (B.14) 
$$J = \begin{bmatrix} -D - Ex_0 & -\mu_0 & Fx_0 & 0 \\ Ex_0 & \mu_0 - D_0 & -Fx_0 & 0 \\ Ex_0 & \mu_0 & -D - Fx_0 - \mu_1'x_1 & -\mu_1 \\ 0 & 0 & \mu_1'x_1 & \mu_1 - D_1 \end{bmatrix},$$

where

$$E = \frac{\partial \mu_0}{\partial s_0}(s_0, s_1) > 0, \quad F = -\frac{\partial \mu_0}{\partial s_1}(s_0, s_1) > 0.$$

For  $SS_0$ , the characteristic polynomial is  $P_0(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda + D)^2$ , where

$$\lambda_1 = \mu_0(s_0^{in}, s_1^{in}) - D_0, \quad \lambda_2 = \mu_1(s_1^{in}) - D_1.$$

447 Thus,  $SS_0$  is LES if and only if

448 (B.15) 
$$\mu_0(s_0^{in}, s_1^{in}) < D_0 \quad \text{and} \quad \mu_1(s_1^{in}) < D_1.$$

If  $D_0 \geq \bar{\mu}_0(s_1^{in})$ , that is,  $D \notin I_0$ , then the first condition of (B.15) is satisfied. If  $D \in I_0$ , using (B.13) and the definition of  $M_0$  in Table 3, it follows that the first condition of (B.15) is equivalent to

$$s_0^{in} < M_0(D_0, s_1^{in}) = F_0(D, s_1^{in}).$$

449 If  $D_1 > \mu_1^{max}$ , that is,  $D \notin \bar{I}_1$ , then the second condition of (B.15) is satisfied. If  $D \in \bar{I}_j$ ,  $j = 1, 2$ ,  
450 using the definition of  $M_1^j$  in Table 3, it follows that the second condition of (B.15) is equivalent to

$$451 \quad (\text{B.16}) \quad s_1^{in} < M_1^1(D_1) \quad \text{with} \quad D \in \bar{I}_1 \quad \text{or} \quad s_1^{in} > M_1^2(D_1) \quad \text{with} \quad D \in \bar{I}_2.$$

452 At  $\text{SS}_1$ , the Jacobian matrix is given by

$$453 \quad J = \begin{bmatrix} -D - Ex_0 & -D_0 & Fx_0 & 0 \\ Ex_0 & 0 & -Fx_0 & 0 \\ Ex_0 & D_0 & -D - Fx_0 & -\mu_1 \\ 0 & 0 & 0 & \mu_1 - D_1 \end{bmatrix}.$$

Denote  $C_i$  and  $L_i$  the columns and lines of the matrix  $J - \lambda I$ . The replacements of  $L_1$  by  $L_1 + L_3$  and then  $C_3$  by  $C_3 - C_1$  preserve the determinant and lead to the following characteristic polynomial

$$P_1(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda^2 + c_1\lambda + c_2),$$

454 where  $\lambda_1 = \mu_1(s_0^{in} + s_1^{in} - s_0) - D_1$ ,  $\lambda_2 = -D$ ,  $c_1 = D + (E + F)x_0$  and  $c_2 = D_0(E + F)x_0$ . Since  
455  $c_1 > 0$  and  $c_2 > 0$ , the real parts of the roots of the quadratic factor are negative. Therefore,  $\text{SS}_1$  is  
456 LES if and only if  $\lambda_1 < 0$ , that is,

$$457 \quad (\text{B.17}) \quad \mu_1(s_0^{in} + s_1^{in} - s_0) < D_1.$$

458 If  $D_1 > \mu_1^{max}$ , that is,  $D \notin \bar{I}_1$ , then condition (B.17) is satisfied. If  $D_1 \leq \mu_1^{max}$ , that is,  $D \in \bar{I}_1$ , then  
459 condition (B.17) is equivalent to

$$460 \quad (\text{B.18}) \quad s_0 > s_0^{in} + s_1^{in} - M_1^1(D_1) \quad \text{or} \quad s_0 < s_0^{in} + s_1^{in} - M_1^2(D_1).$$

Since the function  $s_0 \mapsto \psi(s_0) = \mu_0(s_0, s_0^{in} + s_1^{in} - s_0)$  is increasing, (B.18) is equivalent to

$$\psi(s_0) > \psi(s_0^{in} + s_1^{in} - M_1^1(D_1)) \quad \text{or} \quad \psi(s_0) < \psi(s_0^{in} + s_1^{in} - M_1^2(D_1)).$$

461 At  $\text{SS}_1$ , one has  $\psi(s_0) = D_0$ . Thus, condition (B.18) is equivalent to

$$462 \quad (\text{B.19}) \quad D_0 > \mu_0(s_0^{in} + s_1^{in} - M_1^1(D_1), M_1^1(D_1)) \quad \text{or} \quad D_0 < \mu_0(s_0^{in} + s_1^{in} - M_1^2(D_1), M_1^2(D_1)).$$

If  $D \in \bar{I}_1 \setminus I_1$ , that is,  $\Phi_1(D) < 0$  (or equivalently  $\bar{\mu}_0(M_1^1(D_1)) < D_0$ ) then the first condition of (B.19) is satisfied. If  $D \in \bar{I}_1 \setminus I_2$ , that is,  $\bar{\mu}_0(M_1^2(D_1)) < D_0$ , then the second condition of (B.19) is not satisfied. If  $D \in I_j$ ,  $j = 1, 2$ , then condition (B.19) is equivalent to

$$s_0^{in} + s_1^{in} < M_0(D_0, M_1^1(D_1)) + M_1^1(D_1) \quad \text{or} \quad s_0^{in} + s_1^{in} > M_0(D_0, M_1^2(D_1)) + M_1^2(D_1)$$

463 because the function  $M_0(\cdot, M_1^j(D_1))$  is increasing. These conditions are the same as those in Table 5.

464 For  $\text{SS}_2^j$ ,  $j = 1, 2$ , the characteristic polynomial is  $P_2(\lambda) = \lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4$ , where

$$465 \quad c_1 = G_j x_1 + H x_0 + 2D, \quad c_2 = EG_j x_0 x_1 + (D + D_0)H x_0 + (D + D_1)G_j x_1 + D^2,$$

$$466 \quad c_3 = (D_0 + D_1)EG_j x_0 x_1 + DD_0 H x_0 + DD_1 G_j x_1, \quad c_4 = D_0 D_1 EG_j x_0 x_1,$$

468 with  $H = E + F$  and  $G_1 := \mu_1'(M_1^1(D_1)) > 0$  since  $M_1^1(D_1) < s_1^{max}$  and  $G_2 := \mu_1'(M_1^2(D_1)) < 0$  since  
469  $M_1^2(D_1) > s_1^{max}$ . Note that  $G_1 = G_2 = 0$ , when  $D = \bar{D}_1$  where  $\text{SS}_2^1 = \text{SS}_2^2$ . Using the Liénard-Chipart  
470 stability criteria (see Gantmacher [20], Theorem 11),  $\text{SS}_2^j$  is LES if and only if

$$471 \quad (\text{B.20}) \quad c_i > 0, \quad i = 1, 3, 4, \quad \text{and} \quad c_1 c_2 c_3 - c_1^2 c_4 - c_3^2 > 0.$$

Hence,  $SS_2^2$  is unstable as long as it exists with  $D \neq \bar{D}_1$  because the condition  $c_4 > 0$  in (B.20) is unfulfilled as  $G_2 < 0$ . For  $SS_2^1$ ,  $c_i > 0$ , for all  $i = 1, 3, 4$ , as  $E, F, H$  and  $G_1$  are positive. Following [40], where the particular case  $\alpha_0 = \alpha_1 = 1$  was considered, we obtain

$$c_1 c_2 c_3 - c_1^2 c_4 - c_3^2 = \gamma_5 D^5 + \gamma_4 D^4 + \gamma_3 D^3 + \gamma_2 D^2 + \gamma_1 D + \gamma_0,$$

472 where the coefficients  $\gamma_j$ ,  $j = 0, \dots, 5$ , can be written as follows:

$$\gamma_5 = 2(\alpha_0 H x_0 + \alpha_1 G_1 x_1),$$

$$\gamma_4 = 2[\alpha_0(1 - \alpha_1) + \alpha_1(1 - \alpha_0)]EG_1 x_0 x_1 + ((3 + \alpha_0)H x_0 + (3 + \alpha_1)G_1 x_1)(\alpha_0 H x_0 + \alpha_1 G_1 x_1) + 2a_0 H x_0 + 2a_1 G_1 x_1,$$

$$\gamma_3 = [2(\alpha_1 a_0 + \alpha_0 a_1)H + (a_0(5 - 4\alpha_1) + a_1(5 - 4\alpha_0))E + 3(a_0 + a_1)F]G_1 x_0 x_1 + [\alpha_1(\alpha_0 + 1)H + ((7 - 3\alpha_1)\alpha_0 + 3\alpha_1 + \alpha_0^2)E + \alpha_0(\alpha_0 + \alpha_1 + 2)F]HG_1 x_0^2 x_1 + [\alpha_0(\alpha_1 + 1)H + ((7 - 3\alpha_0)\alpha_1 + 3\alpha_0 + \alpha_1^2)E + \alpha_1(\alpha_0 + \alpha_1 + 2)F]G_1^2 x_0 x_1^2 + (3 + 2\alpha_0)a_0 H^2 x_0^2 + (3 + 2\alpha_1)a_1 G_1^2 x_1^2 + \alpha_0(\alpha_0 + 1)H^3 x_0^3 + \alpha_1(\alpha_1 + 1)G_1^3 x_1^3,$$

$$\gamma_2 = [a_0((2\alpha_0 + \alpha_1 + 2)H + (5 - 3\alpha_1)E + \alpha_1 F) + a_1((\alpha_0 + 1)H + 3(1 - \alpha_0)E + \alpha_0 F)]HG_1 x_0^2 x_1 + [a_0((\alpha_1 + 1)H + 3(1 - \alpha_1)E + \alpha_1 F) + a_1(2(\alpha_0 + \alpha_1 + 1)H + (5 - 4\alpha_0)E)]G_1^2 x_0 x_1^2 + [((3 - 2\alpha_1)\alpha_0 + \alpha_1)H + 2(\alpha_0 + 2\alpha_1)E + ((\alpha_0 + \alpha_1)^2 + 2\alpha_1)F]EG_1^2 x_0^2 x_1^2 + (\alpha_0^2 + 2\alpha_0 + \alpha_1)EH^2 G_1 x_0^3 x_1 + (\alpha_1^2 + 2\alpha_1 + \alpha_0)EG_1^3 x_0 x_1^3 + (1 + 2\alpha_0)a_0 H^3 x_0^3 + (1 + 2\alpha_1)a_1 G_1^3 x_1^3 + (a_0 H x_0 - a_1 G_1 x_1)^2 + 4a_0 a_1 F G_1 x_0 x_1,$$

$$\gamma_1 = (H x_0 + G_1 x_1)(a_0 H x_0 - a_1 G_1 x_1)^2 + 4a_0 a_1 F H G_1 x_0^2 x_1 + 4a_0 a_1 F G_1^2 x_0 x_1^2 + [a_0((5 - 2\alpha_1)E + (2\alpha_0 + 3)F) + a_1((5 - 2\alpha_0)E + (2\alpha_1 + 3)F)]EG_1^2 x_0^2 x_1^2 + (2(\alpha_0 + 1)a_0 + a_1)EH^2 G_1 x_0^3 x_1 + (a_0 + 2(\alpha_1 + 1)a_1)EG_1^3 x_0 x_1^3 + (\alpha_0 + \alpha_1)(H x_0 + G_1 x_1)E^2 G_1^2 x_0^2 x_1^2,$$

$$\gamma_0 = (a_0 + a_1)(H x_0 + G_1 x_1)E^2 G_1^2 x_0^2 x_1^2 + (a_0 + a_1)^2 E F G_1^2 x_0^2 x_1^2 + (a_0 H x_0 - a_1 G_1 x_1)^2 E G_1 x_0 x_1.$$

474 Since  $\alpha_0$  and  $\alpha_1$  are in  $[0, 1]$ , then  $\gamma_j > 0$  for  $j = 0, \dots, 5$ . Thus, the conditions of Liénard-Chipart  
475 stability criteria (B.20) are satisfied for  $SS_2^1$  which is LES as long as it exists with  $D \neq \bar{D}_1$ .

For  $SS_3^j$ ,  $j = 1, 2$ , the characteristic polynomial is

$$P_3(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)(\lambda^2 + c_1 \lambda + c_2),$$

476 where  $\lambda_1 = -D$ ,  $\lambda_2 = \mu_0(s_0^{in}, M_1^j(D_1)) - D_0$ ,  $c_1 = D + G_j x_1$  and  $c_2 = D_1 G_j x_1$ . For  $SS_3^2$ ,  $c_2 < 0$  since  
477  $G_2 < 0$ . Therefore, the roots of the quadratic factor are real and have opposite signs. Consequently,  
478 if  $SS_3^2$  exists, it is unstable. For  $SS_3^1$ , the real parts of the roots of the quadratic factor are negative as  
479  $G_1 > 0$  so that  $c_1 > 0$  and  $c_2 > 0$ . Therefore,  $SS_3^1$  is LES if and only if

$$480 \quad (B.21) \quad \mu_0(s_0^{in}, M_1^1(D_1)) < D_0 \iff s_0^{in} < M_0(D_0, M_1^1(D_1)),$$

481 since the function  $M_0(\cdot, M_1^1(D_1))$  is increasing. ■

**Proof of Proposition 4.1.** Assume that  $s_1^{in} < M_1^1(D_1)$ . Using Table 5,  $SS_3^j$ ,  $j = 1, 2$  does not exist. In this case, we have  $F_1^j(D) < F_2^j(D) - s_1^{in}$ . If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_1$ , then  $s_0^{in} < F_0(D, s_1^{in})$ . From Table 5,  $SS_0$  is LES and  $SS_1$  does not exist. If  $D \notin I_j$ , then the existence condition of  $SS_2^j$  does not hold since  $F_1^j(D) = F_2^j(D) = +\infty$ . Let  $D \in I_j$ . Assume that the existence condition of  $SS_2^j$  holds. Then,

$$M_0(D_0, M_1^j(D_1)) = F_1^j(D) < s_0^{in} < F_0(D, s_1^{in}) = M_0(D_0, s_1^{in}).$$

Using (A.9), we obtain  $M_1^j(D_1) < s_1^{in}$  which is the desired contradiction. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_2$ , then  $F_0(D, s_1^{in}) < s_0^{in} < F_2^1(D) - s_1^{in}$ . From Table 5,  $SS_0$  is unstable and  $SS_1$  exists and is LES. If  $D \notin I_j$ ,

the existence condition of  $SS_2^j$  does not hold. Let  $D \in I_j$ . If  $SS_2^j$  exists, that is,  $s_0^{in} > F_2^j(D) - s_1^{in}$ . This is a contradiction for  $j = 1$ . However, for  $j = 2$ , one has  $F_2^1(D) - s_1^{in} < F_2^2(D) - s_1^{in} < s_0^{in}$  which is a contradiction. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_3$ , then  $F_2^1(D) - s_1^{in} < s_0^{in} < F_2^2(D) - s_1^{in}$ . From Table 5,  $SS_2^1$  exists and is LES while  $SS_2^2$  does not exist. Assume that  $s_0^{in} \leq F_0(D, s_1^{in})$ . Hence,

$$F_1^1(D) < F_2^1(D) - s_1^{in} < F_0(D, s_1^{in}), \quad \text{or (equivalently)} \quad M_1^1(D_1) < s_1^{in},$$

which is a contradiction, that is,  $s_0^{in} > F_0(D, s_1^{in})$ . Therefore,  $SS_0$  exists and is unstable while  $SS_1$  exists and is LES, using Table 5. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_4$ , then  $s_0^{in} > F_2^2(D) - s_1^{in} > F_2^1(D) - s_1^{in} > F_1^1(D)$ . From Table 5,  $SS_2^1$  exists and is LES while  $SS_2^2$  exists and is unstable. Assume that  $s_0^{in} \leq F_0(D, s_1^{in})$ . Hence,

$$F_1^1(D) < F_0(D, s_1^{in}), \quad \text{or (equivalently)} \quad M_1^1(D_1) < s_1^{in},$$

482 which is a contradiction. Thus,  $s_0^{in} > F_0(D, s_1^{in})$ . Therefore,  $SS_0$  is unstable while  $SS_1$  is LES, using  
483 Table 5.

Assume that  $M_1^1(D_1) < s_1^{in} < M_1^2(D_1)$ . Using Table 5,  $SS_0$  is unstable,  $SS_3^1$  exists and  $SS_3^2$  does not exist. In this cas, we have  $F_1^1(D) > F_2^1(D) - s_1^{in}$  and  $F_1^2(D) < F_2^2(D) - s_1^{in}$ . If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_5$ , then  $s_0^{in} > F_2^2(D) - s_1^{in} > F_1^2(D) > F_1^1(D)$ . Assume that  $s_0^{in} \leq F_0(D, s_1^{in})$ . Hence,

$$F_1^2(D) < F_0(D, s_1^{in}), \quad \text{or (equivalently)} \quad M_1^2(D_1) < s_1^{in}$$

which is a contradiction. Thus,  $s_0^{in} > F_0(D, s_1^{in})$ . From Table 5,  $SS_1$  and  $SS_2^1$  exist and are LES while  $SS_2^2$  exists and is unstable. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_6$ , then

$$F_2^1(D) - s_1^{in} < F_1^1(D) < F_0(D, s_1^{in}) < s_0^{in} < F_2^2(D) - s_1^{in}$$

because  $M_1^1(D_1) < s_1^{in}$ . Using Table 5,  $SS_1$  and  $SS_3^1$  exist and are unstable,  $SS_2^1$  exists and is LES,  $SS_2^2$  does not exist. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_7$ , then

$$F_1^1(D) < s_0^{in} < F_0(D, s_1^{in}) < F_1^2(D) < F_2^2(D) - s_1^{in},$$

as  $s_1^{in} < M_1^2(D_1)$ . From Table 5,  $SS_1$  and  $SS_2^2$  do not exist, and  $SS_2^1$  exists and is LES, and  $SS_3^1$  exists and is unstable. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_8$ , then

$$s_0^{in} < F_1^1(D) < F_0(D, s_1^{in}) < F_1^2(D) < F_2^2(D) - s_1^{in}.$$

484 From Table 5,  $SS_1$ ,  $SS_2^1$  and  $SS_2^2$  do not exist and  $SS_3^1$  exists and is LES.

Assume that  $M_1^2(D_1) < s_1^{in}$ . Using Table 5,  $SS_3^1$  and  $SS_3^2$  exist. In this case, we have  $F_1^1(D) > F_2^1(D) - s_1^{in}$  and  $F_1^2(D) > F_2^2(D) - s_1^{in}$ . If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_9$ , then

$$s_0^{in} < F_1^1(D) < F_1^2(D) < F_0(D, s_1^{in}).$$

From Table 5,  $SS_1$ ,  $SS_2^1$  and  $SS_2^2$  do not exist,  $SS_0$  and  $SS_3^1$  are LES and  $SS_3^2$  is unstable. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_{10}$ , then

$$F_1^1(D) < s_0^{in} < F_1^2(D) < F_0(D, s_1^{in}).$$

From Table 5,  $SS_1$  and  $SS_2^2$  do not exist,  $SS_0$  and  $SS_2^1$  are LES, and  $SS_3^1$  and  $SS_3^2$  are unstable. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_{11}$ , then

$$F_1^1(D) < F_1^2(D) < s_0^{in} < F_0(D, s_1^{in}).$$

From Table 5,  $SS_1$  does not exist,  $SS_0$  and  $SS_2^1$  are LES, and  $SS_2^2$ ,  $SS_3^1$  and  $SS_3^2$  are unstable. If  $(D, s_0^{in}, s_1^{in}) \in \mathcal{J}_{12}$ , then

$$F_2^1(D) - s_1^{in} < F_1^1(D) < F_1^2(D) < F_0(D, s_1^{in}) < s_0^{in}.$$

485 From Table 5,  $SS_1$  and  $SS_2^1$  are LES, and  $SS_0$ ,  $SS_2^2$ ,  $SS_3^1$  and  $SS_3^2$  are unstable. ■

**Proof of Proposition 4.2.** Let  $D \in \bar{I}_j$ . We have  $s_{1j}^{in*} = M_1^j(D_1) \geq 0$ ,  $j = 1, 2$  such that  $s_{11}^{in*} < s_{12}^{in*}$  because  $M_1^1(D_1) \leq M_1^2(D_1)$ , for all  $D \in \bar{I}_2$ . For all  $D \in I_1$ , one has

$$F_0(D, s_{11}^{in*}) = M_0(D_0, M_1^1(D_1)) = F_1^1(D) < +\infty = F_0(D, \bar{s}_1^{in}).$$

As the function  $F_0(D, \cdot)$  is increasing, we obtain  $s_{11}^{in*} < \bar{s}_1^{in}$ . For all  $D \in I_1$ , we have

$$F_1^1(D) = F_1^1(D) + M_1^1(D_1) - s_{11}^{in*} = F_2^1(D) - s_{11}^{in*},$$

that is, the curves  $\gamma_0$ ,  $\gamma_1^1$  and  $\gamma_2^1$  intersect at  $s_{11}^{in*}$ . For all  $s_1^{in} \in [0, s_{11}^{in*})$ , one has  $M_1^j(D_1) > s_1^{in}$  and therefore

$$M_0(D_0, s_1^{in}) < M_0(D_0, M_1^1(D_1)) < M_0(D_0, M_1^1(D_1)) + M_1^1(D_1) - s_1^{in},$$

486 that is, (4.2) holds. Inversely, for all  $s_1^{in} \in (s_{11}^{in*}, \bar{s}_1^{in})$ , (4.3) holds. The second assertion is proved in a  
487 similar manner. ■

**Proof of Proposition 4.3.** Let  $s_1^{in} \leq s_1^{max}$ . The function  $D \mapsto M_1^2(\alpha_1 D + a_1) - s_1^{in}$  is nonnegative for all  $D \in \bar{I}_2$  since it is decreasing from  $M_1^2(a_1) - s_1^{in}$  for  $D = 0$  to  $s_1^{max} - s_1^{in} \geq 0$  for  $D = \bar{D}_1$ . Thus, for all  $D \in I_2$ ,

$$F_1^2(D) = M_0(D_0, M_1^2(D_1)) \leq M_0(D_0, M_1^2(D_1)) + M_1^2(D_1) - s_1^{in} = F_2^2(D) - s_1^{in}.$$

Since  $M_0$  is increasing with respect to the second variable (see formula (A.9)), we have for all  $D \in I_2$ ,

$$F_0(D, s_1^{in}) = M_0(D_0, s_1^{in}) \leq M_0(D_0, M_1^2(D_1)) = F_1^2(D).$$

Since the function  $D \mapsto M_1^1(\alpha_1 D + a_1) - s_1^{in}$  is increasing from  $M_1^1(a_1) - s_1^{in}$  for  $D = 0$  to  $s_1^{max} - s_1^{in}$  for  $D = \bar{D}_1$ , there exists a solution  $D_1^* \in \bar{I}_1$  of equation  $M_1^1(\alpha_1 D + a_1) = s_1^{in}$  if and only if (4.6) holds. If such  $D_1^*$  exists then it is unique. If  $D_1^* \in I_1$ , the function  $F_i^1$  is defined for  $D = D_1^*$  where

$$F_2^1(D_1^*) - s_1^{in} = M_0(\alpha_0 D_1^* + a_0, M_1^1(\alpha_1 D_1^* + a_1)) = F_1^1(D_1^*) = M_0(\alpha_0 D_1^* + a_0, s_1^{in}) = F_0(D_1^*, s_1^{in}).$$

Since  $M_1^1(D_1) < s_1^{in}$  if  $D < D_1^*$ , one has

$$F_2^1(D) - s_1^{in} = M_0(D_0, M_1^1(D_1)) + M_1^1(D_1) - s_1^{in} < M_0(D_0, M_1^1(D_1)) = F_1^1(D) < M_0(D_0, s_1^{in}),$$

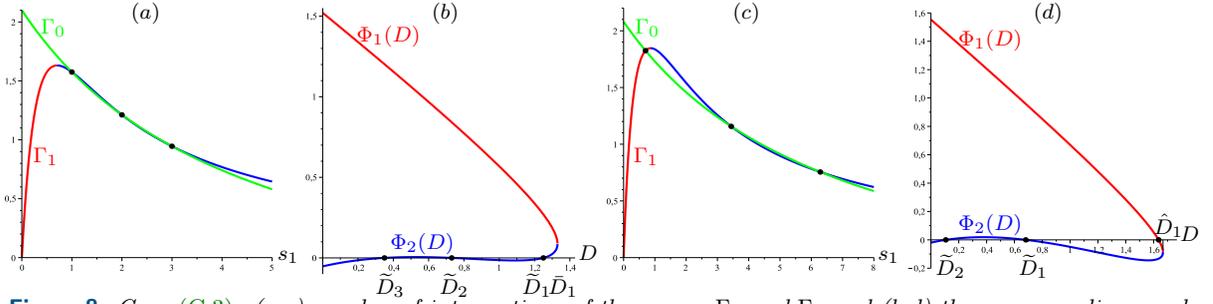
488 that is, (4.3) holds. Inversely, if  $D > D_1^*$ , then (4.2) holds. If  $D_1^* \in \bar{I}_1 \setminus I_1$ , that is,  $D_1^* \in [\hat{D}_1, \bar{D}_1]$ , then  
489  $M_1^1(\alpha_1 D + a_1) < s_1^{in}$  for all  $D \in [0, \hat{D}_1)$ . Therefore, (4.3) holds where  $\bar{D}_0(s_1^{in}) < \hat{D}_1$ . If  $D_1^*$  does not  
490 exist, then  $M_1^1(\alpha_1 D + a_1) > s_1^{in}$  for all  $D \in I_1$  and consequently (4.2) holds. ■

491 **Proof of Proposition 4.5.** From Table 6, the surface  $\gamma_0$  is defined by  $s_0^{in} = F_0(D, s_1^{in})$ . Using  
492 Tables 4 and 5 and Proposition 3.1, we can see that  $SS_0$  and  $SS_1$  coalesce and are nonhyperbolic steady  
493 states on the surface  $\gamma_0$ . Using Table 5, if  $s_1^{in} < M_1^1(D_1)$ , we have a transition from  $\mathcal{J}_1$  to  $\mathcal{J}_2$  where  
494  $SS_0$  becomes unstable and  $SS_1$  emerges stable in the positive octant  $\mathbb{R}_+^4$ . All other cases are left to  
495 the reader since they can be treated similarly. ■

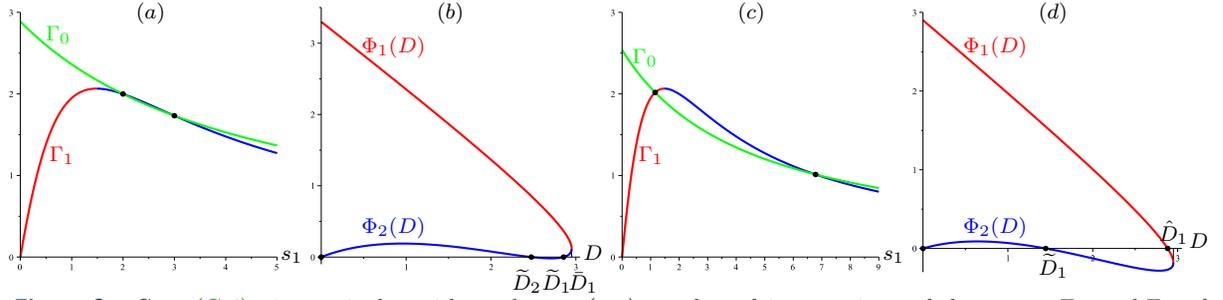
496 **Appendix C. The particular case for growth functions (C.1).** The Hypotheses 2.1 to 2.5 are  
497 satisfied by the following growth rates of Monod-type with hydrogen inhibition and of Haldane-type,  
498 respectively,

$$499 \quad (C.1) \quad \mu_0(s_0, s_1) = \frac{m_0 s_0}{K_0 + s_0} \frac{1}{1 + s_1/K_i}, \quad \mu_1(s_1) = \frac{m_1 s_1}{K_1 + s_1 + s_1^2/K_I},$$

500 where  $m_j$  and  $K_j$ ,  $j = 0, 1$ , denote the maximum growth rates (units are 1/d) and the Michaelis-Menten  
501 constants with units of concentration (kg COD/m<sup>3</sup>);  $K_i$  and  $K_I$  represent the inhibition factor due  
502 to  $s_1$  for the growth of the species  $x_0$  and  $x_1$ , respectively, with units of concentration. The following  
503 result determines the maximal number of solutions of the equation  $\Phi_2(D) = 0$  in the particular case  
504 of growth functions (C.1) when  $\alpha_0 > 0$  and  $\alpha_1 > 0$ .



**Figure 8.** Case (C.3): (a,c) number of intersections of the curves  $\Gamma_0$  and  $\Gamma_1$  and (b,d) the corresponding number of solutions of equation  $\Phi_j(D) = 0$ . (a-b) In case 1 of (4.1), the equation  $\Phi_2(D) = 0$  has three solutions on  $[0, \bar{D}_1]$ . (c-d) In case 2 of (4.1), the equation  $\Phi_2(D) = 0$  has two solutions on  $[0, \bar{D}_1]$ .



**Figure 9.** Case (C.4), in particular without decay: (a,c) number of intersections of the curves  $\Gamma_0$  and  $\Gamma_1$  of the functions  $\tilde{\mu}_0$  and  $\mu_1$ , respectively, and (b,d) the corresponding number of solutions of equation  $\Phi_j(D) = 0$ . (a-b) In case 1 of (4.1), the equation  $\Phi_2(D) = 0$  has two solutions on  $[0, \bar{D}_1]$ . (c-d) In case 2 of (4.1), the equation  $\Phi_2(D) = 0$  has one solution on  $[0, \bar{D}_1]$ .

505 **Proposition C.1.** Let  $\alpha_0 > 0$  and  $\alpha_1 > 0$ . The equations  $\Phi_1(D) = 0$  and  $\Phi_2(D) = 0$  are equivalent  
506 to

$$507 \quad (C.2) \quad \mu_1(y) = \tilde{\mu}_0(y) := \frac{\alpha_1}{\alpha_0} \bar{\mu}_0(y) + a_1 - \frac{\alpha_1}{\alpha_0} a_0, \quad \text{with } y = \bar{\mu}_0^{-1}(D_0).$$

508 When the growth functions  $\mu_0$  and  $\mu_1$  are of type (C.1), the equation  $\Phi_2(D) = 0$  has at most three  
509 solutions in the case 1 of (4.1) when

$$510 \quad (C.3) \quad a_1/\alpha_1 \neq a_0/\alpha_0,$$

511 and at most two solutions in the case 2 of (4.1) (see Figure 8(b-d)). It has at most two solutions in  
512 the case 1 of (4.1) when

$$513 \quad (C.4) \quad a_1/\alpha_1 = a_0/\alpha_0,$$

514 and at most one solution in the case 2 of (4.1), (see Figure 9(b-d)).

*Proof.* From definition of the function  $\Phi_j$  in Table 9 and Hypothesis 2.5, we have, for  $j = 1, 2$ ,

$$\Phi_j(D) = 0 \iff M_1^j(D_1) = \bar{\mu}_0^{-1}(D_0) \iff \mu_1(\bar{\mu}_0^{-1}(D_0)) = D_1.$$

Let  $y = \bar{\mu}_0^{-1}(D_0)$ . Thus,  $D_0 = \bar{\mu}_0(y)$  and  $D_1 = \mu_1(y)$ . From definition (1.3) of  $D_i$ ,  $i = 0, 1$ , we have  $D_1 = \alpha_1(D_0 - a_0)/\alpha_0 + a_1$ . Consequently, equation (C.2) holds. When the growth functions  $\mu_0$  and  $\mu_1$  are of type (C.1), we obtain

$$\frac{m_1 y}{K_1 + y + y^2/K_I} = \frac{K_i m_0 \alpha_1 / \alpha_0 + (K_i + y)(a_1 - a_0 \alpha_1 / \alpha_0)}{K_i + y}.$$

515 When condition (C.3) holds, we obtain an algebraic equation of degree three in  $y$  and consequently  
516 the equation (C.2) has at most three solutions. Hence, if case 1 of (4.1) holds, that is, the equation  
517  $\Phi_1(D) = 0$  has no solution, then the equation  $\Phi_2(D) = 0$  has at most three solutions. However, if case  
518 2 of (4.1) holds, that is, the equation  $\Phi_1(D) = 0$  has one solution, then the equation  $\Phi_2(D) = 0$  has  
519 at most two solutions. When condition (C.4) holds, we obtain an algebraic equation of degree two in  
520  $y$ . Thus, the rest of the results follows similarly.  $\blacksquare$

521 When the growth functions are given by (C.1), we succeeded in finding a set of parameters such  
 522 that we show the maximum number of intersections of the curves  $\Gamma_0$  and  $\Gamma_1$  and the corresponding  
 523 number of solutions of the equation  $\Phi_j(D) = 0$  (see Figures 8 and 9).

524 **Appendix D. Tables.** In this section, we give some tables used in the paper. Tables 10 and 11  
 525 describe the intersections of the surfaces of  $\Gamma$  with a two-dimensional operating plane where  $D$  or  $s_1^{in}$   
 526 is constant, respectively. Table 12 presents the auxiliary functions defined in Table 3 in the particular  
 527 case of the Monod-type with hydrogen inhibition and of the Haldane-type given by (C.1). Table 13  
 provides the biological parameter values used in all the figures.

**Table 10**

*Intersections of the surfaces of  $\Gamma$  with a  $(s_1^{in}, s_0^{in})$  plane where  $D$  is constant.*

$\Gamma$	Condition	$\Gamma \cap \{D = \text{constant}\}$
$\gamma_0$	$D < \bar{D}_0(0)$	Curve of the function $s_0^{in} = F_0(D, s_1^{in})$
	$D \geq \bar{D}_0(0)$	Empty
$\gamma_1^j$	$D \in I_j$	Horizontal line $s_0^{in} = F_1^j(D)$
	$D \notin I_j$	Empty
$\gamma_2^j$	$D \in I_j$	Oblique line $s_0^{in} = F_2^j(D) - s_1^{in}$
	$D \notin I_j$	Empty
$\gamma_3^j$	$D \in \bar{I}_j$	Vertical line $s_1^{in} = s_1^{in*} = M_1^j(D_1)$
	$D \notin \bar{I}_j$	Empty
$\gamma_4$	$D = \bar{D}_1$	Whole plane $(s_1^{in}, s_0^{in})$
	$D \neq \bar{D}_1$	Empty

**Table 11**

*Intersections of the surfaces of  $\Gamma$  with a  $(D, s_0^{in})$  plane where  $s_1^{in}$  is constant.*

$\Gamma$	Condition	$\Gamma \cap \{s_1^{in} = \text{constant}\}$
$\gamma_0$	$D < \bar{D}_0(s_1^{in})$	Curve of the function $s_0^{in} = F_0(D, s_1^{in})$
	$D \geq \bar{D}_0(s_1^{in})$	Empty
$\gamma_1^j$	$D \in I_j$	Curve of the function $s_0^{in} = F_1^j(D)$
	$D \notin I_j$	Empty
$\gamma_2^j$	$D \in I_j$ and $s_1^{in} < F_2^j(D)$	Curve of the function $s_0^{in} = F_2^j(D) - s_1^{in}$
	$D \notin I_j$ or $s_1^{in} > F_2^j(D)$	Empty
$\gamma_3^1$	$s_1^{in} \in (M_1^1(a_1), s_1^{max}]$	Vertical line $D = D_1^*$
	$s_1^{in} \notin (M_1^1(a_1), s_1^{max}]$	Empty
$\gamma_3^2$	$s_1^{in} \in [s_1^{max}, M_1^2(a_1))$	Vertical line $D = D_2^*$
	$s_1^{in} \notin [s_1^{max}, M_1^2(a_1))$	Empty
$\gamma_4$	$s_0^{in} \geq \max(0, s_1^{max} - s_1^{in})$	Vertical line $D = \bar{D}_1$

**Table 12**

*Auxiliary functions with the specific growth functions (C.1) where  $I_j, j = 1, 2$  are defined by (A.2), (A.5), and (A.6).*

Auxiliary function	Definition domain
$M_0(y, s_1) = \frac{K_0 y(1+s_1/K_i)}{m_0 - y(1+s_1/K_i)}$	$0 \leq y < \frac{m_0}{1+s_1/K_i}$
$M_1^j(y) = \frac{(m_1 - y)K_I \pm \sqrt{(K_I(m_1 - y))^2 - 4K_1 K_I y^2}}{2y}$	$0 < y < \frac{m_1}{1+2\sqrt{K_1/K_I}}$
$F_0(D, s_1^{in}) = \frac{K_0(\alpha_0 D + a_0)(1+s_1^{in}/K_i)}{m_0 - (\alpha_0 D + a_0)(1+s_1^{in}/K_i)}$	$0 \leq \alpha_0 D + a_0 < \frac{m_0}{1+s_1^{in}/K_i}$
$F_1^j(D) = \frac{K_0(\alpha_0 D + a_0)(1+M_1^j(\alpha_1 D + a_1)/K_i)}{m_0 - (\alpha_0 D + a_0)(1+M_1^j(\alpha_1 D + a_1)/K_i)}$	$D \in I_j$
$F_2^j(D) = M_1^j(\alpha_1 D + a_1) + F_1^j(D)$	$D \in I_j$

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Table 13

The biological parameter values used for system (2.1) with the specific growth functions (C.1).

Parameter	$m_0$	$K_0$	$K_i$	$m_1$	$K_1$	$K_I$	$\alpha_0$	$a_0$	$\alpha_1$	$a_1$
Figures 1, 3, and 5, Figure 7(a)	3.5	1.5	5	4	0.5	0.95	0.9	1.2	0.8	0.7
Figures 2, 4, and 6	3.5	1.5	5	3.5	0.5	0.95	0.95	1.4	0.5	0.5
Figure 7(b)	4	1.5	1.2	5.32	0.5	0.95	1	1	0.8	1.18
Figure 7(c), Figure 8(a,b)	3.3	1	4.5	3.94	0.5	1	0.8	1.7	0.7	0.7
Figure 8(c,d)	3.2	1	7	3.98	0.5	1.5	0.8	1.6	0.7	0.68
Figure 9(a-b)	3.3	1	4.5	8.21	2.21	1	0.8	0	0.7	0
Figure 9(c-d)	2.9	1	4.5	8.21	2.21	1	0.8	0	0.7	0

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