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

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

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

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

where a substrate s_0 (Volatile Fatty Acid) is consumed by a biomass x_0 (acetogenic bacteria) to produce a product s_1 (hydrogen). The substrate s_1 is consumed in the second reaction by another biomass x_1 (hydrogenotrophic methanogenic bacteria). μ_0 and μ_1 are the bacterial growth rates, depending eventually on one or both substrates. The substrates s_0 and s_1 are introduced in the reactor with the inflowing concentrations s_0^{in} and s_1^{in} , respectively, and a dilution rate D . These reactions are described by the following system of differential equations

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

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

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

where the nonnegative death (or decay) rate parameters a_0 and a_1 are taken into consideration with units of the dilution rate (D has units 1/d). These decay terms included in model (1.2) are related to consumption of energy, other than growth; see for instance [23] or [33]. The coefficients α_0 and α_1 belong to $[0, 1]$ and represent, respectively, the first and the second biomass proportion that leaves the reactor. For example, in [7] these coefficients are proposed to model a biomass reactor attached to the support or to decouple the residence time of solids and the hydraulic residence time ($1/D$). Thus, the study will not be restricted to the case $\alpha_i = 1$, $i = 0, 1$, as in most of the studies in the literature (see Tables 1 and 2 below), and the case $0 \leq \alpha_i \leq 1$, which is of biological interest, will be investigated.

If the growth rate μ_0 depends only on substrate s_0 and μ_1 depends only on s_1 , that is,

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

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

affected by the growth of the commensal species x_1 . If μ_0 depends on both substrates s_0 and s_1 , and μ_1 depends on substrate s_1 , that is,

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

then system (1.2) describes a syntrophic relationship where two microbial species depend on each other for survival by the production of a required substrate s_1 . In this case, each species benefits from the presence of the other species. Tables 1 and 2 summarize the modeling assumptions made in the literature on two-tiered model (1.2) describing the commensalistic and the syntrophic relationships, 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]	≥ 0	αD	Monod	Haldane
Simeonov and Diop [46]	0	D	Monod or Contois	Haldane
Sbarciog et al. [42]	≥ 0	D	Monotonic	Nonmonotonic
Benyahia et al. [5]	≥ 0	αD	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]	≥ 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]	≥ 0	$D + a_i$	Increasing in s_0 , decreasing in s_1	Increasing

Harvey et al. [24] have studied model (1.2) in the particular case where $s_1^{in} = 0$, $D_i = D$, and 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 study provides an extension of the results in [24] to the case where D_1 and D_2 are distinct from D . Notice that most of the studies in the existing literature (see Table 2) consider the case of equal removal rates ($D_1 = D_2 = D$), where the model can be reduced to a two-dimensional system. In this paper, we generalize [10, 16, 24, 26], by allowing distinct removal rates. In this case, the study of the stability is much more delicate and requires the Liénard-Chipart stability criteria [20] for a four-dimensional system. Furthermore, it is reported in the literature [5, 7, 18, 24, 42, 46, 48] that at many times the second reaction of (1.1) is inhibited by large values of s_1 , which instigates to consider a Haldane-type growth function for μ_1 . The goal of the present work is to understand the joined effects of syntrophy, mortality of two microbial species, substrate inhibition on their growth and inflowing substrate concentration of the second species, which have not been studied in the literature. Moreover, here, we do not specify kinetics but we consider qualitative properties on the growth functions and we assume that the second species is inhibited when the concentration of substrate becomes significant. The particular case $s_1^{in} = 0$ was considered in [18]. The case where μ_1 does not present inhibition was considered in [11, 40, 54].

On the other hand, our study provides an important tool for the experimentation which is the operating diagram showing the behavior of the syntrophic model (1.2) according to the control parameters 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 μ_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 μ_0 and μ_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 μ_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

introduce in Table 3 the auxiliary functions for determining the existence and stability conditions. Some comments and details on their definition domains are given in Appendix A. In the particular 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 $y \in (0, \mu_1^{\max}]$.
$F_0(D, s_1^{\text{in}})$	$F_0(D, s_1^{\text{in}}) = M_0(\alpha_0 D + a_0, s_1^{\text{in}})$ defined for $(D, s_1^{\text{in}}) \in \text{dom}(F_0)$
$F_1^j(D)$	$F_1^j(D) = M_0(\alpha_0 D + a_0, M_1^j(\alpha_1 D + a_1))$, $D \in I_j$
$F_2^j(D)$	$F_2^j(D) = M_1^j(\alpha_1 D + a_1) + F_1^j(D)$, $D \in I_j$

The following result gives all the steady states of (2.1) and the necessary and sufficient conditions of their existence and stability. For convenience, we shall use the abbreviation LES for Locally Exponentially Stable.

Proposition 3.1. Assume that Hypotheses 2.1 to 2.4 hold. Then, the six steady states of (2.1) are 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 ₀	$s_0 = s_0^{\text{in}}, s_1 = s_1^{\text{in}}$	$x_0 = 0, x_1 = 0$
SS ₁	s_0 is a solution of equation $\mu_0(s_0, s_0^{\text{in}} + s_1^{\text{in}} - s_0) = D_0$ $s_1 = s_0^{\text{in}} + s_1^{\text{in}} - s_0$	$x_0 = \frac{D}{D_0} (s_0^{\text{in}} - s_0)$ $x_1 = 0$
SS ₂ ^j	$s_0 = F_1^j(D)$ $s_1 = M_1^j(D_1)$	$x_0 = \frac{D}{D_0} (s_0^{\text{in}} - s_0)$ $x_1 = \frac{D}{D_1} (s_0^{\text{in}} + s_1^{\text{in}} - s_0 - s_1)$
SS ₃ ^j	$s_0 = s_0^{\text{in}}$ $s_1 = M_1^j(D_1)$	$x_0 = 0$ $x_1 = \frac{D}{D_1} (s_1^{\text{in}} - M_1^j(D_1))$

Table 5

Necessary and sufficient conditions of existence and local stability of steady states of model (2.1).

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

Remark 3.2. Since the function $F_0(D, s_1^{\text{in}})$ is defined for $(D, s_1^{\text{in}}) \in \text{dom}(F_0)$ (see Proposition A.1), the condition $s_0^{\text{in}} > F_0(D, s_1^{\text{in}})$ means that $(D, s_1^{\text{in}}) \in \text{dom}(F_0)$ and the inequality is satisfied. Conversely, if $(D, s_1^{\text{in}}) \notin \text{dom}(F_0)$, we let $F_0(D, s_1^{\text{in}}) = +\infty$. Thus, the condition $s_0^{\text{in}} < F_0(D, s_1^{\text{in}})$ means that $(D, s_1^{\text{in}}) \notin \text{dom}(F_0)$ or the inequality is satisfied and $(D, s_1^{\text{in}}) \in \text{dom}(F_0)$. Similarly, the condition $s_1^{\text{in}} > M_1^j(D_1)$ means that $D \in \bar{I}_j$, $j = 1, 2$ and the inequality is satisfied, while the condition $s_1^{\text{in}} < M_1^j(D_1)$ means $D \notin \bar{I}_j$ or the inequality is satisfied and $D \in \bar{I}_j$. The other conditions involving functions $F_i^j(D)$, $i, j = 1, 2$, follow similarly.

As we will see in Proposition 4.5, the limit case $D = \bar{D}_1$ corresponds to saddle-node bifurcations of SS₂¹ with SS₂² and SS₃¹ with SS₃² 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 Γ
 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 Γ , 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
$\gamma_3^1 = \{(D, s_0^{in}, s_1^{in}) : s_1^{in} = M_1^1(D_1), D \in \bar{I}_1\}$ $= \{(D, s_0^{in}, s_1^{in}) : D = D_1^*\} = \{(D, s_0^{in}, s_1^{in}) : s_1^{in} = s_{11}^{in*}, D \in \bar{I}_1\}$	Pink
$\gamma_3^2 = \{(D, s_0^{in}, s_1^{in}) : s_1^{in} = M_1^2(D_1), D \in \bar{I}_2\}$ $= \{(D, s_0^{in}, s_1^{in}) : D = D_2^*\} = \{(D, s_0^{in}, s_1^{in}) : s_1^{in} = s_{12}^{in*}, D \in \bar{I}_2\}$	Violet
$\gamma_4 = \{(D, s_0^{in}, s_1^{in}) : D = \bar{D}_1\}$	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_0	SS_1	SS_2^1	SS_2^2	SS_3^1	SS_3^2
$s_1^{in} < M_1^1(D_1)$	$s_0^{in} < F_0(D, s_1^{in})$	$\mathcal{J}_1$	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
	$F_1^1(D) < s_0^{in} < F_2^1(D)$	$\mathcal{J}_{10}$	Gray	S		S		U	U
	$F_2^1(D) < s_0^{in} < F_0(D, s_1^{in})$	$\mathcal{J}_{11}$	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 γ_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 γ_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 γ_0 with the straight lines γ_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 Γ 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 γ_0 , γ_1^1 and γ_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) $F_0(D, s_1^{in}) > F_1^1(D) > F_2^1(D) - s_1^{in}$.

For all $D \in I_2$, the three curves γ_0 , γ_1^2 and γ_2^2 intersect at the same point $s_1^{in} = s_{12}^{in*}$ (see Figure 1) such that $s_{12}^{in*} < \bar{s}_1^{in}$. For all $s_1^{in} \in [0, s_{12}^{in*})$,

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

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

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

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 defined in Table 9, the regions of the operating diagram in the (s_1^{in}, s_0^{in}) plane where D is kept constant are cataloged as follows:

1. if $D \in I_2$, then the twelve regions exist (see Figure 1);
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 (see Figure 2(c));
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 $\mathcal{J}_9$ exist (see Figure 2(b));
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 Figure 2(b) where $\mathcal{J}_2$ is empty);
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));
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 $\mathcal{J}_2$ is empty).

4.2. Operating diagrams in the (D, s_0^{in}) plane when s_1^{in} fixed. The intersection of the surfaces γ_0 and γ_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 . However, the intersections of the surfaces γ_3^j , $j = 1, 2$ with this plane are straight lines (see Table 11). To determine the operating diagram when s_1^{in} is fixed, we show the following result which determines the relative positions of the curves γ_0 and γ_i^j , $i, j = 1, 2$ according to the values of D and D_1^* . We 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 $D \in I_2$,

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

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

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

It is unique if it exists. If $D_1^* \in I_1$, the three curves γ_0 , γ_1^1 and γ_2^1 intersect at the same point $D = D_1^*$ (see Figures 3 and 4(b)) such that for all $D \in [0, D_1^*)$, (4.3) holds and for all $D \in (D_1^*, \bar{D}_1) \cap I_0 \cap I_1$, (4.2) holds. The curves γ_0 , γ_1^1 and γ_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 (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)).

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

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) and Figure 4(a,d) in case 2).
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 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 regions $\mathcal{J}_1$ and $\mathcal{J}_5$ to $\mathcal{J}_8$ (see Figure 4(c,f)).

The operating diagram of Figure 4(b,e) shows the existence of seven regions $\mathcal{J}_1$ to $\mathcal{J}_8$ where the region $\mathcal{J}_4$ 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 $\mathcal{J}_4$ can be not empty for another set of parameters such that $D_1^* < \tilde{D}_1$.

By similar arguments to that in the proof of Proposition 4.3, we can prove the following result which determines the relative positions of the curves γ_0 and γ_i^j , $i, j = 1, 2$ according to the values of D and D_2^* in the case $s_1^{in} > s_1^{max}$.

Figure 3. The curves C_1 , C_2 and those of Γ 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 Γ 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 γ_0 , γ_1^1 and γ_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 $D \in (D_2^*, \bar{D}_1) \cap I_0 \cap I_2$, (4.5) holds. The curves γ_0 , γ_1^1 and γ_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 Γ 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 Γ 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.

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

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 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 up to nine regions in the operating diagram (see Figure 6(b,e) in case 2). If case 2 holds and $D_2^* \in \bar{I}_2 \setminus I_2$, there exist at most seven regions $\mathcal{J}_1$ and $\mathcal{J}_5$ to $\mathcal{J}_{10}$ (see Figure 6(a,d)).
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 1 and Figure 6(c,f) in case 2).

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

we show that this equation has at most three solutions $\tilde{D}_j$, $j = 1, 2, 3$ such that $\lim_{D \rightarrow \tilde{D}_j^-} F_i^2(D) = +\infty$, $i = 1, 2$ (see [Proposition A.4](#)). The operating diagrams of [Figure 7\(b-c\)](#) show that in the case of two or three solutions of the equation $\Phi_2(D) = 0$, we have the same number of regions but there is a change in the shape and the connectivity of the regions. This property is the same for the various 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 $\Phi_2(D) = 0$ (a) has no solution, (b) has two solutions (c) has three solutions. The operating diagram (a) is the same in [Figure 3\(c\)](#).

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

Proposition 4.5. *The bifurcation analysis of the steady states of (2.1) by crossing the surfaces of Γ 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 Γ . The letter TB (resp. SNB) means a transcritical bifurcation (resp. saddle-node bifurcation). Note that $k = 2, 3$.

Γ	Conditions	Transition	Bifurcation
γ_0	$s_1^{in} < M_1^1(D_1)$	$\mathcal{J}_1$ to $\mathcal{J}_2$	TB: $SS_0 = SS_1$
	$M_1^1(D_1) < s_1^{in} < M_1^2(D_1)$	$\mathcal{J}_6$ to $\mathcal{J}_7$	
	$M_1^2(D_1) > s_1^{in}$	$\mathcal{J}_{11}$ to $\mathcal{J}_{12}$	
γ_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 $\mathcal{J}_{10}$	
γ_1^2	$s_1^{in} > M_1^2(D_1)$	$\mathcal{J}_{10}$ to $\mathcal{J}_{11}$	TB: $SS_2^2 = SS_3^2$
γ_2^1	$s_1^{in} < M_1^1(D_1)$	$\mathcal{J}_2$ to $\mathcal{J}_3$	TB: $SS_1 = SS_2^1$
γ_2^2	$s_1^{in} < M_1^1(D_1)$	$\mathcal{J}_3$ to $\mathcal{J}_4$	TB: $SS_1 = SS_2^2$
	$M_1^1(D_1) < s_1^{in} < M_1^2(D_1)$	$\mathcal{J}_5$ to $\mathcal{J}_6$	
γ_3^1	$s_0^{in} > F_2^2 - s_1^{in}$	$\mathcal{J}_4$ to $\mathcal{J}_5$	TB: $SS_0 = SS_3^1$
	$F_2^1 - s_1^{in} < s_0^{in} < F_2^2 - s_1^{in}$ if $D < D_1^*$, if not $F_0 < s_0^{in} < F_2^2 - s_1^{in}$	$\mathcal{J}_3$ to $\mathcal{J}_6$	
	$s_0^{in} < F_0$ if $D < D_1^*$, if not $s_0^{in} < F_1^1$	$\mathcal{J}_1$ to $\mathcal{J}_8$	
γ_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 $\mathcal{J}_{12}$	TB: $SS_0 = SS_3^2$
	$F_1^1 < s_0^{in} < F_0$ if $D < D_2^*$, if not $F_1^1 < s_0^{in} < F_1^2$	$\mathcal{J}_7$ to $\mathcal{J}_{10}$	
	$s_0^{in} < F_1^1$	$\mathcal{J}_8$ to $\mathcal{J}_9$	
γ_4	$s_1^{in} < s_1^{max}$	$\mathcal{J}_2$ to $\mathcal{J}_4$	SNB: $SS_2^1 = SS_2^2$
γ_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 $\mathcal{J}_{11}$	
		$\mathcal{J}_1$ to $\mathcal{J}_9$	SNB: $SS_3^1 = SS_3^2$

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

5. Discussion and conclusion. In this paper, we have generalized the mathematical analysis of the simplified model (2.1) of anaerobic digestion in the form of a two-tiered microbial food chain describing a syntrophic relationship between two microbial species in a chemostat. To this end, we 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 μ_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, μ_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 μ_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 μ_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	
$\bar{D}_0(s_1^{in})$	$\bar{D}_0(s_1^{in}) = (\bar{\mu}_0(s_1^{in}) - a_0) / \alpha_0$
$\bar{D}_1$	$\bar{D}_1 = (\mu_1^{max} - a_1) / \alpha_1$
$\Phi_j(D)$	$\Phi_j(D) = \bar{\mu}_0(M_1^j(D_1)) - D_0, \text{ for } D \in \bar{I}_j, j = 1, 2$
$\hat{D}_1$	$\hat{D}_1$ 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 α_0 and α_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

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

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

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

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 $D \in [0, \bar{D}_1]$ 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*

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

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

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

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 $\tilde{D}_i > \tilde{D}_j$, 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

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

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

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

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

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 Φ_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,

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

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

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

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

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

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

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

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

By applying Gronwall's lemma, we obtain

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

We deduce that

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

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

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

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

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

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

$$(B.5) \quad (\mu_1(s_1) - D_1)x_1 = 0.$$

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

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

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

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

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

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

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

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

For 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, SS_0 always exists.

For 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

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

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

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

Thus, SS_1 exists if and only if equation (B.11) has a nonnegative solution and the s_1 and x_0 -components are positive. This condition is equivalent to say that $0 \leq s_0 < s_0^{in}$. From Hypotheses 2.1 and 2.3, we

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 $s_0 = s_0^{in}$. Therefore, there exists a solution of equation (B.11) in $[0, s_0^{in}]$ if and only if

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

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

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

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

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

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 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

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

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

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

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

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

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

Thus, SS_0 is LES if and only if

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

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

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

452 At 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

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

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, SS_1 is
456 LES if and only if $\lambda_1 < 0$, that is,

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

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

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

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 SS_1 , one has $\psi(s_0) = D_0$. Thus, condition (B.18) is equivalent to

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

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 $M_0(\cdot, M_1^1(D_1))$ is increasing. These conditions are the same as those in Table 5.

464 For 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 $SS_2^1 = SS_2^2$. Using the Liénard-Chipart
470 stability criteria (see Gantmacher [20], Theorem 11), SS_2^j is LES if and only if

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

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

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

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

$$\begin{aligned} \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) \\ &\quad + 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 \\ &\quad + [\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 \\ &\quad + [\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 \\ &\quad + (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 \\ &\quad + [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 \\ &\quad + [((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 \\ &\quad + (\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 \\ &\quad + (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 \\ &\quad + [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 \\ &\quad + (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 \\ &\quad + (\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. \end{aligned}$$

Since α_0 and α_1 are in $[0, 1]$, then $\gamma_j > 0$ for $j = 0, \dots, 5$. Thus, the conditions of Liénard-Chipart 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

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

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 $G_2 < 0$. Therefore, the roots of the quadratic factor are real and have opposite signs. Consequently, 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 $G_1 > 0$ so that $c_1 > 0$ and $c_2 > 0$. Therefore, SS_3^1 is LES if and only if

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

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 γ_0 , γ_1^1 and γ_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

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

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 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

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

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 $M_1^1(\alpha_1 D + a_1) < s_1^{in}$ 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 exist, then $M_1^1(\alpha_1 D + a_1) > s_1^{in}$ for all $D \in I_1$ and consequently (4.2) holds. ■

Proof of Proposition 4.5. From Table 6, the surface γ_0 is defined by $s_0^{in} = F_0(D, s_1^{in})$. Using Tables 4 and 5 and Proposition 3.1, we can see that SS_0 and SS_1 coalesce and are nonhyperbolic steady states on the surface γ_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 SS_0 becomes unstable and SS_1 emerges stable in the positive octant $\mathbb{R}_+^4$. All other cases are left to the reader since they can be treated similarly. ■

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

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

where m_j and K_j , $j = 0, 1$, denote the maximum growth rates (units are 1/d) and the Michaelis-Menten constants with units of concentration (kg COD/m³); K_i and K_I represent the inhibition factor due to s_1 for the growth of the species x_0 and x_1 , respectively, with units of concentration. The following result determines the maximal number of solutions of the equation $\Phi_2(D) = 0$ in the particular case 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 Γ_0 and Γ_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 Γ_0 and Γ_1 of the functions $\tilde{\mu}_0$ and μ_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 $[0, \bar{D}_1]$.

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

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

When the growth functions μ_0 and μ_1 are of type (C.1), the equation $\Phi_2(D) = 0$ has at most three solutions in the case 1 of (4.1) when

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

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

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

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

Proof. From definition of the function Φ_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 μ_0 and μ_1 are of type (C.1), we obtain

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

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

When the growth functions are given by (C.1), we succeeded in finding a set of parameters such that we show the maximum number of intersections of the curves Γ_0 and Γ_1 and the corresponding number of solutions of the equation $\Phi_j(D) = 0$ (see Figures 8 and 9).

Appendix D. Tables. In this section, we give some tables used in the paper. Tables 10 and 11 describe the intersections of the surfaces of Γ with a two-dimensional operating plane where D or s_1^{in} is constant, respectively. Table 12 presents the auxiliary functions defined in Table 3 in the particular 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 Γ with a (s_1^{in}, s_0^{in}) plane where D is constant.

Γ	Condition	$\Gamma \cap \{D = \text{constant}\}$
γ_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
γ_1^j	$D \in I_j$	Horizontal line $s_0^{in} = F_1^j(D)$
	$D \notin I_j$	Empty
γ_2^j	$D \in I_j$	Oblique line $s_0^{in} = F_2^j(D) - s_1^{in}$
	$D \notin I_j$	Empty
γ_3^j	$D \in \bar{I}_j$	Vertical line $s_1^{in} = s_{1j}^{in*} = M_1^j(D_1)$
	$D \notin \bar{I}_j$	Empty
γ_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 Γ with a (D, s_0^{in}) plane where s_1^{in} is constant.

Γ	Condition	$\Gamma \cap \{s_1^{in} = \text{constant}\}$
γ_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
γ_1^j	$D \in I_j$	Curve of the function $s_0^{in} = F_1^j(D)$
	$D \notin I_j$	Empty
γ_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
γ_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
γ_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
γ_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
$M_0(y, s_1) = \frac{K_0 y (1 + s_1 / K_i)}{m_0 - y (1 + s_1 / K_i)}$	$0 \leq y < \frac{m_0}{1 + s_1 / K_i}$
$M_1^j(y) = \frac{(m_1 - y) K_I \pm \sqrt{(K_I (m_1 - y))^2 - 4 K_1 K_I y^2}}{2y}$	$0 < y < \frac{m_1}{1 + 2\sqrt{K_1 / K_I}}$
$F_0(D, s_1^{in}) = \frac{K_0(\alpha_0 D + a_0)(1 + s_1^{in} / K_i)}{m_0 - (\alpha_0 D + a_0)(1 + s_1^{in} / K_i)}$	$0 \leq \alpha_0 D + a_0 < \frac{m_0}{1 + s_1^{in} / K_i}$
$F_1^j(D) = \frac{K_0(\alpha_0 D + a_0)(1 + M_1^j(\alpha_1 D + a_1) / K_i)}{m_0 - (\alpha_0 D + a_0)(1 + M_1^j(\alpha_1 D + a_1) / K_i)}$	$D \in I_j$
$F_2^j(D) = M_1^j(\alpha_1 D + a_1) + F_1^j(D)$	$D \in I_j$

REFERENCES

- [1] N. Abdellatif, R. Fekih-Salem, and T. Sari, *Competition for a single resource and coexistence of several species in the chemostat*, Math. Biosci. Eng., 13 (2016), pp. 631–652, <https://doi.org/10.3934/mbe.2016012>.
- [2] B. Bar and T. Sari, *The operating diagram for a model of competition in a chemostat with an external lethal inhibitor*, Discrete & Continuous Dyn. Syst. - B, 25 (2020), pp. 2093–2120, <https://doi.org/10.3934/dcdsb.2019203>.

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	α_0	a_0	α_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

- [3] D. Batstone, J. Keller, I. Angelidaki, S. Kalyuzhnyi, S. Pavlosthathis, A. Rozzi, W. Sanders, H. Siegrist, and V. Vavilin, *The IWA Anaerobic Digestion Model No 1 (ADM1)*, Water Sci Technol., 45 (2002), pp. 66–73, <https://doi.org/10.2166/wst.2002.0292>.
- [4] B. Benyahia and T. Sari, *Effect of a new variable integration on steady states of a two-step anaerobic digestion model*, Math. Biosci. Eng., 17 (2020), pp. 5504–5533.
- [5] B. Benyahia, T. Sari, B. Cherki, and J. Harmand, *Bifurcation and stability analysis of a two step model for monitoring anaerobic digestion processes*, J. Proc. Control, 22 (2012), pp. 1008–1019, <https://doi.org/10.1016/j.jprocont.2012.04.012>.
- [6] B. Benyahia, T. Sari, B. Cherki, and J. Harmand, *Anaerobic membrane bioreactor modeling in the presence of Soluble Microbial Products (SMP) - the Anaerobic Model AM2b*, Chem. Eng. J., 228 (2013), pp. 1011–1022, <https://doi.org/10.1016/j.cej.2013.05.073>.
- [7] O. Bernard, Z. Hadj-Sadok, D. Dochain, A. Genovesi, and J.-P. Steyer, *Dynamical model development and parameter identification for an anaerobic wastewater treatment process*, Biotechnol. Bioeng., 75 (2001), pp. 424–438, <https://doi.org/10.1002/bit.10036>.
- [8] M. Boer, B. Kooi, and S. Kooijman, *Food chain dynamics in the chemostat*, Math. Biosci., 150 (1998), pp. 43–62, [https://doi.org/10.1016/S0025-5564\(98\)00010-8](https://doi.org/10.1016/S0025-5564(98)00010-8).
- [9] A. Bornhöft, R. Hanke-Rauschenbach, and K. Sundmacher, *Steady-state analysis of the anaerobic digestion model No. 1 (ADM1)*, Nonlinear Dyn., 73 (2013), pp. 535–549, <https://doi.org/10.1007/s11071-013-0807-x>.
- [10] A. Burchard, *Substrate degradation by a mutualistic association of two species in the chemostat*, J. Math. Biol., 32 (1994), pp. 465–489, <https://doi.org/10.1007/BF00160169>.
- [11] Y. Daoud, N. Abdellatif, T. Sari, and J. Harmand, *Steady state analysis of a syntrophic model: The effect of a new input substrate concentration*, Math. Model. Nat. Phenom., 13 (2018), pp. 1–22, <https://doi.org/10.1051/mmnp/2018037>.
- [12] M. Dellal and B. Bar, *Global analysis of a model of competition in the chemostat with internal inhibitor*, Discrete & Continuous Dyn. Syst. - B, (2020), <https://doi.org/10.3934/dcdsb.2020156>.
- [13] M. Dellal, M. Lakrib, and T. Sari, *The operating diagram of a model of two competitors in a chemostat with an external inhibitor*, Math. Biosci., 302 (2018), pp. 27–45, <https://doi.org/10.1016/j.mbs.2018.05.004>.
- [14] S. Di and A. Yang, *Analysis of productivity and stability of synthetic microbial communities*, J. R. Soc. Interface, 16 (2019), pp. 1–19, <https://doi.org/10.1098/rsif.2018.0859>.
- [15] A. Donoso-Bravo, J. Mailier, C. Martin, J. Rodríguez, C. A. Aceves-Lara, and A. Vande Wouwer, *Model selection, identification and validation in anaerobic digestion: A review*, Water Research, 45 (2011), pp. 5347–5364, <https://doi.org/10.1016/j.watres.2011.08.059>.
- [16] M. El-Hajji, F. Mazenc, and J. Harmand, *A mathematical study of a syntrophic relationship of a model of anaerobic digestion process*, Math. Biosci. Eng., 7 (2010), pp. 641–656, <https://doi.org/10.3934/mbe.2010.7.641>.
- [17] R. Fekih-Salem, N. Abdellatif, T. Sari, and J. Harmand, *Analyse mathématique d'un modèle de digestion anaérobie à trois étapes*, ARIMA J., 17 (2014), pp. 53–71, <http://arima.inria.fr/017/017003.html>.
- [18] R. Fekih-Salem, N. Abdellatif, and A. Yahmadi, *Effect of inhibition on a syntrophic relationship model in the anaerobic digestion process*, in Proceedings of the 8th conference on Trends in Applied Mathematics in Tunisia, Algeria, Morocco, 2017, pp. 391–396, <https://indico.math.cnrs.fr/event/1335>.
- [19] R. Fekih-Salem, C. Lobry, and T. Sari, *A density-dependent model of competition for one resource in the chemostat*, Math. Biosci., 286 (2017), pp. 104–122, <https://doi.org/10.1137/18M1171801>, <http://www.sciencedirect.com/science/article/pii/S0025556417300792>.
- [20] F. Gantmacher, *Application of the theory of matrices*, Interscience Publishers, INC. New York, 2004.
- [21] A. Ghouali, T. Sari, and J. Harmand, *Maximizing biogas production from the anaerobic digestion*, J. Process Control, 36 (2015), pp. 79–88, <https://doi.org/10.1016/j.jprocont.2015.09.007>.
- [22] G. Giovannini, M. Sbarciog, J.-P. Steyer, R. Chamy, and A. Vande Wouwer, *On the derivation of a simple dynamic model of anaerobic digestion including the evolution of hydrogen*, Water Research, 134 (2018), pp. 209–225, <https://doi.org/10.1016/j.watres.2018.01.036>.
- [23] J. Harmand, C. Lobry, A. Rapaport, and T. Sari, *The Chemostat: Mathematical Theory of Microorganism Cultures*, vol. 1, Chemical Eng. Ser., Chemostat Bioprocesses Set, Wiley, New York, 2017, <https://doi.org/10.1002/9781119437215>.
- [24] E. Harvey, J. Heys, and T. Gedeon, *Quantifying the effects of the division of labor in metabolic pathways*, J. Theor. Biol., 360 (2014), pp. 222–242, <https://doi.org/10.1016/j.jtbi.2014.07.011>.

- [25] Z. Khedim, B. Benyahia, B. Cherki, T. Sari, and J. Harmand, *Effect of control parameters on biogas production during the anaerobic digestion of protein-rich substrates*, Appl. Math. Model., 61 (2018), pp. 351–376, <https://doi.org/10.1016/j.apm.2018.04.020>.
- [26] R. Kreikenbohm and E. Bohl, *A mathematical model of syntrophic cocultures in the chemostat*, FEMS Microbiol. Ecol., 38 (1986), pp. 131–140, <https://doi.org/10.1111/j.1574-6968.1986.tb01722.x>.
- [27] J. Mailier, M. Remy, and A. Vande Wouwer, *Stoichiometric identification with maximum likelihood principal component analysis*, J. Math. Biol., 67 (2013), pp. 739–765, <https://doi.org/10.1007/s00285-012-0559-0>.
- [28] F. Mairet, O. Bernard, E. Cameron, M. Ras, L. Lardon, J.-P. Steyer, and B. Chachuat, *Three-reaction model for the anaerobic digestion of microalgae*, Biotechnol. Bioeng., 109 (2012), pp. 415–425, <https://doi.org/10.1002/bit.23350>.
- [29] S. Marsili-Libelli and S. Beni, *Shock load modelling in the anaerobic digestion process*, Ecol. Model., 84 (1996), pp. 215–232, [https://doi.org/10.1016/0304-3800\(94\)00125-1](https://doi.org/10.1016/0304-3800(94)00125-1).
- [30] C. Martinez, A. Ávila, F. Mairet, L. Meier, and D. Jeison, *Modeling and analysis of an absorption column connected to a microalgae culture*, SIAM J. Appl. Math., 80 (2020), pp. 772–791, <https://doi.org/10.1137/18M1225641>.
- [31] T. Meadows, M. Weeder mann, and G. Wolkowicz, *Global analysis of a simplified model of anaerobic digestion and a new result for the chemostat*, SIAM J. Appl. Math., 79 (2019), pp. 668–689, <https://doi.org/10.1137/18M1198788>.
- [32] T. Mtar, R. Fekih-Salem, and T. Sari, *Interspecific density-dependent model of predator-prey relationship in the chemostat*, Int. J. Biomath., (2020), <https://hal.archives-ouvertes.fr/hal-02445761>.
- [33] B.-J. Ni, G.-P. Sheng, and H.-Q. Yu, *Model-based characterization of endogenous maintenance, cell death and predation processes of activated sludge in sequencing batch reactors*, Chem. Eng. Sci., 66 (2011), pp. 747–754, <https://doi.org/10.1016/j.ces.2010.11.033>.
- [34] S. Nouaoura, N. Abdellatif, R. Fekih-Salem, and T. Sari, *Mathematical analysis of a three-tiered model of anaerobic digestion*, hal-02540350, (2020), <https://hal.archives-ouvertes.fr/hal-02540350>.
- [35] S. Nouaoura, R. Fekih-Salem, N. Abdellatif, and T. Sari, *Mathematical analysis of a three-tiered food-web in the chemostat*, To appear in Discrete & Continuous Dyn. Syst. - B, (2020), <https://hal.archives-ouvertes.fr/hal-02878246>.
- [36] S. Pavlou, *Computing operating diagrams of bioreactors*, J. Biotechnol., 71 (1999), pp. 7–16, [https://doi.org/10.1016/S0168-1656\(99\)00011-5](https://doi.org/10.1016/S0168-1656(99)00011-5).
- [37] P. J. Reilly, *Stability of commensalistic systems*, Biotechnol. Bioeng., 16 (1974), pp. 1373–1392, <https://doi.org/10.1002/bit.260161006>.
- [38] T. Sari and B. Benyahia, *The operating diagram for a two-step anaerobic digestion model*, hal-02557464, (2020), <https://hal.archives-ouvertes.fr/hal-02557464>.
- [39] T. Sari, M. E. Hajji, and J. Harmand, *The mathematical analysis of a syntrophic relationship between two microbial species in a chemostat*, Math. Biosci. Eng., 9 (2012), pp. 627–645, <https://doi.org/10.3934/mbe.2012.9.627>.
- [40] T. Sari and J. Harmand, *A model of a syntrophic relationship between two microbial species in a chemostat including maintenance*, Math. Biosci., 275 (2016), pp. 1–9, <https://doi.org/10.1016/j.mbs.2016.02.008>.
- [41] T. Sari and M. Wade, *Generalised approach to modelling a three-tiered microbial food-web*, Math. Biosci., 291 (2017), pp. 21–37, <https://doi.org/10.1016/j.mbs.2017.07.005>.
- [42] M. Sbarciog, M. Loccufier, and E. Noldus, *Determination of appropriate operating strategies for anaerobic digestion systems*, Biochem. Eng. J., 51 (2010), pp. 180–188, <https://doi.org/10.1016/j.bej.2010.06.016>.
- [43] M. Sbarciog, M. Loccufier, and A. Vande Wouwer, *An optimizing start-up strategy for a bio-methanator*, Bioprocess Biosyst Eng, 35 (2012), pp. 565–578, <https://doi.org/10.1007/s00449-011-0629-5>.
- [44] M. Sbarciog, J. A. Moreno, and A. Vande Wouwer, *A biogas-based switching control policy for anaerobic digestion systems*, IFAC Proceedings, 45 (2012), pp. 603–608, <https://doi.org/10.3182/20120710-4-SG-2026.00056>.
- [45] S. Shen, G. C. Premier, A. Guwy, and R. Dinsdale, *Bifurcation and stability analysis of an anaerobic digestion model*, Nonlinear Dynam., 48 (2007), pp. 391–408, <https://doi.org/10.1007/s11071-006-9093-1>.
- [46] I. Simeonov and S. Diop, *Stability analysis of some nonlinear anaerobic digestion models*, Int. J. Bioautomation, 14 (2010), pp. 37–48.
- [47] I. Simeonov and S. Stoyanov, *Modelling and dynamic compensator control of the anaerobic digestion of organic wastes*, Chem. Biochem. Eng. Q., 17 (2003), pp. 285–292.
- [48] G. Stephanopoulos, *The dynamics of commensalism*, Math. Biosci., 23 (1981), pp. 2243–2255, <https://doi.org/10.1002/bit.260231008>.
- [49] E. Volcke, M. Sbarciog, E. Noldus, B. D. Baets, and M. Loccufier, *Steady state multiplicity of two-step biological conversion systems with general kinetics*, Math. Biosci., 228 (2010), pp. 160–170, <https://doi.org/10.1016/j.mbs.2010.09.004>.
- [50] M. Wade, *Not just numbers: Mathematical modelling and its contribution to anaerobic digestion processes*, Processes, 8 (2020), p. 888, <https://doi.org/10.3390/pr8080888>.
- [51] M. Wade, R. Pattinson, N. Parker, and J. Dolfing, *Emergent behaviour in a chlorophenol-mineralising three-tiered microbial ‘food web’*, J. Theor. Biol., 389 (2016), pp. 171–186, <https://doi.org/10.1016/j.jtbi.2015.10.032>.
- [52] M. Weeder mann, G. Seo, and G. S. Wolkowicz, *Mathematical model of anaerobic digestion in a chemostat: effects of syntrophy and inhibition*, J. Biol. Dyn., 7 (2013), pp. 59–85, <https://doi.org/10.1080/17513758.2012.755573>.
- [53] M. Weeder mann, G. S. Wolkowicz, and J. Sasara, *Optimal biogas production in a model for anaerobic digestion*, Nonlinear Dyn, 81 (2015), pp. 1097–1112, <https://doi.org/10.1007/s11071-015-2051-z>.
- [54] A. Xu, J. Dolfing, T. Curtis, G. Montague, and E. Martin, *Maintenance affects the stability of a two-tiered microbial ‘food chain’?*, J. Theor. Biol., 276 (2011), pp. 35–41, <https://doi.org/10.1016/j.jtbi.2011.01.026>.