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Coexistence phenomena and global bifurcation structure in a chemostat-like model with species-dependent diffusion rates

François Castella · Sten Madec

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Abstract We study the competition of two species for a single resource in a chemostat. In the simplest space-homogeneous situation, it is known that only one species survives, namely the best competitor. In order to exhibit *coexistence* phenomena, where the two competitors are able to survive, we consider a space dependent situation: we assume that the two species and the resource follow a diffusion process in space, on top of the competition process. Besides, and in order to consider the most general case, we assume each population is associated with a *distinct* diffusion constant. This is a key difficulty in our analysis: the specific (and classical) case where all diffusion constants are equal, leads to a particular conservation law, which in turn allows to eliminate the resource in the equations, a fact that considerably simplifies the analysis and the qualitative phenomena. Using the global bifurcation theory, we prove that the underlying 2-species, stationary, diffusive, chemostat-like model, does possess *coexistence solutions*, where both species survive. On top of that, we identify the domain, in the space of the relevant bifurcation parameters, for which the system does have coexistence solutions.

Keywords Global bifurcation · Elliptic systems · Heterogeneous environment · Coexistence · Chemostat

Mathematics Subject Classification (2000) 35B32 · 35J61 · 35Q92 · 58J20 · 92D25

F. Castella
Université de Rennes 1, UMR CNRS 6625 Irmar,
Campus de Beaulieu, 35042 Rennes Cedex, France
e-mail: francois.castella@univ-rennes1.fr

S. Madec (✉)
Université de Tours, UMR 7350 LMPT, 37200 Tours, France
e-mail: sten.madec@lmpt.univ-tours.fr

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1 Introduction

The present paper is devoted to the study of *coexistence solutions* in some chemostat like systems, where various species compete for a single resource. The starting point of our analysis is the fact that in the simplest models, i.e. in the space-homogeneous situation, only one species survives, namely the best competitor. Therefore, and in order to observe situations where all species are able to survive, we readily consider a space-inhomogeneous situation, where the various species and the single resource follow a diffusion process in space. Technically speaking, and in order to tackle the most general situation, we assume that each population possesses its own *distinct* diffusion coefficient. This is a major difficulty and originality in the present text, as we discuss later in this introduction.

The main result of this paper is that the underlying 2-species chemostat-like model does possess *coexistence solutions*, i.e. solutions where all species survive. Besides, we are able to identify a domain in the space of the relevant parameters, for which coexistence holds.

Our construction relies on global bifurcations in elliptic systems. Although we conjecture that our analysis may be generalized to the case of N competing species for any $N \geq 2$, our results can only be proved in the case $N = 2$ for the time being.

Let us come to technical statements.

We study the nonnegative steady-state solutions of the reaction–diffusion system

$$\begin{cases} \partial_t R = a_0 \Delta R - F_1(x, R)U - F_2(x, R)V - m_0(x)R + I, \\ \partial_t U = a_1 \Delta U + (F_1(x, R) - m_1(x))U, \\ \partial_t V = a_2 \Delta V + (F_2(x, R) - m_2(x))V, \end{cases} \qquad (x \in \Omega,\ t > 0),$$

where Ω is a bounded region in $\mathbb{R}^n$ with smooth boundary. The above system is supplemented with Neumann[1] boundary conditions

$$\partial_n R(t, x) = \partial_n U(t, x) = \partial_n V(t, x) = 0 \quad (x \in \partial\Omega,\ t > 0),$$

where ∂_n is the normal derivative on the boundary $\partial\Omega$.

The above system describes a situation where two species with density $U = U(t, x)$ and $V = V(t, x)$, respectively, compete for the same resource with density $R = R(t, x)$, through the nonlinear terms $F_i(x, R)U$ and $F_i(x, R)V$ $(i = 1, 2)$. Besides, the space dependent resource R, as well as the two species U, V, follow a diffusion process in space, with the *distinct* diffusion constants $a_0 > 0, a_1 > 0, a_2 > 0$, respectively.[2] The space dependent functions $m_i(x) > 0$ on $\overline{\Omega}$ $(i = 0, 1, 2)$, are death

[1] Robin boundary conditions, of the form $a_0 \partial_n R + b_0(x)R = g(x)$, $a_1 \partial_n U + b_1(x)U = a_2 \partial_n V + b_1(x)V = 0$ on $\partial\Omega$, with $g(x) \geq 0$ and $b_i(x) \geq 0$ $(i = 0, 1, 2)$, would do as well, as we discuss later in this text.

[2] Our analysis is valid when the various constant coefficients diffusion operators $a_i \Delta$ become div $a_i(x)\nabla$ for some smooth, space-dependent coefficients $a_i(x) > 0$ on $\overline{\Omega}$, *provided* all coefficients $a_i(x)$ are *proportional*, i.e. $a_i(x) = \lambda_i a_0(x)$ $(i = 1, 2)$ for some constants $\lambda_1 > 0$ and $\lambda_2 > 0$. This easy extension is discussed later in the text. Needless to say, in that case, Robin boundary conditions become $a_0(x)\partial_n R + b_0(x)R = g(x)$ on $\partial\Omega$, and so on, with $g(x) \geq 0$ and $b_i(x) \geq 0$ on $\partial\Omega$ $(i = 0, 1, 2)$.

rates, while the space dependent functions $F_i(x, R) = F_i(x, R(t, x)) \geq 0$ are the consumption rates. The given, time-independent function $I = I(x) \gneqq 0$ is the nutrient input. All these data are assumed smooth.

In order to implement a bifurcation method, we normalize the consumption rates as follows. We readily choose *given*, smooth, functions $f_1 = f_1(x, R)$, $f_2 = f_2(x, R)$, and introduce two bifurcation parameters $c_1 > 0$ and $c_2 > 0$, which somehow measure the strength of the interaction between the species and the resource, through

$$F_1(x, R) \equiv c_1 f_1(x, R), \quad F_2(x, R) \equiv c_2 f_2(x, R). \tag{1.1}$$

Note that, since we are only interested in nonnegative solutions (R, U, V), the only important data is the value of $f_i(x, R)$ for $R \geq 0$: as shown by our analysis, any smooth extension of $f_i(x, R)$ may be retained for values $R \leq 0$, provided $f_i(x, R) \leq 0$ whenever $R \leq 0$.

With the above notation, in this paper we look for stationary solutions $U = U(x)$, $V = V(x)$, $R = R(x)$ to the above system, namely[3]

$$\begin{cases} (m_0(x) - a_0 \Delta) R + c_1 f_1(x, R) U + c_2 f_2(x, R) V = I(x), & \\ (m_1(x) - a_1 \Delta) U - c_1 f_1(x, R) U = 0, & (x \in \Omega) \\ (m_2(x) - a_2 \Delta) V - c_2 f_2(x, R) V = 0, & \\ \partial_n R = \partial_n U = \partial_n V = 0 & (x \in \partial\Omega). \end{cases} \tag{1.2}$$

More precisely, our goal is to exhibit *coexistence solutions* in (1.2), i.e. solutions R, U, V for which $R > 0$, $U > 0$, $V > 0$. Our approach relies on a global bifurcation method, where c_1 and c_2 are used as bifurcation parameters. In that respect, we also aim at identifying a domain in the (c_1, c_2)-plane for which coexistence holds.

Let us come to some bibliographical comments.

Bifurcation methods have been used in many texts concerning interacting species (competition models, predator–prey systems), see Blat and Brown (1986), Conway (1983), Brown and Du (1994) and more recently see Walker (2010) for the study of some age structured models, as well as Du and Hsu (2010) in a non-local situation. In that respect, we wish to stress that the chemostat involves a fairly specific mathematical structure, a fact that plays a crucial role below: the nonlinear coupling in (1.2), say, only involves terms of the form $f_i(x, R)U$ or $f_i(x, R)V$; in other words the two species U and V in (1.2) are only coupled through the resource R. This observation holds in any chemostat model and allows, in some situations, to reduce the original model to a standard competition system by eliminating the equation on the resource (see Dung et al. 1999; Hsu et al. 1994; Hsu and Waltman 1993; Smith and Waltman 1995; Wu 2000; Nie and Wu 2010; Zhang 2005).

Steady states of unstirred chemostats have been first studied by Hsu and Waltman (1993). The authors consider two species evolving in the one-dimensional situation $\Omega = [0, 1]$. A generalisation in the case of two species evolving in a higher dimensional domain Ω is studied by Wu (2000) and Nie and Wu (2010). Using the index

[3] Recall that Robin boundary conditions are covered by our analysis, as well as variable coefficients diffusion operators $\operatorname{div} a_i(x)\nabla$, provided $a_i(x) = \lambda_i a_0(x)$ $(i = 1, 2)$, see Footnotes 1 and 2.

in a positive cone (see Dancer 1984), Guo et al. (2008) and Liu and Zheng (2003) show coexistence results in systems with various trophic levels. In all these texts, the heterogeneity in space, that is crucial to recover coexistence phenomena, is introduced by imposing a gradient of the resource, which in turn is obtained through the boundary condition, of Robin type. All other coefficients are space independent. In the present text at variance, we allow the reaction terms (and other less crucial coefficients) to actually depend on space.

A key point is the following. In all the above works, the authors assume that the competing species, and the resource, have the *same* diffusion rate and the *same* death rate. This assumption provides a specific conservation law, that links the resource and the competing species. In our case it reads (taking $a_0 = a_1 = a_2 = a$ and $m_0(x) = m_1(x) = m_2(x) = m(x)$)

$$m(x)(R + U + V) - a\Delta(R + U + V) = I(x). \tag{1.3}$$

Relation (1.3) allows to eliminate the resource R from the equations, and to write a reduced system whose *semi-trivial solutions* satisfy a simple, scalar, elliptic equation. Semi-trivial solutions are those corresponding to either $(U > 0, V = 0)$ or to $(U = 0, V > 0)$. They correspond to the case where one and only one species survives. Once the semi-trivial solutions are constructed, global bifurcation techniques can be applied to obtain true coexistence solutions, i.e. solutions of the form $(U > 0, V > 0)$, from the semi-trivial ones,.

When the conservation law (1.3), is not available, very little is known. Some perturbation results are available. In Dung et al. (1999), the authors use a perturbation method to extend the above mentioned result when the Eq. (1.3) is *nearly* verified. Baxley and Robinson (1998) study a very general system in the case of N competing species, and they establish a result *close to* the bifurcation point.

In this paper, we propose a *global* method using the more general conservation equation

$$(m_0(x) - a_0\Delta)R + (m_1(x) - a_1\Delta)U + (m_2(x) - a_2\Delta)V = I. \tag{1.4}$$

Eliminating the unknown R in (1.4) leads to *nonlocal* semi-trivial problems. We are able to study these semi-trivial problems by using a lower–upper solutions technique in the so-obtained scalar, nonlocal, elliptic equations. In an independent step, a specific use of global bifurcation techniques then allows to construct true coexistence solutions $(U > 0, V > 0)$, starting from the semi-trivial solutions $(U > 0, V = 0)$ or $(U = 0, V > 0)$. This is a key step of our approach. We wish to stress that the lower–upper solutions part of our analysis requires (see Assumption 2 below) the crucial hypothesis[4]

$$\forall x \in \Omega, \quad \frac{m_i(x)}{a_i} \leq \frac{m_0(x)}{a_0} \quad (i = 1, 2). \tag{1.5}$$

[4] In the case when the diffusion operators $a_i\Delta$ become $\operatorname{div} a_i(x)\nabla$ with $a_i(x) = \lambda_i a_0(x)$ $(i = 1, 2)$, the condition below becomes $m_i(x)/a_i(x) \leq m_0(x)/a_0(x)$ for $x \in \Omega$ $(i = 1, 2)$.

It means that the ratio between death rate and diffusion rate should be larger for the resource than for the competing species, or, in other words, that the two species should diffuse relatively faster than the resource. Since spatial heterogeneity, and the associated diffusion processes, are the key to obtaining systems which allow coexistence, this assumption is quite natural: diffusion of the competing species helps obtaining coexistence situations. To be complete, let us mention that in the case when Robin boundary conditions are retained, another crucial assumption appears, namely[5]

$$\forall x \in \partial\Omega, \quad \frac{b_i(x)}{a_i} \le \frac{b_0(x)}{a_0} \quad (i = 1, 2). \tag{1.6}$$

Assumption (1.6) is similar to (1.5) in spirit, in that a stronger ratio between the escape rate and the diffusion rate is required for the resource R at the boundary, in comparison with the analogous ratio for populations U and V.

The organization of the paper is as follows. In Sect. 2 we present the notation and recall some technical results used in the paper. We also state our main results, namely Theorems 2.15 and 2.17. In Sect. 4, we construct the above mentioned semi-trivial solutions. Under Assumption 2, the lower–upper solutions method, in conjunction with bifurcation arguments, allows to prove existence, uniqueness, and non-degeneracy of the semi-trivial solutions. Section 5 is the main step of our study, in that we prove the existence of solutions (R, U, V) to (1.2) that satisfy $R > 0, U > 0, V > 0$. A global bifurcation theorem is used to construct these coexistence solutions, by joining the two families of semi-trivial solutions. Our construction allows to define a domain $\Theta \subset \mathbb{R}^2_+$ in the space of bifurcation parameters (c_1, c_2), called the *coexistence domain*. This domain is such that whenever $(c_1, c_2) \in \Theta$, a coexistence solution is at hand. In Sect. 6, we state some consequences of our analysis, which provide an ecological point of view. Section 7 concludes this paper.

2 Preliminaries and statement of our results

2.1 Generalities

For $i = 0, 1, 2$, the constants a_i are supposed positive, and the functions $m_i(x)$ and $I(x)$ are assumed smooth, with $m_i(x) > 0$ on $\overline{\Omega}$ and $I(x) \ge 0$ and $I(x) \not\equiv 0$ on $\overline{\Omega}$.

Taking a given $\alpha \in (0, 1)$ whose value is irrelevant, we define the spaces[6]

$$\begin{aligned} &X = \{u \in C^{2+\alpha}(\overline{\Omega}), \quad \partial_n u = 0 \text{ on } \partial\Omega\} \\ &X_+ = \{u \in X, \ \forall x \in \overline{\Omega}, \ u(x) \ge 0\}, \quad X_+^* = \{u \in X_+, \ \forall x \in \overline{\Omega}, \ u(x) > 0\}. \end{aligned} \tag{2.1}$$

[5] This assumption obviously becomes $b_i(x)/a_i(x) \le b_0(x)/a_0(x)$ for $x \in \partial\Omega$ $(i = 1, 2)$, when the a_i's depend on x.

[6] With the obvious adaptation if Robin boundary conditions and/or variable coefficients a_i's are retained: to each operator div $a_i(x)\nabla - m_i(x)$ with boundary condition $a_i(x)\partial_n \cdot + b_i(x) \cdot = 0$ is associated the space $X_i = \{u \in C^{2+\alpha}(\overline{\Omega}), a_i(x)\partial_n u + b_i(x)u = 0 \text{ on } \partial\Omega\}$, and the triple (R, U, V) then is to be exhibited in $X_{0,+} \times X_{1,+} \times X_{2,+}$.

In the sequel, a *solution* to (1.2) is a triple $(R, U, V) \in X_+^3$ that satisfies (1.2). A *coexistence solution* is a solution that lies in $X_+^* \times X_+^* \times X_+^*$. For $i = 0, 1, 2$, we note

$$A_i := m_i(x) - a_i \Delta. \tag{2.2}$$

It is well known that, for all $\alpha \in (0, 1)$, we have

$$A_i : \{w \in C^{2+\alpha}(\Omega),\ \partial_n w = 0 \text{ on } \partial\Omega\} \longrightarrow C^\alpha(\Omega) \quad \text{is one-to-one.}$$

In order to keep a simple notations, the above operator will always be denoted by the same symbol A_i for any choice of α. In the similar spirit we note

$$K_i := A_i^{-1}. \tag{2.3}$$

For each $i = 0, 1, 2$, the operator K_i is compact when seen as (more precisely : when extended to) an operator from $C^1(\Omega)$ to $C^1(\Omega)$ and from $L^2(\Omega)$ to $L^2(\Omega)$. Note that each operator K_i maps X to X compactly as well. Recall that the strong maximum principle for elliptic operators with Neumann (or Robin) boundary conditions reads, whenever $u \in X$,

$$\begin{cases} A_i u \geq 0 \\ \partial_n u \geq 0 \\ u \not\equiv 0 \end{cases} \Longrightarrow \min_{x \in \overline{\Omega}} u(x) = m > 0. \tag{2.4}$$

We last recall the following standard lemmas.

Lemma 2.1 *Take $m(x) \in C^\alpha(\overline{\Omega})$ and $q(x) \in C^\alpha(\overline{\Omega})$. Assume $m(x) > 0$ for all $x \in \overline{\Omega}$. Take $a \in \mathbb{R}_+^*$. Then the eigenvalue problem*

$$(m(x) - a\Delta)\phi + q(x)\phi = \lambda\phi \text{ on } \Omega, \quad \partial_n \phi = 0 \text{ on } \partial\Omega$$

has an infinite sequence of eigenvalues

$$\lambda_1(q) < \lambda_2(q) \leq \cdots$$

Moreover, $\lambda_1(q) = \min_{\phi \in H^1(\Omega), \phi \neq 0} \frac{\int a(\nabla\phi)^2 + \int (m+q)\phi^2}{\int \phi^2}$ is a simple eigenvalue and the corresponding eigenfunction does not change sign on Ω. The quantity $\lambda_1(q)$ is the only eigenvalue whose associated eigenfunction does not change sign on Ω. Finally $\lambda_1(q)$ depends continuously on q and, if $q_1 \leq q_2$ with $q_1 \neq q_2$, then $\lambda_1(q_1) < \lambda_1(q_2)$.

Lemma 2.2 *Take $q(x) \in C^\alpha(\overline{\Omega})$, $a \in \mathbb{R}_+^*$ such that $q(x) > 0$ for any $x \in \overline{\Omega}$. Then the eigenvalue problem*

$$(m(x) - a\Delta)\phi = \mu q(x)\phi, \quad \partial_n \phi = 0,$$

has an infinite sequence of eigenvalues

$$0 < \mu_1(q) < \mu_2(q) \leq \cdots$$

Moreover, $\mu_1(q) = \min_{\phi \in H^1(\Omega), \phi \neq 0} \frac{\int a(\nabla\phi)^2 + \int m\phi^2}{\int q\phi^2}$ *is a simple eigenvalue and the corresponding eigenfunction does not change sign on* Ω*. The quantity* $\mu_1(q)$ *is the only eigenvalue whose associated eigenfunction does not change sign on* Ω*. Moreover,* $\mu_1(q)$ *depends continuously on* q *and, if* $q_1 \leq q_2$ *with* $q_1 \neq q_2$*, then* $\mu_1(q_1) < \mu_1(q_2)$*.*

2.2 Lower- and upper-solutions

In order to make use of a lower–upper solution technique later in this text, we readily introduce the following assumption

Assumption 1 For $i = 1, 2$, we assume $f_i(x, R) \in C^1(\overline{\Omega} \times \mathbb{R})$, with $f_1(x, R) \leq 0$ whenever $R \leq 0$.[7] Besides, we assume that for any $x \in \overline{\Omega}$, we have

$$\forall R > 0, \quad f_i(x, R) > 0, \quad \text{and} \quad \frac{\partial f_i}{\partial R}(x, R) > 0.$$

In other words, the consumption rate is supposed to be a non-negative and increasing function of the resource. We also introduce the following *crucial* one-sided condition[8]

Assumption 2 For $i = 1, 2$ and $x \in \Omega$, we have

$$m_i(x)/a_i \leq m_0(x)/a_0.$$

As we show now, this condition provides a monotonicity property that plays a key role in our analysis. Whenever $w \in X_+$, define $R_i(w) \in X$ as the unique solution in X to

$$A_0 R_i(w) + A_i w = I. \tag{2.5}$$

The operator $w \mapsto R_i(w)$ is introduced for the following reason. The one-species problem (corresponding to semi-trivial solutions ($U > 0$, $V = 0$) say), reads

$$A_0 R + c_1 f_1(x, R) U = I, \quad A_1 U - c_1 f_1(x, R) U = 0. \tag{2.6}$$

This in turn is equivalent to

$$R = R_1(U), \quad A_1 U - c_1 f_1(x, R_1(U)) U = 0, \tag{2.7}$$

[7] Recall that we are only interested in situations with $R \geq 0$, hence the way we extend f_i for negative values of R is irrelevant.

[8] See Footnote 4 in the case of variable coefficients diffusion operators.

and $R_1(U)$ may be seen as the resource at hand in the presence of the population U. In any circumstance, the one-species problem leads to considering the above nonlinear and *nonlocal* elliptic problem, with nonlinearity $w \mapsto f_1(R_1(w))w$.

Now, an easy computation provides the alternative formula.[9]

$$R_i(w) = K_0(I) - \frac{a_i}{a_0} K_0 A_0 w + \frac{1}{a_0} K_0((a_i m_0(x) - a_0 m_i(x))w). \tag{2.8}$$

A key point is the fact that the nonlocal term $K_0(a_i m_0 - a_0 m_i)w$ above satisfies

$$K_0(a_i m_0 - a_0 m_i)w \geq 0 \quad \text{whenever } w \geq 0, \tag{2.9}$$

as an obvious consequence of Assumption 2 together with the maximum principle. Another remark is in order. In the case of Neumann boundary conditions, we have the obvious relation $K_0 A_0 w = w$. The reader's attention is drawn to the fact that in the case of Robin boundary condition, $K_0 A_0 w$ always lies in X_0 so that if w lies in X_1 or X_2, then $K_0 A_0 w$ and w do not satisfy the same boundary condition in general. Note however that the following holds. Provided we assume $b_i/a_i \leq b_0/a_0$ ($i = 1, 2$)—see Eq. (1.6) and Footnote 5—we have

$$K_0 A_0 w \leq w \quad \text{whenever } w \geq 0. \tag{2.10}$$

This comes from the maximum principle together with the fact that, when $w \geq 0$, the function $v = K_0 A_0 w$ satisfies $A_0(v - w) = 0$ with the boundary condition $(a_0 \partial_n + b_0)(v - w) = +(a_0 b_1 - b_0 a_1) w / a_1 \leq 0$.

We readily show that Assumption 2 implies the following one-sided Lipschitz condition for the nonlinearity $w \mapsto f_1(R_1(w))w$ in (2.7).

Lemma 2.3 *Suppose Assumption 2 is true. Let M be a positive constant and take $i = 1, 2$. Then, there exists $\gamma = \gamma_i(M) > 0$ such that*

$$w_1(x) f_i(x, R_i(w_1))(x) - w_2(x) f_i(x, R_i(w_2))(x) \geq -\gamma (w_1(x) - w_2(x))$$

whenever $w_1, w_2 \in X$ satisfy $0 \leq w_2 \leq w_1 \leq M$.

Remark 2.4 The point is, the above estimate is *pointwise* in x, though it involves the *nonlocal* operator R_i. □

Remark 2.5 If all diffusion operators are the same, as in the previously quoted papers, namely if $A_i \equiv A_0$ ($i = 1, 2$), then the nonlocal terms of the form $K_0(a_i m_0 - a_0 m_i)w$ vanish in the course of the analysis. In that particular case, the method we develop coincides with that of Wu (2000). The nonlocal terms constitute the main difficulty we treat. □

[9] When the diffusion operators become div $a_i(x)\nabla$ with $a_i(x) = \lambda_i a_0(x)$, see Footnotes 2 and 4, the formula below becomes $R_i(w) = K_0(I) - \lambda_i K_0 A_0 w + K_0((\lambda_i m_0(x) - m_1(x))w)$, with $\lambda_i m_0(x) - m_1(x) \geq 0$ for all x, and our analysis is unchanged.

Admitting Lemma 2.3 is proved for the moment, we readily state that this result allows us to apply a lower–upper solution method in the nonlocal elliptic equation

$$A_i w - c_i f_i(x, R_i(w)(x))w = 0, \tag{2.11}$$

where $w \in X$ is the unknown. Indeed, using Lemma 2.3, the following definition and theorem are standard (see Smoller 1993).

Definition 2.6 *(lower- and upper-solutions)* An upper-solution to Eq. (2.11) is a function $w \in C^{2+\alpha}(\overline{\Omega})$ verifying[10]

$$A_i w(x) - c_i f_i(x, R_i(w)(x))w(x) \geq 0 \text{ for all } x \in \Omega, \quad \text{and} \quad \partial_n w \geq 0 \text{ on } \partial\Omega.$$

A lower-solution is defined in the similar way with reversed inequalities.

Theorem 2.7 (lower–upper solutions method—see Smoller (1993)) *Assume there exists a lower resp. upper solution W^1 resp. W^2 to Eq. (2.11), which satisfies $0 \leq W^1 \leq W^2$.*

Then, Eq. (2.11) admits a pair (W^-, W^+) of solutions, with $W^1 \leq W^- \leq W^+ \leq W^2$.

If W^1 and W^2 are not solutions to (2.11), we have $W^1 < W^- \leq W^+ < W^2$ on $\overline{\Omega}$.

The pair (W^-, W^+) is maximal in the sense that each solution W to (2.11) which satisfies $W \in [W^1, W^2]$ necessarily verifies $W \in [W^-, W^+]$ as well.

Remark 2.8 Stricto sensu the above theorem is not to be found in Smoller (1993). Smoller requires the nonlinear term be Lipschitz in w, a property that we do not have at hand in the present case. It is standard to observe that the key of the proof, which relies on an iteration of the maximum principle, is the following. When writing the equation $A_i w = c_i f_i(x, R_i(w))w =: G_i(x, w)$, the point is to find a (large) $K > 0$ and a (large) $M > 0$ such that whenever $0 \leq W_1(x) \leq W_2(x) \leq M$ for all x, we have $G(x, W_1)(x) + K W_1(x) \leq G(x, W_2)(x) + K W_2(x)$ for all x as well. The one-sided Lipschitz estimate of Lemma 2.3 is enough in that respect.

Note that Pao (1982, 1996) establishes variants of the above techniques for *systems*, in the case where the nonlinear terms, which are vector-valued, satisfy so-called quasi-monotonicity properties. □

There remains to prove Lemma 2.3.

Proof of Lemma 2.3 Firstly, when $w \in X$ satisfies $0 \leq w \leq M$, the maximum principle provides easily[11]

$$\begin{aligned}\|R_i(w)\|_{L^\infty} &\leq \|K_0(I)\|_{L^\infty} + \|K_0 A_0\left(\frac{w}{a_0}\right)\|_{L^\infty} + \left\|K_0\left((a_i m_0 - a_0 m_i)\frac{w}{a_0}\right)\right\|_{L^\infty} \\ &=: M_\infty < +\infty.\end{aligned}$$

10 With the obvious extension in the case of Robin boundary conditions.

11 In the case of Robin boundary conditions, the only additional difficulty is to show that $v := K_0 A_0(w)$ is bounded provided w is bounded. The function $v - w$ verifies $A_0(v - w) = 0$ on Ω and $a_0 \partial_n(v - w) + b_0(v - w) = (a_0 b_1 - b_0 a_1)\frac{w}{a_1}$ on $\partial\Omega$. Since w is bounded, the boundary term is bounded as well and the maximum principle shows that $v - w$ and then v is bounded.

The assumed smoothness of f_i ensures that f_i is globally Lipschitz on $\overline{\Omega} \times [-M_\infty, M_\infty]$. We call C_i the Lipschitz constant associated with f_i.

Next, whenever $0 \leq w_2 \leq w_1 \leq M$, with $w_i \in X$ $(i = 1, 2)$, we have

$$\begin{aligned} R_i(w_1) - R_i(w_2) &= -\frac{a_i}{a_0} K_0 A_0(w_1 - w_2) \\ &\quad + \frac{1}{a_0} K_0((a_i m_0(x) - a_0 m_i(x))(w_1 - w_2)) \\ &\geq -\frac{a_i}{a_0} K_0 A_0(w_1 - w_2) \\ &\geq -\frac{a_i}{a_0}(w_1 - w_2). \end{aligned}$$

where the first lower bound uses Assumption 2 while the second uses the observation (2.9). Hence, writing

$$\begin{aligned} & w_1(x) f_i(x, R_i(w_1)(x)) - w_2(x) f_i(x, R_i(w_2)(x)) \\ &\quad = f_i(x, R_i(w_1)(x))(w_1 - w_2)(x) \\ &\qquad + w_2(x)(f_i(x, R_i(w_1)(x)) - f_i(x, R_i(w_2)(x))) \\ &\quad \geq w_2(x)(f_i(x, R_i(w_1)(x)) - f_i(x, R_i(w_2)(x))), \end{aligned}$$

we distinguish two cases. If x is such that $R_i(w_1)(x) \geq R_i(w_2)(x)$, then f_i being an increasing function of R, we recover

$$w_1(x) f_i(x, R_i(w_1)(x)) - w_2(x) f_i(x, R_i(w_2)(x)) \geq 0.$$

In the opposite case we have

$$\begin{aligned} & w_1(x) f_i(x, R_i(w_1)(x)) - w_2(x) f_i(x, R_i(w_2)(x)) \\ &\quad \geq w_2(x)(f_i(x, R_i(w_1)(x)) - f_i(R_i(w_2)(x))) \\ &\quad \geq +C_i w_2(x)(R_i(w_1)(x) - R_i(w_2)(x)) \\ &\quad \geq -C_i \frac{a_i}{a_0} w_2(x)(w_1(x) - w_2(x)) \geq -C_i \frac{a_i}{a_0} M(w_1(x) - w_2(x)). \end{aligned}$$

The proposition is proved. □

2.3 Bifurcation methods

We state a version of two global bifurcation theorems we use in the sequel, for equations of the form,

$$T(c, W) = W,$$

where $c \in \mathbb{R}$ is the bifurcation parameter, $W \in Y$ is the seeked solution, and Y is a Banach space, while $T(c, W) \in C^0(\mathbb{R} \times Y; Y)$ is a given, continuous map. In the following we assume that T is C^2 in (c, W), and we denote by D_c resp. D_W the derivatives of T with respect to c resp. W. We assume also that $D_W T(c, W)$ is compact for any c and W.

We start with the following bifurcation theorem from a simple eigenvalue. Note that the first part (the local part) is a classical result of Crandall and Rabinowitz (1971) while the second part (the global part) is a classical result of Rabinowitz (1971).

Theorem 2.9 (Bifurcation from a simple eigenvalue—see Crandall and Rabinowitz 1971; Rabinowitz 1971) *With the above notation, we assume that*

$$\forall c \in \mathbb{R}, \quad T(c, 0) = 0.$$

We note $L(c) = \mathrm{Id} - D_W T(c, 0)$ and we also assume that for some value $c^0 \in \mathbb{R}$, the following holds:

$$\begin{cases} \textit{dim Ker } (L(c^0)) = 1, \\ \quad \textit{and, whenever } W_0 \textit{ satisfies } \mathrm{Ker}\ (L(c^0)) = \mathrm{span}(W_0), \ \textit{we have} \\ D_c L(c^0) \cdot W_0 \notin \mathrm{Im}(L_0). \end{cases}$$

Then, there exists $\varepsilon > 0$ and a map $(c(s), X(s)) \in C^0((-\varepsilon, \varepsilon); \mathbb{R} \times Y)$, with $c(0) = c^0$, $X(0) = 0$, such that close to $(c^0, 0)$ in $\mathbb{R} \times Y$, the only nontrivial solution to $T(c, W) = W$ is given by $\Gamma_\varepsilon = \{(c(s), sW_0 + X(s)), s \in (-\varepsilon, \varepsilon)\}$. Moreover Γ_ε is contained in a continuum[12] *$\mathscr{C}$ of nontrivial solutions to $T(c, W) = W$ in $\mathbb{R} \times Y$ which either joins $(c_1^0, 0)$ to ∞ in $\mathbb{R} \times Y$ or joins $(c_1^0, 0)$ to another trivial solution $(\widehat{c}, 0)$ with $\widehat{c} \neq c_1^0$.*

In many application, one needs to select positive solutions of $T(c, W) = 0$. In that case, one defines the two following subsets of Γ_ε :

$$\Gamma_\varepsilon^+ = \{(c(s), sW_0 + X(s)); s \in (0, \varepsilon)\}; \Gamma_\varepsilon^- = \{(c(s), sW_0 + X(s)); s \in (-\varepsilon, 0)\}.$$

Typically, Γ_ε^+ consists in positive solutions and one wants to construct a global curve made of positive solutions. Such "unilateral" global bifurcation results first appears in Rabinowitz (1971) but, as noted for instance in López-Gómez (2001), there is a gap in the original proofs. However López-Gómez (2001) and Shi and Wang (2009) contain rigorous proof of a weaker version of the original theorems. We follow here the presentation of Shi and Wang (2009).

Theorem 2.10 (Unilateral bifurcation—see Shi and Wang (2009)) *Suppose that all conditions in Theorem 2.9 are satisfied and assume that both Y and Y^* are separable. Let $\mathscr{C}^+$ be the connected set of $\mathscr{C} \backslash \Gamma_\varepsilon^-$ which contains Γ_ε^+. Then $\mathscr{C}^+$ satisfies one of the following:*

(i) The closure $\overline{\mathscr{C}^+}$ joins the trivial solution $(c^0, 0)$ to another trivial solution $(\widehat{c}, 0)$, for some $\widehat{c} \in \mathbb{R}$, $\widehat{c} \neq c_0$, where $\mathrm{Id} - D_W T(\widehat{c}, 0)$ is not invertible.

[12] We call a continuum of solutions a connected family of solutions $(c, W) \in R \times Y$.

(ii) The closure $\overline{\mathscr{C}^+}$ *joins* $(c_0, 0)$ *to* ∞ *in* $\mathbb{R} \times Y$.
(iii) The closure $\overline{\mathscr{C}^+}$ *contains a point* $(c, z) \in \mathbb{R} \times Z$ *where* Z *is a supplementary space of* $span(W_0)$ *in* Y.

2.4 Statement of our results

Our whole construction relies on a recursive procedure. We construct coexistence solutions to (1.2) (we do not rewrite the boundary conditions),

$$\begin{cases} A_0 R + c_1 f_1(x, R)U + c_2 f_2(x, R)V = I, \\ A_1 U - c_1 f_1(x, R)U = 0, \\ A_2 V - c_2 f_2(x, R)V = 0, \end{cases} \tag{2.12}$$

by starting from the 0-species problem (namely trivial solutions corresponding to $R > 0, U = 0, V = 0$). Then we construct 1-species, or semi-trivial, solutions (corresponding to $R > 0$, and either $(U > 0, V = 0)$ or $(U = 0, V > 0)$), by using lower–upper solutions techniques. Then we prove the non-degeneracy of the so-obtained semi-trivial solutions. This step is crucial, and makes a strong use of our Assumption 2. It is the most difficult and technical part of our analysis. Armed with these results, we then use bifurcations to construct true coexistence solutions $R > 0, U > 0, V > 0$. This last step uses all informations gathered on the semi-trivial solutions.

We start with the 0-species problem.

Theorem 2.11 (Trivial solution)

(i) The following equation has a unique solution $S \in X_+^*$,

$$A_0 S = I. \tag{2.13}$$

(ii) If $(R, U, V) \in X_+^3$ *is a solution to* (1.2) *with* $U \not\equiv 0$ *or* $V \not\equiv 0$, *then*[13] $0 < R < S$.
(iii) Let $w \in X_+$. *The equation*

$$A_0 R + c_i f_i(x, R) \quad w = I$$

has a unique solution[14] $R_w^{(i)} \in X_+^*$. *It satisfies* $0 < R_w^{(i)} \leq S$.

The map $w \mapsto R_w^{(i)}$ *is decreasing from* X_+ *to* X_+.

We postpone the (easy) proof of this statement.

We next focus our attention on *semi-trivial* solutions to (1.2).

[13] Recall that throughout this text the notation $R < S$ means $S - R \in X_+^*$, or, in other words, that for any $x \in \overline{\Omega}$ we have $R(x) < S(x)$

[14] Note that $R_w^{(i)} \neq R_i(w)$, see (2.8), unless we have $A_i w = c_i f_i(x, R_w^{(i)})w$.

If $V \equiv 0$ (the case $U \equiv 0$ is similar), system (1.2) reduces to (we do not rewrite the boundary conditions)

$$\begin{cases} A_0 R + c_1 f_1(x, R)U = I, \\ A_1 U - c_1 f_1(x, R)U = 0. \end{cases} \tag{2.14}$$

We define the operator

$$T_1(c_1, R, U) = \begin{pmatrix} K_0(I - c_1 f_1(x, R)U) \\ K_1(c_1 f_1(x, R)U) \end{pmatrix} = \begin{pmatrix} S \\ 0 \end{pmatrix} + c_1 \begin{pmatrix} -K_0(f_1(x, R)U) \\ K_1(f_1(x, R)U) \end{pmatrix}. \tag{2.15}$$

Clearly, $T_1 : \mathbb{R} \times X^2 \to X^2$ is continuous and compact, any fixed point $(R, U) \in X^2$ of $T_1(c_1, \cdot, \cdot)$, i.e. such that $T_1(c_1, R, U) = {}^t(R, U)$, is clearly a solution to (2.14), and the trivial solution is $T_1(c_1, S, 0) = {}^t(c_1, S, 0)$.

The following theorem describes two solution branches to (2.14). It is proved in Sect. 4, using a global bifurcation technique with c_1 used as the bifurcation parameter.

Theorem 2.12 (Semi-trivial solutions)
Under Assumptions 1 and 2, the following holds.

(i) *There exists $c_1^0 > 0$ such that:*
- *if $c_1 \le c_1^0$, then $(S, 0)$ is the only solution to (2.14) in X_+^2,*
- *if $c_1 > c_1^0$, the system (2.14) has a unique solution in $(X_+^*)^2$, noted*

$$(R_u^*(c_1), U^*(c_1)).$$

(ii) *Whenever $c_1 > c_1^0$, the solution $(R_u^*(c_1), U^*(c_1))$ is non-degenerate*[15]

(iii) *The map $R_u^* : c_1 \mapsto R_u^*(c_1)$ is decreasing and belongs to $C^1((c_1^0, +\infty), X_+^*)$. Moreover, the following two limits hold uniformly on $\overline{\Omega}$, namely,*

$$R_u^*(c_1) \underset{c_1 \to c_1^0}{\longrightarrow} S, \quad \textit{and} \quad R_u^*(c_1) \underset{c_1 \to +\infty}{\longrightarrow} 0,$$

(iv) *The map $U^* : c_1 \mapsto U^*(c_1)$ is increasing and belongs to $C^1((c_1^0, +\infty), X_+^*)$. Moreover, the following two limits hold uniformly on $\overline{\Omega}$, namely,*

$$U^*(c_1) \underset{c_1 \to c_1^0}{\longrightarrow} 0, \quad \textit{and} \quad U^*(c_1) \underset{c_1 \to +\infty}{\longrightarrow} U_\infty,$$

where $U_\infty \in X_+^*$ is the unique solution to $A_1 U_\infty = I$.

[15] In other words, $\mathrm{Ker}(\mathrm{Id} - D_{(R,U)} T_1(c_1, R_u^*(c_1), U^*(c_1))) = \{0\}$.
This apparently technical statement is the key to constructing true coexistence solutions and obtaining Theorem 2.15 below.

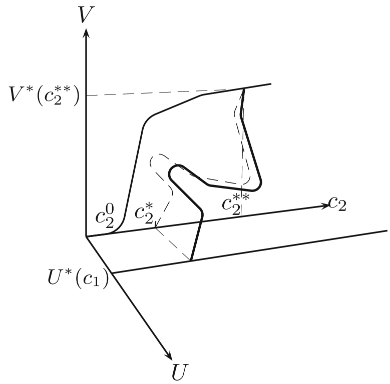


Fig. 1 Coexistence solution in the space $\mathbb{R} \times X_+ \times X_+$. The parameter c_1 is *fixed* here, with $c_1 > c_1^0$. The *full line* in the (U, c_2)-plane represent (the projection of) the particular semi-trivial solution associated with $U^*(c_1)$—see Theorem 2.12. Due to its very definition, this solution does not depend on c_2. The *full curve* in the (c_2, V)-plane represents the (projection of the) family of semi-trivial solutions $(R, 0, V^*(c_2))$. Finally, the *bold curve* joining the two planes (c_2, U) and (c_2, V) represents the (projection of the) coexistence solutions $(c_1, c_2, R, U, V) \in (c_1^0, \infty) \times (\underline{c_2}(c_1), \overline{c_2}(c_1)) \times (X_+^*)^3$ obtained in part (i) of the theorem. In the present figure we have assumed $c_2^*(c_1) < c_2^{**}(c_1)$

Remark 2.13 It can be shown using a local bifurcation argument (Crandall and Rabinowitz 1971) that for c_1 near c_1^0 the semi-trivial solution is a stable solution of the associated time dependent one species problem.

Remark 2.14 In fact, the mere *existence* of semi-trivial solutions may be obtained using a simple global bifurcation argument, *without* making use of our Assumption 2. Assumption 2 is required at variance to obtain *uniqueness* of these solutions. This assumption also plays a key role in establishing non-degeneracy.

Naturally, the similar results hold in the case $U \equiv 0$ and $V > 0$. This provides a critical value c_2^0, and a solution branch $(R_v^*(c_2), V^*(c_2)) \in (X_+^*)^2$ whenever $c_2 > c_2^0$, which satisfies the properties similar to the ones listed before. The natural semi-trivial solutions to (1.2) are $(R, U, V) = (R_u^*(c_1), U^*(c_1), 0)$ (with $c_1 > c_1^0$) and $(R, U, V) = (R_v^*(c_2), 0, V^*(c_2))$ (with $c_2 > c_2^0$). We define the following two subsets of $\mathbb{R}_+^2 \times X_+^3$, namely

$$\mathscr{C}_u = \left\{(c_1, c_2, R_u^*(c_1), U^*(c_1), 0);\ c_1 > c_1^0\right\},$$
$$\mathscr{C}_v = \left\{(c_1, c_2, R_v^*(c_2), 0, V^*(c_2));\ c_2 > c_2^0\right\}. \tag{2.16}$$

With this notation at hand, the following Theorem is the main result of the present paper. It establishes that coexistence solutions to (1.2) may be defined using bifurcations from the two sets $\mathscr{C}_u$ and $\mathscr{C}_v$. The proof is provided in Sect. 5.2. Figure 1 illustrates the situation.

Theorem 2.15 (Coexistence solutions)
Under Assumptions 1 and 2, there is a bifurcation from $\mathscr{C}_u$ to $\mathscr{C}_v$ in the following sense. Let $c_1 > c_1^0$ be fixed.

There exist $c_2^* = c_2^*(c_1) > c_2^0$ *and* $c_2^{**} = c_2^{**}(c_1) > c_2^0$*, and there is a continuum of positive solutions to* (1.2)*, noted* $(c_1, c_2, R, U, V) \in (c_1^0, +\infty) \times (c_2^0, +\infty) \times (X_+^*)^3$*, whose closure joins the semi-trivial* $(c_1, c_2^*, R_u^*(c_1), U^*(c_1), 0) \in \mathscr{C}_u$ *to the semi-trivial* $(c_1, c_2^{**}, R_v^*(c_2^{**}), 0, V^*(c_2^{**})) \in \mathscr{C}_v$*.*

In particular, noting $\underline{c_2}(c_1) = min(\{c_2^*, c_2^{**}\}) \leq max(\{c_2^*, c_2^{**}\}) = \overline{c_2}(c_1)$*, we have*

$$\forall c_2 \in (\underline{c_2}(c_1), \overline{c_2}(c_1)), \quad \exists (R, U, V) \in (X_+^*)^3 \text{ coexistence solution to (1.2).}$$

Naturally, the similar results hold for a bifurcation from $\mathscr{C}_v$ to $\mathscr{C}_u$ which provides for any $c_2 > c_2^0$ the definition of $c_1^*(c_2)$, $c_1^{**}(c_2)$, $\underline{c_1}(c_2)$ and $\overline{c_1}(c_2)$.

Remark 2.16 Note that the situation where $c_2^*(c_1) = c_2^{**}(c_1)$, say, may very well happen. In that case the interval $(\underline{c_2}(c_1), \overline{c_2}(c_1))$ is void. Hence, as we can see, the second statement of the theorem is a weak byproduct of the first one, which exhibits at variance an actual branch of coexistence solutions. We refer to the conjecture stated in Sect. 7 below for a discussion of this point.

With the use of the above Theorem, one may define a *coexistence domain* Θ, as

$$\begin{aligned} \Theta = \{&(c_1, c_2) \in (c_1^0, +\infty) \times (c_2^0, +\infty), \text{ s.t.} \\ &c_1 \in (\underline{c_1}(c_2), \overline{c_1}(c_2)) \quad \text{and} \quad c_2 \in (\underline{c_2}(c_1), \overline{c_2}(c_1))\}. \end{aligned} \tag{2.17}$$

It corresponds to values of the parameters (c_1, c_2) for which a coexistence solution may be exhibited (a subset of the set of *all* values (c_1, c_2) such that a coexistence solution may be exhibited—see Sect. 7 on that point).

The following theorem is proved in Sect. 5.3. It explores the structure of Θ.

Theorem 2.17 (Coexistence domain)

Under Assumptions 1 *and* 2*, and with the notation of Theorem* 2.15*, the following holds.*

(i) Whenever $c_1 > c_1^0$*, the quantity* $c_2^{**}(c_1)$ *is characterised by the relation*

$$c_1^*(c_2^{**}(c_1)) = c_1,$$

and similarly when indices 1 *and* 2 *are reversed.*

(ii) The two maps $c_i^*(c_j) : (c_j^0, +\infty) \longrightarrow (c_i^0, +\infty)$, $\{i, j\} = \{1, 2\}$ *are continuous and increasing. Moreover, for* $\{i, j\} = \{1, 2\}$*, we have*

$$\lim_{c_i \to c_i^0} c_j^*(c_i) = c_j^0, \quad \text{and} \quad \lim_{c_i \to +\infty} c_j^*(c_i) = +\infty.$$

(iii) With the notation (2.17)*, whenever* $(c_1, c_2) \in \Theta$*, system* (1.2) *has a coexistence solution* $(R, U, V) \in (X_+^*)^3$*, and we have*

$$\begin{aligned} \Theta = \Theta_- \cup \Theta_+, \quad &\text{with } \Theta_- = \{(c_1, c_2), \quad c_1 < c_1^*(c_2) \text{ and } c_2 < c_2^*(c_1)\}, \\ &\text{and } \Theta_+ = \{(c_1, c_2), \quad c_1 > c_1^*(c_2) \text{ and } c_2 > c_2^*(c_1)\}. \end{aligned}$$

The next sections are devoted to the proof of Theorem 2.11 (trivial solutions), Theorem 2.12 (semi-trivial solutions), as well as Theorems 2.15 and 2.17 (coexistence solutions and coexistence domain).

3 Zero species: trivial solutions—Proof of Theorem 2.11

We prove here the various statements of Theorem 2.11. Recall that the problem with zero species reads, shortly, $A_0 R = I$.
Point (i) Existence and uniqueness of S is clear.
Point (ii) Let $(R, U, V) \in X_+^3$ be a solution to (1.2) with $U \geq 0$ and $V \geq 0$.
We have $A_0 R = I - c_1 f_1(x, R)U - c_2 f_2(x, R)V \leq I$. Hence $A_0 R \leq I$ with $A_0 R \not\equiv I$ whenever $U \not\equiv 0$ or $V \not\equiv 0$. The strong maximum principle provides $0 < R < S$, with $R < S$ whenever $U \not\equiv 0$ or $V \not\equiv 0$.
Point (iii) Take $w \in X_+^*$. Due to Assumption 1, for $\varepsilon > 0$ small enough, S resp. ε are upper resp. lower solutions to

$$A_0 R + c_i f_i(x, R)w = I. \tag{3.1}$$

As a consequence, there exists a pair $(R^-, R^+) \in X^2$ of maximal solutions to (3.1), with $0 < R^- \leq R^+ < S$. Let us show that $R^- \equiv R^+$. We have $A_0(R^+ - R^-) + c_i(f_i(x, R^+) - f_i(x, R^-))w = 0$. Integrating over Ω and taking the boundary conditions into account,[16] we obtain

$$\int_\Omega [m_0(R^+ - R^-) + c_i(f_i(x, R^+) - f_i(x, R^-))w]\, dx = 0.$$

Since $R \mapsto f_i(x, R)$ is an increasing function of R for any value of x, we recover $R^- = R^+$. Existence and uniqueness of $R_w^{(i)}$ in the theorem follows.

Lastly, take $0 < w_1 < w_2$, with $w_1, w_2 \in X$. We have $A_0 R_{w_2}^{(i)} + c_i f_i(x, R_{w_2}^{(i)})w_1 \leq I$. Hence, $R_{w_2}^{(i)} \in X$ is a lower-solution to $A_0 R + c_i f_i(x, R)w_1 = I$. As a consequence, there exists an actual solution $\widetilde{R}_{w_1}^{(i)} \in X$ to $A_0 R + c_i f_i(x, R)w_1 = I$, which satisfies $R_{w_2}^{(i)} < \widetilde{R}_{w_1}^{(i)} < S$. Uniqueness then provides $\widetilde{R}_{w_1}^{(i)} = R_{w_1}^{(i)}$. We recover the necessary relation $R_{w_2}^{(i)} < R_{w_1}^{(i)}$. This ends the proof.

4 One species: semi-trivial solutions—Proof of Theorem 2.12

In this section, we study the one species problem (2.14), corresponding to the semi-trivial solution $(R, U, 0) \in X_+^* \times X_+^* \times X_+$ to (1.2). Recall that the one species problem reads

$$\begin{cases} A_0 R + c_1 f_1(x, R)U = I, \\ A_1 U - c_1 f_1(x, R)U = 0. \end{cases}$$

[16] Robin boundary conditions would add a term $\int_{\partial\Omega} b_0(x)[R^+ - R^-] \geq 0$, and the conclusion would remain unchanged.

4.1 General facts about the one species problem

Lemma 4.1 *Let $c_1 > 0$ be fixed. There exists $M_0 > 0$ such that each solution $(R, U) \in (X^*_+)^2$ to (2.14) verifies*

$$0 \leq U \leq M_0.$$

Proof of Lemma 4.1 Let $(R, U) \in (X^*_+)^2$ be a solution to (2.14). Summing the equations on R and U provides, as already noted, $A_0 R + A_1 U = I$. As a consequence, for some $\alpha > 0$ small enough we have $(\alpha - \Delta)(a_0 R + a_1 U) \leq I \leq \|I\|_\infty$. The strong maximum principle[17] then provides $0 \leq a_0 R + a_1 U \leq \frac{1}{\alpha}\|I\|_{L^\infty}$. □

Lemma 4.2 *The eigenvalue problem $A_1\phi - \mu f_1(x, S)\phi = 0$ with $\phi \in X$ has a principal eigenvalue $c_1^0 > 0$ and a corresponding eigenfunction $\phi_0 \in X^*_+$, unique up to a multiplicative constant. We have*

$$A_1\phi_0 - c_1^0 f_1(x, S)\phi_0 = 0, \tag{4.1}$$

with c_1^0 given by $c_1^0 = \min_{\phi \in H^1(\Omega), \phi \neq 0} \left[\int a_1 \nabla\phi^2 + m_1\phi^2\right] / \left[\int f_1(x, S)\phi^2\right]$.

Proof of Lemma 4.2 This is a direct application of Lemma 2.2. □

Proposition 4.3 *Let $c_1 > 0$ be fixed. Suppose there exists $(R, U) \in (X^*_+)^2$ solution to (2.14). Then we necessarily have $c_1 > c_1^0$.*

Proof of Proposition 4.3 The function $U > 0$ verifies $A_1 U - c_1 f_1(R)U = 0$. Multiplying by ϕ_0, defined in Lemma 4.2, and integrating over Ω leads to

$$0 = \int_\Omega A_1 U\phi_0 - c_1 \int_\Omega f_1(x, R)U\phi_0 = \int_\Omega U\phi_0(c_1^0 f_1(x, S) - c_1 f_1(x, R)).$$

Since Proposition 2.11 ensures $R < S$ hence $f_1(x, R) < f_1(x, S)$, we recover the necessary condition $c_1 > c_1^0$. □

4.2 Existence, uniqueness, and some properties of solutions to the one species problem

The main result of this paragraph is the

Proposition 4.4 *Suppose Assumptions 1 and 2 are verified. Assume $c_1 > c_1^0$. Then, system (2.14) has a unique solution in $(X^*_+)^2$ denoted by $(R^*_u(c_1), U^*(c_1))$.*

---

[17] With the obvious adaptation in the case of Robin boundary conditions. In the case of variable coefficients $a_i(x)$ with $a_i(x) = \lambda_i a_0(x)$, see Footnote 2, the argument is the same, due to the bound $(\alpha - \operatorname{div} a_0(x)\nabla)(R + \lambda_1 U) \leq I(x) = (m_0(x) - \operatorname{div} a_0(x)\nabla)R + (m_1(x) - \lambda_1 \operatorname{div} a_0(x)\nabla)U$.

Proof of Proposition 4.4 Take a solution $(R, U) \in (X_+^*)^2$ to (2.14). Defining, as in (2.8), the quantity $R_1(U) \in X$ by the relation $A_0 R_1(U) + A_1 U = I$ we recover the necessary condition $R = R_1(U)$, and system (2.14) can be rewritten (with $\partial_n U = 0$ on $\partial\Omega$),

$$A_1 U - c_1 f_1(x, R_1(U))U = 0, \tag{4.2}$$

Let $\phi_0 > 0$ be the eigenfunction defined in Lemma 4.2, which satisfies $A_1\phi_0 - c_1^0 f_1(x, S)\phi_0 = 0$. We claim that for $\varepsilon > 0$ small enough and $M > 0$ large enough, the pair $(\varepsilon\phi_0, M)$ is a pair of lower–upper solutions to (4.2). Indeed, on the one hand, choosing $M > 0$ large enough leads to $R_1(M) < 0$ (since $A_0 R_1(M) = I - A_1 M = I - m_1(x)M$). Therefore, we obtain

$$A_1 M - c_1 M f_1(x, R_1(M)) \geq m_1 M \geq 0,$$

with $\partial_n M = 0$ on $\partial\Omega$, and M is an upper-solution to (4.2). On the other hand, taking $\varepsilon > 0$ small enough leads to

$$A_1(\varepsilon\phi_0) - c_1 f_1(x, R_1(\varepsilon\phi_0)) \cdot (\varepsilon\phi_0) = \varepsilon\phi_0(c_1^0 f_1(x, S) - c_1 f_1(x, R_1(\varepsilon\phi_0))),$$
$$\text{with } A_0 R_1(\varepsilon\phi_0) + \varepsilon c_1^0 f_1(x, S)\phi_0 = I.$$

It is clear that $\lim_{\varepsilon\to 0} \|R_1(\varepsilon\phi_0) - S\|_\infty = 0$. Therefore, we recover

$$A_1(\varepsilon\phi_0) - c_1 f_1(x, R_1(\varepsilon\phi_0)) \cdot (\varepsilon\phi_0) = \varepsilon(c_1^0 - c_1)\phi_0 f_1(x, S) + o_{\varepsilon\to 0}(1) \leq 0,$$

with $\partial_n(\varepsilon\phi_0) = 0$ on $\partial\Omega$. Therefore $\varepsilon\phi_0$ is a lower solution to (4.2) for ε small enough.

These considerations allow us to conclude (see Theorem 2.7) that there exists a pair (U^-, U^+) of maximal solutions to (4.2), satisfying $\varepsilon\phi_0 < U^- \leq U^+ < M$, and for any solution $U \in [\varepsilon\phi_0, M]$ to (4.2) we necessarily have $U^- \leq U \leq U^+$. Besides, let $U \in X_+^*$ be a solution to (4.2). Lemma 4.1 and maximum principle ensure one can choose $M \geq M_0$ and $\varepsilon > 0$ such that $\varepsilon\phi_0 \leq U \leq M$ and $0 < U \leq U^+$ as well.

Let us show that $U = U^+$. We first observe that the relation $0 < U \leq U^+$ implies

$$0 \leq R_1(U^+) \leq R_1(U).$$

This is due to Theorem 2.11, together with the fact that $R_1(U) = R_U^{(1)}$ and $R_1(U^+) = R_{U^+}^{(1)}$ in the present case (for U and U^+ solve the auxiliary equation $A_1 U = c_1 f_1(\ldots)U$ and similarly for U^+). We deduce $f_1(x, R_1(U^+)) \leq f_1(x, R_1(U))$. On the other hand, the definition of U and U^+, provide

$$0 = \int_\Omega (A_1 U \cdot U^+ - A_1 U^+ \cdot U) = \int_\Omega c_1 U U^+(f_1(\cdot, R_1(U)) - f_1(\cdot, R_1(U^+)))$$

so that $f_1(x, R_1(U)) = f_1(x, R_1(U^+))$ and $R_1(U) = R_1(U^+)$. Eventually we deduce, using the equations satisfied by U and U^+ again, the relation $U = U^+$.

The same proof works in the case of Robin boundary conditions. □

With the above proposition at hand, we complete the picture by stating some properties of the pair $(R_u^*(c_1), U^*(c_1))$.

Proposition 4.5 *With the notation of Proposition 4.4, we have*

(i) $\lim_{c_1 \to c_1^0}(\|R_u^*(c_1) - S\|_\infty + \|U^*(c_1)\|_\infty) = 0$
(ii) $\lim_{c_1 \to +\infty}(\|R_u^*(c_1)\|_\infty + \|U^*(c_1) - U_\infty\|_\infty) = 0$,

where U_∞ *is the unique solution to* $A_1 U = I$ *in* X_+.

Proof of Proposition 4.5 *Proof of (i).* Let ϕ_0 be the only positive eigenfunction of $A_1\phi_0 - c_1^0 f_1(S)\phi_0 = 0$ verifying $\|\phi_0\|_\infty = 1$. Now let $\varepsilon > 0$ be fixed. For $c_1 > c_1^0$ close enough to c_1^0, the function $\varepsilon\phi_0$ is an upper-solution to

$$A_1 U - c_1 f_1(x, R_1(U))U = 0$$

in X_+^*.

Indeed, we have $R_1(\varepsilon\phi_0) = K_0(I) - \varepsilon c_1^0 K_0(f_1(x, S)\phi_0) < S$ on $\overline{\Omega}$, so that $f_1(x, S) > f_1(x, R_1(\varepsilon\phi_0))$ and

$$\begin{aligned} &\varepsilon A_1\phi_0 - c_1 f_1(x, R_1(\varepsilon\phi_0))\varepsilon\phi_0 \\ &\quad = \varepsilon\phi_0[c_1^0 f_1(x, S) - c_1 f_1(x, R_1(\varepsilon\phi_0))] > 0, \end{aligned}$$

provided c_1 is close enough to c_1^0.

Now take c_1 as before. Arguing as in the proof of the Proposition 4.4 one sees that for $\varepsilon_1 \in (0, \varepsilon)$ small enough, the function $\varepsilon_1\phi_0$ is a lower-solution to

$$A_1 U - c_1 f_1(x, R_1(U))U = 0.$$

The maximum principle, as stated in Theorem 2.7, establishes that there is a maximal pair (U^-, U^+) of solutions to $A_1 U - c_1 f_1(x, R_1(U))U = 0$, satisfying $0 < \varepsilon_1\phi_0 \le U^- \le U^+ \le \varepsilon\phi_0$. Lastly, we readily know that $U^*(c_1)$ is the *unique* positive solution of $A_1 U - c_1 f_1(x, R_1(U))U = 0$ so that $U^- = U^+ = U^*(c_1)$. In particular, we recover $0 \le U^*(c_1) \le \varepsilon\phi_0$. This shows $\lim_{c_1 \to c_1^0} \|U^*(c_1)\|_\infty = 0$.

The relation $R_u^*(c_1) = R_1(U^*(c_1))$ then provides the limit $\lim_{c_1 \to c_1^0} \|R^*(c_1) - S\|_\infty = 0$.

Proof of (ii). Firstly, the function U_∞ is an upper-solution to

$$A_1 U - c_1 f_1(x, R_1(U))U = 0$$

in X_+^*. Indeed, we clearly have, using the definition of U_∞ and R_1, the relation $R_1(U_\infty) = 0$, from which it follows that $A_1 U_\infty - c_1 f_1(x, R_1(U_\infty))U_\infty = I \ge 0$.

On the other hand, take an $\varepsilon > 0$ fixed. For c_1 large enough, one checks easily that the function $(1-\varepsilon)U_\infty$ is a lower-solution to $A_1 U - c_1 f_1(x, R_1(U))U = 0$ in X_+^*. Arguing as before using the *uniqueness* of solution, we recover $(1-\varepsilon)U_\infty \le U^*(c_1) \le U_\infty$. This shows $\lim_{c_1\to+\infty} \|U^*(c_1) - U_\infty\|_\infty = 0$.

Next, we observe that $R_u^*(c_1)$ satisfies $A_0 R_u^*(c_1) + A_1 U^*(c_1) = I = A_1 U_\infty$, so that formula (2.8) provides[18]

$$R_u^*(c_1) = -\frac{a_1}{a_0} K_0 A_0 (U^*(c_1) - U_\infty) + \frac{1}{a_0} K_0[(a_1 m_0 - a_0 m_1)(U^*(c_1) - U_\infty)].$$

Using the fact that $U^*(c_1) \le U_\infty$, Assumption 2, and, more precisely, relations (2.9) and (2.10), give $0 \le R_u^*(c_1) \le \frac{a_1}{a_0}(U_\infty - U^*(c_1))$. Using the established limiting behaviour of $U^*(c_1)$ we deduce $\lim_{c_1\to+\infty} \|R_u^*(c_1)\|_\infty = 0$. □

The next result is a monotonicity property.

Proposition 4.6 *With the notation of Proposition 4.4 the map $c_1 \mapsto U^*(c_1)$ is increasing from $(c_1^0, +\infty)$ to X_+^*, while the map $c_1 \mapsto R_u^*(c_1)$ is decreasing from $(c_1^0, +\infty)$ to X_+^*.*

Proof of Proposition 4.6 Take $b_2 > b_1 > c_1^0$. For $i = 1, 2$ the function $U^*(b_i)$ is the only solution in X_+ to

$$A_1 U^*(b_i) - b_i f_1(x, R_1(U^*(b_i)))U^*(b_i) = 0.$$

We observe that

$$A_1 U^*(b_1) - b_2 f_1(x, R_1(U^*(b_1)))U^*(b_1) = (b_1 - b_2) f_1(x, R_1(U^*(b_1)))U^*(b_1) < 0,$$

hence $U^*(b_1)$ is a lower-solution to $A_1 U - b_2 f_1(x, R_1(U))U = 0$ in X_+. On the other hand, we have already established that $U_\infty > U^*(b_1)$ is an upper-solution as well. Hence the maximum principle, as stated in Theorem 2.7, allows to conclude that there exists a solution $\widetilde{U}(b_2)$ to $A_1 U - b_2 f_1(x, R_1(U))U = 0$ in X which satisfies $U(b_1) < \widetilde{U}(b_2) \le U_\infty$. The uniqueness we proved in Proposition 4.4 then provides $\widetilde{U}(b_2) = U(b_2)$. Therefore we have $U^*(b_1) < U^*(b_2)$.

From this we deduce, using the already observed fact that $R_1(U^*(b_i)) \equiv R^{(1)}_{U^*(b_i)}$ (by definition of the various objects), and using Theorem 2.11 part (iii), the relation $R_u^*(b_1) > R_u^*(b_2)$. This ends the proof. □

We finish this list of propositions with a continuity property.

Proposition 4.7 *With the notation of Proposition 4.4 the maps $c_1 \mapsto U^*(c_1)$ and $c_1 \mapsto R_u^*(c_1)$ are continuous from $(c_1^0, +\infty)$ to X_+^*.*

[18] With the similar formula if the coefficients a_i become space-dependent, with $a_1(x) = \lambda_1 a_0(x)$ and $a_2(x) = \lambda_2 a_0(x)$—see Footnotes 2, 4 and 9.

Proof Let $c_1 > c_1^0$ and $\varepsilon > 0$ be fixed. We claim that if c is close enough to c_1 then $(1 \pm \varepsilon)U^*(c_1)$ is a pair of lower–upper solutions to

$$A_1 U - c f_1(R(U))U = 0.$$

Indeed, one has $R_1((1-\varepsilon)U^*(c_1)) = R_1(U^*(c_1)) + \varepsilon c_1 K_0[f_1(x, R_1^*(c_1))]$ so that $f_1(x, R_1(U^*(c_1))) > f_1(x, R_1((1-\varepsilon)U^*(c_1)))$, which implies

$$\begin{aligned}&(1-\varepsilon)[A_1 U^*(c_1) - c f_1(x, R_1((1-\varepsilon)U^*(c_1)))]U^*(c_1)\\&\quad = (1-\varepsilon)U^*(c_1)[c_1 f_1(x, R_1(U^*(c_1))) - c f_1(x, R_1((1-\varepsilon)U^*(c_1)))] > 0\end{aligned}$$

provided $|c - c_1|$ is small enough. Hence, $(1-\varepsilon)U^*(c_1)$ is a lower solution. We see similarly that $(1+\varepsilon)U^*(c_1)$ is an upper solution. It follows arguing as below and using uniqueness that $(1-\varepsilon)U^*(c_1) < U^*(c) < (1+\varepsilon)U^*(c_1)$ which shows that $U^*(c)$ tends to $U^*(c_1)$ in $C^0(\overline{\Omega})$ as $c \to c_1$. The fact that $R_u^*(c) = R_1(U^*(c))$ shows the similar convergence for $R_u^*(c)$. Sobolev's embeddings and elliptic regularity shows that the convergence holds in X. This ends the proof. □

4.3 Non-degeneracy of the semi-trivial solutions

This section is devoted to the proof of the non-degeneracy of the semi-trivial solutions. This result allow us to end the proof of the Theorem 2.12 in that it establishes the key technical fact that the mapping $c_1 \to (R^*(c_1), U^*(c_1))$ is continuously differentiable.

Proposition 4.8 *With the notation of Proposition 4.4, for each $c_1 > c_1^0$, we have*

$$\mathrm{Ker}(\mathrm{Id} - D_{(R,U)}T_1(c_1, R_u^*(c_1), U^*(c_1))) = \{0\}.$$

Proof of Proposition 4.8 Take $c_1 > c_1^0$ and note for convenience $L(c_1) = \mathrm{Id} - D_{(R,U)}T_1(c_1, R_u^*(c_1), U^*(c_1))$. The proof is by contradiction.

Assume 0 is an eigenvalue of $L(c_1)$. We define, for each $u \in X$, the following auxiliary operator, acting on X. Taking a large, fixed number $K > 0$, we introduce

$$u \in X \mapsto H(u) := (A_1 + K)^{-1}[f_1(R_1(U))U + KU] \in X \tag{4.3}$$

where $A_0 R_1(u) + A_1 u = I$ as usual (see (2.8)). Up to the introduction of the terms involving K, the function H is essentially the second component of T_1, evaluated at $(R_1(U), U)$. From the definition of H, the following equivalence is clear whenever $U \in X_+^*$, namely

$$T_1(c_1, R, U) = {}^t(R, U) \Leftrightarrow [R = R_1(U) \text{ and } H(U) = U.] \tag{4.4}$$

Hence we readily have $H(U^*(c_1)) = U^*(c_1)$, and the equivalence (4.4) also implies, since 0 is an eigenvalue of $L(c_1)$, that 1 is an eigenvalue of $D_u H(U^*(c_1))$ as well.

We claim that the operator H is nondecreasing, i.e. whenever U and V belong to X, we have

$$U \geq V \geq 0 \Longrightarrow H(U) \geq H(V). \tag{4.5}$$

This property is actually the reason for our introduction of the parameter K. It comes from the fact that, according to Lemma 2.3, from $U \geq V \geq 0$, we deduce $f_1(R_1(U))U - f_1(R_1(V))V \geq -\gamma(U - V)$ hence $f_1(R_1(U))U - f_1(R_1(V))V + K(U - V) \geq (K - \gamma)(U - V) \geq 0$, and the maximum principle allows to conclude.

Our second claim is

$$D_u H(U^*(c_1)) \cdot U^*(c_1) = kU^*(c_1), \quad \text{where } k < 1. \tag{4.6}$$

(Note that k is a function in X). This is the key ingredient. It comes from the following computation. We have

$$\begin{aligned} D_u H(U^*(c_1)) \cdot U^*(c_1) &= \frac{d}{dt}\Big|_{t=0} H((1+t)U^*(c_1)) \\ &= \frac{d}{dt}\Big|_{t=0} (A_1 + K)^{-1}[f_1(R_1((1+t)U^*(c_1))) + K](1+t)U^*(c_1) \\ &= (A_1 + K)^{-1}[f_1(R_1(U^*(c_1))) + K]U^*(c_1) \\ &\quad + (A_1 + K)^{-1}[D_R f_1(R_1(U^*(c_1)))U^*(c_1) \frac{d}{dt}\Big|_{t=0} R_1((1+t)U^*(c_1))]. \end{aligned}$$

On the other hand, we have

$$(A_1 + K)^{-1}[f_1(R_1(U^*(c_1))) + K]U^*(c_1) = H(U^*(c_1)),$$

while

$$\begin{aligned} \frac{d}{dt}\Big|_{t=0} R_1((1+t)U^*(c_1)) &= \frac{d}{dt}\Big|_{t=0} K_0[I - (1+t)A_1 U^*(c_1)] \\ &= -\frac{d}{dt}\Big|_{t=0} (1+t)K_0[c_1 f_1(R_1(U^*(c_1)))U^*(c_1)] \\ &= -K_0[c_1 f_1(R_1(U^*(c_1)))U^*(c_1)] = R_1(U^*(c_1)) - S < 0. \end{aligned}$$

Eventually we have established

$$D_u H(U^*(c_1)) \cdot U^*(c_1) = U^*(c_1) + (R_1(U^*(c_1)) - S) =: kU^*(c_1),$$

with $k < 1$ as claimed. This proves relation (4.6).

Our third claim is a consequence of the previous one. It somehow asserts that the function $(1 + \varepsilon)U^*(c_1)$ is an upper solutions to $H(u) = u$ in a strong sense. Namely, taking a (fixed) parameter $\mu > 0$ such that

$$k + \mu < 1.$$

We define

$$H_\mu(u) := H(u) + \mu(u - U^*(c_1)). \tag{4.7}$$

We claim that whenever $\varepsilon > 0$ is small enough, we have

$$H_\mu((1+\varepsilon)U^*(c_1)) \leq (1+\varepsilon)U^*(c_1). \tag{4.8}$$

This comes from the following expansion

$$\begin{aligned} H_\mu((1+\varepsilon)U^*(c_1)) &= H_\mu(U^*(c_1)) + \varepsilon D_u H_\mu(U^*(c_1)) \cdot U^*(c_1) + \mathcal{O}(\varepsilon^2) \\ &= U^*(c_1) + \varepsilon(k+\mu)U^*(c_1) + \mathcal{O}(\varepsilon^2) \\ &\leq (1+\varepsilon)U^*(c_1), \end{aligned}$$

provided ε is small enough. We have used relation (4.6) together with the fact that $U^*(c_1) > 0$.

Gathering all the above claims, let us now show that $D_u H(U^*(c_1))$ cannot have 1 as an eigenvalue. Take $\phi \in X$ ($\phi \not\equiv 0$) such that

$$D_u H(U^*(c_1)) \cdot \phi = \phi.$$

Up to rescaling ϕ, we may assume that

$$-U^*(c_1) \leq \phi \leq U^*(c_1).$$

For technical reasons that become clear later, we may rescale ϕ again, so as to ensure that there is a point $x_0 \in \Omega$ such that

$$(1+\mu)\phi(x_0) > U^*(c_1)(x_0),$$

where $\mu > 0$ is as before. The idea is to compute $H_\mu(U^*(c_1) + \varepsilon\phi)$ in two different ways, to obtain the desired contradiction.

On the one hand we have, from the relation $U^*(c_1) + \varepsilon\phi \leq (1+\varepsilon)U^*(c_1)$, and using (4.8), the bounds

$$H_\mu(U^*(c_1) + \varepsilon\phi) \leq H_\mu((1+\varepsilon)U^*(c_1)) \leq (1+\varepsilon)U^*(c_1).$$

On the other hand, we may expand (the expansion holds in X)

$$\begin{aligned} H_\mu(U^*(c_1) + \varepsilon\phi) &= H_\mu(U^*(c_1)) + \varepsilon D_u H_\mu(U^*(c_1)) \cdot \phi + \mathcal{O}(\varepsilon^2) \\ &= U^*(c_1) + (1+\mu)\varepsilon\phi + \mathcal{O}(\varepsilon^2) \\ &= (1+\varepsilon)U^*(c_1) + \varepsilon((1+\mu)\phi - U^*(c_1)) + \mathcal{O}(\varepsilon^2). \end{aligned}$$

Hence, at the point x_0, we have $H_\mu(U^*(c_1)+\varepsilon\phi)(x_0) > (1+\varepsilon)U^*(c_1)(x_0)$, provided ε is small enough, which contradicts the fact that $H_\mu(U^*(c_1)+\varepsilon\phi) \leq (1+\varepsilon)U^*(c_1)$.

To summarize, the whole idea of our contradiction argument is that on the one hand $(1+\varepsilon)U^*(c_1)$ satisfies $H(U) < U$ in a *strict* fashion [as a consequence of (4.6)], while the upper–lower solution technique, together with the fact that ϕ is associated with the eigenvalue 1 of the linear part of H, imply that when perturbing $U^*(c_1)$ in the direction ϕ, the function H must at the same time be almost constant in that direction. $\square$

As an immediate consequence of the non-degeneracy of the semi-trivial solution, together with the implicit function theorem, we deduce the next proposition which ends the proof of Theorem 2.12

Proposition 4.9 *The mapping $c_1 \mapsto (R_u^*(c_1), U^*(c_1))$ is continuously differentiable from $(c_1^0, +\infty)$ to $X_+^* \times X_+^*$.*

5 Coexistence solutions

We now show the main result of this paper, namely we exhibit coexistence solutions to the full 2-species system (1.2), i.e. solutions (R, U, V) to (1.2) that lie in $(X_+^*)^3$. Recall that the system with 2 species reads, shortly,

$$\begin{cases} A_0 R + c_1 f_1(x, R)U + c_2 f_2(x, R)V = I, \\ A_1 U - c_1 f_1(x, R)U = 0, \\ A_2 V - c_2 f_2(x, R)V = 0, \end{cases} \tag{5.1}$$

5.1 Preliminary results

The following fact summarizes the work we have performed at this stage.

Proposition 5.1 *The system (1.2) has the trivial solution $(S, 0, 0) \in X_+^3$. Besides,*

(i) if $c_1 > c_1^0$, system (1.2) has the semi-trivial solution $(R_u^*(c_1), U^*(c_1), 0) \in X_+^3$.
(ii) if $c_2 > c_2^0$, system (1.2) has the semi-trivial solution $(R_v^*(c_2), 0, V^*(c_2)) \in X_+^3$.

We denote these two families by

$$\mathscr{C}_u = \{(c_1, c_2, R_u^*(c_1), U^*(c_1), 0), (c_1, c_2) \in (c_1^0, +\infty) \times (c_2^0, +\infty)\},$$
$$\mathscr{C}_v = \{(c_1, c_2, R_v^*(c_2), 0, V^*(c_2)), (c_1, c_2) \in (c_1^0, +\infty) \times (c_2^0, +\infty)\}.$$

Our first result in the direction of obtaining coexistence solutions to (5.1) is the

Proposition 5.2 *Let $(c_1, c_2) \in \mathbb{R}^2$. Assume that $(R, U, V) \in (X_+^*)^3$ is a coexistence solution to (5.1).*

Then, the following holds:

(i) We necessarily have $c_1 > c_1^0$ and $c_2 > c_2^0$.
(ii) With the above notation, the function $R - R_u^*(c_1)$ (resp. $R - R_v^*(c_2)$) either changes sign on Ω, or it vanishes identically.
(iii) We have $0 < U < U^*(c_1)$ and $0 < V < V^*(c_2)$ (on $\overline{\Omega}$).

Proof of Proposition 5.2 Let $(R, U, V) \in (X_+^*)^3$ be a coexistence solution to (1.2).

Point (i) By Theorem 2.11 we have $R < S$. Hence, as in the proof of Proposition 4.3, we deduce that $c_i > c_i^0$ for $i = 1, 2$.

Point (ii) We have

$$0 = \int_\Omega A_1 U \cdot U^*(c_1) - A_1 U^*(c_1) \cdot U = c_1 \int_\Omega (f_1(R) - f_1(R_u^*(c_1)))UU^*(c_1)$$

with $U > 0$ and $U^*(c_1) > 0$. Point (ii) therefore comes as a direct consequence of the fact that $R \mapsto f_1(R)$ increases with R.

Point (iii) We use a lower–upper solution method. Whenever u and v belong to X, denote by $R(u, v)$ the only solution in X to $A_0 R + A_1 u + A_2 v = I$. With this notation at hand, the function $u = U$ is seen to satisfy the following, nonlinear, nonlocal, elliptic problem

$$A_1 u - c_1 f_1(R(u, V)) \quad u = 0. \tag{5.2}$$

We first claim that U is the only positive solution to (5.2). To prove this, we observe that whenever $M > 0$ is large enough, the constant function $u = M$ is an upper-solution to (5.2). Indeed, it is clear that $R(M, V) \leq 0$ when M is large [for $A_0(R(M, V)) \leq 0$ under these circumstances], from which it follows $A_1 M - c_1 f_1(R(M, V))M \geq m_1 M \geq 0$. The function $u = \varepsilon\phi_0$ being clearly a lower-solution to (5.2) for small enough $\varepsilon > 0$, it follows that there exist a maximal solution $\varepsilon\phi_0 \leq U^+ \leq M$ such that any solution u to (5.2) such that $0 < u \leq M$ also satisfies $0 < u \leq U^+$. In particular, taking $M > U$, we deduce $0 < U \leq U^+$.

To prove that $U = U^+$, we define for convenience $R^+ = R(U^+, V)$ and $R = R(U, V)$. We clearly have[19]

$$0 = \int_\Omega (A_1 U^+ \cdot U - A_1 U \cdot U^+) = c_1 \int_\Omega [f_1(R^+) - f_1(R)]U^+ U,$$

which proves $U^+ = U$ provided we establish $R^+ \leq R$. On the other hand, the function $r = R$ satisfies

$$A_0 r + c_1 f_1(r) U = I - c_2 f_2(r) V, \tag{5.3}$$

while the function $r = R^+$ satisfies

$$A_0 r + c_1 f_1(r) U^+ = I - c_2 f_2(r) V.$$

Since $U \leq U^+$, we see that R^+ is a lower-solution to (5.3). This implies, similarly to the proof of the Theorem 2.11, that $R^+ \leq R$. Hence $U^+ = U$ and U is the only positive solution to (5.2).

[19] With the obvious adaptation in the case of Robin boundary conditions

Let $s \in (0,1)$, we now claim $U^*(c_1)$ resp. sU are (strict) upper resp. lower solutions to (5.2). Indeed, on the one hand, we have

$$A_0(R(U^*(c_1), V) - R(U^*(c_1), 0)) = -A_2 V = -c_2 f_2(R(U, V)) < 0,$$

so that $R(U^*(c_1), V) < R(U^*(c_1), 0)$. We deduce

$$\begin{aligned} &A_1 U^*(c_1) - c_1 f_1(R(U^*(c_1), V)) U^*(c_1) \\ &\quad = c_1 [f_1(R(U^*(c_1), 0)) - f_1(R(U^*(c_1), V))] U^*(c_1) > 0. \end{aligned}$$

On the other hand, we have

$$A_0(R(sU, V) - R(U, V)) = (1-s) c_1 f_1(R(U, V)) > 0,$$

so that $R(sU, V) > R(U, V)$. We deduce

$$A_1(sU) - c_1 f_1(R(sU, V)) sU = c_1 [f_1(R(U, V)) - f_1(R(sU, V))] sU < 0.$$

Now, since $\inf_{\overline{\Omega}} U^*(c_1) > 0$, one can choose $s \in (0,1)$ small enough such that $sU < U^*(c_1)$ and it follows that there exists a solution $\widetilde{U}$ to (5.2) such that $sU < \widetilde{U} < U^*(c_1)$ [the inequalities being strict because sU and $U^*(c_1)$ are not true solutions]. Uniqueness of the positive solution yields $\widetilde{U} = U$ hence $U < U^*(c_1)$. The same proof shows that $V < V^*(c_2)$. □

To conclude this section, we also state the following two Lemmas.

Lemma 5.3 *Let $c_1 > c_1^0$. Then the eigenvalue problem $A_2 \psi - \mu f_2(R_u^*(c_1)) \psi = 0$ has a principal eigenvalue $c_2^*(c_1) > 0$ and a corresponding eigenfunction $\psi^*(c_1) > 0$. We have $c_2^*(c_1) = \min_{\phi \in H^1(\Omega), \phi \neq 0} \frac{\int_\Omega a_2 \nabla \phi^2 + m_2 \phi^2}{\int_\Omega f_2(R_u^*(c_1)) \phi^2}$. In particular, there holds $c_2^*(c_1) > c_2^0$.*

Proof of Lemma 5.3 We only need to prove the inequality $c_2^*(c_1) > c_2^0$, which comes from the formulae giving $c_2^*(c_1)$ resp. c_2^0, in conjunction with the maximum principle. □

Lemma 5.4 *Let $c_1 > c_1^0$ be fixed.*
Then, there exists $c_2^{\max} = c_2^{\max}(c_1) > c_2^0$ such that, if $(R, U, V) \in (X_+^*)^3$ is a solution of (1.2), we necessarily have $c_2 < c_2^{\max}$.

Proof of Lemma 5.4 Let $c_1 > c_1^0$ be given fixed. We suppose by contradiction that there exists a sequence of solutions $(c_2^k, R_k, U_k, V_k) \in (c_2^0, +\infty) \times (X_+^*)^3$ with $c_2^k \to +\infty$.
As in the proof of Lemma 4.1, from the relation $A_0 R_k + A_1 U_k + A_2 V_k = I$ we deduce that for some $\alpha > 0$ we have $(\alpha - \Delta)(a_0 R_k + a_1 U_k + a_2 V_k) \leq I$ (with the obvious adaptation in the case of variable coefficients $a_i = a_i(x)$, see the proof of Lemma 4.1), hence $0 \leq a_0 R_k + a_1 U_k + a_2 V_k \leq M$ for some $M \geq 0$ independent of k. We deduce that all functions R_k, U_k, and V_k are bounded in L^∞, uniformly in k. In

turn we recover that $A_0 R_k$, $A_1 U_k$, and $A_2 V_k$ are uniformly bounded in L^∞ as well, and a bootstrap argument shows that R_k, U_k, and V_k are uniformly bounded in some $C^{2+\beta}$ space ($\beta > 0$), hence converge towards some R_∞, U_∞, V_∞ in X_+, say.

We claim that $R_\infty = 0$. Indeed, the function $v_k := \frac{V_k}{c_2^k \|V_k\|_\infty}$ verifies $A_2 v_k = f_2(R_k) v_k$. It follows that v_k converges in X_+^* to some nonnegative function v_∞ verifying $A_2 v_\infty = f_2(R_\infty) v_\infty$. If $R_\infty \neq 0$ then $v_\infty > 0$ which contradicts the fact that $\|v_k\|_\infty = \frac{1}{c_2^k} \to 0$. We recover $R_k \to 0$ in X.

Now, the fact that $U_k > 0$ provides $\lambda_1(A_1 - c_1 f_1(R_k)) = 0$. We deduce $0 = \lambda_1(A_1 - c_1 f_1(R_k)) \to \lambda_1(A_1)$ as $k \to \infty$. The known fact $\lambda_1(A_1) > 0$ provides the contradiction. □

5.2 Proof of Theorem 2.15

Let us now come to the construction of coexistence solutions.

For a given value of $c_1 > c_1^0$, we introduce the (compact, continuous, twice continuously differentiable) operator $T_2 : (c_2^0, \infty) \times X^3 \to X^3$ as

$$T_2(c_2, R, U, V) = \begin{pmatrix} K_0(I - c_1 f_1(R)U - c_2 f_2(R)V) \\ c_1 K_1(f_1(R)U) \\ c_2 K_2(f_2(R)V) \end{pmatrix}$$
$$= \begin{pmatrix} S \\ 0 \\ 0 \end{pmatrix} + c_1 \begin{pmatrix} -K_0(f_1(R)U) \\ K_1(f_1(R)U) \\ 0 \end{pmatrix} + c_2 \begin{pmatrix} -K_0(f_2(R)V) \\ 0 \\ K_2(f_2(R)V) \end{pmatrix}. \tag{5.4}$$

Clearly $(c_2, R, U, V) \in (c_2^0, \infty) \times (X_+^*)^3$ is a coexistence solution if and only if

$$T_2(c_2, R, U, V) = {}^t(R, U, V).$$

We readily know that the semi-trivial solution $(c_2, R_u^*(c_1), U^*(c_1), 0)$ satisfies

$$T_2(c_2, R_u^*(c_1), U^*(c_1), 0) = {}^t(R_u^*(c_1), U^*(c_1), 0),$$

for any value of c_2. We now construct coexistence solutions using bifurcations from the (family of) point(s) $(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)$, where $c_2^*(c_1) > c_2^0$ is provided by Lemma 5.3.

Proposition 5.5 *Take $c_1 > c_1^0$. Let $c_2^* = c_2^*(c_1) > c_2^0$ be the eigenvalue defined in Lemma 5.3 and $\psi^* = \psi^*(c_1) \in X_+^*$ be the associated eigenfunction.*

Then $(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)$ is a bifurcation point for T_2, in that the bifurcation Theorem 2.9 applies.

In particular, there exists $\rho^* = \rho^*(c_1) \in X$ and $\phi^* = \phi^*(c_1) \in X$, there exists $\varepsilon > 0$, there exists a map $(\widetilde{r}, \widetilde{u}, \widetilde{v}) \in C^1((-\varepsilon, \varepsilon), X^3)$ verifying $\widetilde{r}(0) = \widetilde{u}(0) = \widetilde{v}(0) = 0$, together with a map $c_2 \in C^1((-\varepsilon, \varepsilon), \mathbb{R}^+)$ verifying $c_2(0) = c_2^*(c_1)$, such that the following holds. The branch

$$\Gamma_\varepsilon^+ = \{(c_2(s), \widetilde{R}(s), \widetilde{U}(s), \widetilde{V}(s));\ 0 < s < \varepsilon\}$$

is a family of positive solutions to (5.1)*, where we set*

$$\widetilde{R}(s) = R_u^*(c_1) + s(\rho^*(c_1) + \widetilde{r}(s)), \quad \widetilde{U}(s) = U^*(c_1) + s(\phi^*(c_1) + \widetilde{u}(s)),$$
$$\widetilde{V}(s) = s(\psi^*(c_1) + \widetilde{v}(s)).$$

Moreover, any solution $(c_2, R, U, V) \in \mathbb{R} \times X^3$ *to* (5.1) *near the bifurcation point* $(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)$ *is either the semi-trivial solution* $(c_2, R_u^*(c_1), U^*(c_1), 0)$*, or it coincides for some* $s \in (-\varepsilon, \varepsilon)$ *with* $(c_2(s), \widetilde{R}(s), \widetilde{U}(s), \widetilde{V}(s))$*. Finally, there exist a continuum of nontrivial solutions* $\mathscr{C}_0 \subset \mathbb{R} \times X^2 \times (X \setminus \{0\})$ *containing* Γ_ε^+*.*

Proof of Proposition 5.5 Recall that the value of $c_1 > c_1^0$ is fixed. We set

$$L_2(c_2) = \mathrm{Id} - D_{(R,U,V)}T_2(c_2, R_u^*(c_1), U^*(c_1), 0). \tag{5.5}$$

Using again the operator T_1 of the one species problem, see (2.15), we have, whenever $(\rho, \phi, \psi) \in X^3$, the relation

$$L_2(c_2^*(c_1)) \cdot {}^t(\rho, \phi, \psi) = {}^t(\rho, \phi, \psi)$$
$$- \begin{pmatrix} D_{(R,U)}T_1(c_1, R_u^*(c_1), U^*(c_1)) \cdot \begin{pmatrix} \rho \\ \phi \end{pmatrix} \\ 0 \end{pmatrix} - c_2^*(c_1) \begin{pmatrix} -K_0(f_2(R_u^*(c_1))\psi) \\ 0 \\ K_2(f_2(R_u^*(c_1))\psi) \end{pmatrix}. \tag{5.6}$$

Take now $(\rho, \phi, \psi) \in \mathrm{Ker}(L_2(c_2^*(c_1)))$. We have

$$(\mathrm{Id} - D_{(R,U)}T_1(c_1, R_u^*(c_1), U^*(c_1))) \cdot {}^t(\rho, \phi) = {}^t(c_2^*(c_1)K_0(f_2(R_u^*(c_1))\psi), 0), \tag{5.7}$$

$$\psi - c_2^*(c_1)K_2(f_2(R_u^*(c_1))\psi) = 0. \tag{5.8}$$

Equation (5.8) on ψ, and the definition of $c_2^*(c_1)$, implies that $\psi = \psi^*(c_1) > 0$ up to a multiplicative constant. Equation (5.7) on (ρ, ϕ), together with the already proved invertibility of $\mathrm{Id} - D_{(R,U)}T_1(c_1, R_u^*(c_1), U^*(c_1))$ (see Proposition 4.8), then provides $(\rho, \phi) = (\rho^*(c_1), \phi^*(c_1))$, where we have set

$$\begin{aligned} &{}^t(\rho^*(c_1), \phi^*(c_1)) \\ &\quad := (\mathrm{Id} - D_{(R,U)}T_1(c_1, R_u^*(c_1), U^*(c_1)))^{-1\,t}(c_2^*(c_1)K_0(f_2(R_u^*(c_1))\psi^*(c_1)), 0). \end{aligned} \tag{5.9}$$

Hence $\mathrm{Ker}(L_2(c_2^*(c_1))) = \mathrm{span}(\rho^*(c_1), \phi^*(c_1), \psi^*(c_1))$.

There remains to show that

$$D_{c_2}L_2(c_2^*(c_1)) \cdot {}^t(\rho^*(c_1), \phi^*(c_1), \psi^*(c_1)) \notin \mathrm{Im}(L_2(c_2^*(c_1))). \tag{5.10}$$

We clearly have

$$D_{c_2} L_2(c_2^*(c_1)) \cdot {}^t(\rho^*(c_1), \phi^*(c_1), \psi^*(c_1))$$
$$= {}^t(-K_0(f_2(R_u^*(c_1))\psi^*(c_1)), 0, -K_2(f_2(R_u^*(c_1))\psi^*(c_1))).$$

If relation (5.10) is false, we can find ψ_1 such that

$$-K_2(f_2(R_u^*(c_1))\psi^*(c_1)) = \psi_1 - c_2^*(c_1) K_2(f_2(R_u^*(c_1))\psi_1).$$

We get easily $\int f_2(R_u^*(c_1))(\psi^*(c_1))^2 = 0$, which contradicts $\psi^*(c_1) > 0$.

Eventually we have proved that the bifurcation Theorem 2.9 applies, and the proposition follows. ◻

At this stage we have exhibited the continuum of nontrivial solutions $\mathscr{C}_0 \subset \mathbb{R} \times X^2 \times (X \setminus \{0\})$. We need to select *positive* solutions (i.e. coexistence solutions) out of $\mathscr{C}_0$.

Close to the bifurcation point $(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)$, the only solutions that belong to $(X_+^*)^3$ necessarily belong to the branch Γ_ε^+ as stated in Proposition 5.5. To transform this construction into a global one, we now define

$$\begin{aligned} &\mathscr{C}_0^+ \text{ is the closure of the maximal connected component of} \\ &\quad \mathscr{C}_0 \backslash \{(c_2(s), \widetilde{R}(s), \widetilde{U}(s), \widetilde{V}(s));\ -\varepsilon < s < 0\}. \end{aligned} \tag{5.11}$$

Define for convenience,

$$\dot{\mathscr{C}}_0^+ := \mathscr{C}_0^+ \backslash \{(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)\}.$$

The question we need to address now is whether $\dot{\mathscr{C}}_0^+ \subset \mathbb{R} \times (X_+^*)^3$. The following proposition states that this set cannot remain in $\mathbb{R} \times (X_+^*)^3$ *globally*.

Proposition 5.6 *We have*

$$\dot{\mathscr{C}}_0^+ \not\subset \mathbb{R} \times (X_+^*)^3.$$

Proof of Proposition 5.6 We argue by contradiction.
Assume that $\mathscr{C}_0^+ \backslash \{(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)\} \subset \mathbb{R} \times (X_+^*)^3$.
Let Z be a complement of $span(\rho^*(c_1), \phi^*(c_1), \psi^*(c_1))$ in X^3. Clearly any component u_i of any $(u_1, u_2, u_3) \in Z$ is neither positive nor negative. According to Theorem 2.10 (whose assumptions are easily verified in the present case), the key point is that one of the three following situations occurs:

(i) The set $\mathscr{C}_0^+$ joins $(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)$ to $(\widehat{c}_2, R_u^*(c_1), U^*(c_1), 0)$ with $\widehat{c}_2 \neq c_2^*$.
(ii) The set $\mathscr{C}_0^+$ joins $(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)$ to ∞ in $\mathbb{R} \times X^3$.
(iii) The set $\mathscr{C}_0^+$ contains a point $(c_2, R_u^*(c_1) + r, U^*(c_1) + u, v)$ where $(r, u, v) \in Z \backslash \{(0, 0, 0)\}$.

In the present contradiction argument, case (iii) cannot occur, nor can case (i) occur. On top of that, take a point $(c_2, R, U, V) \in \mathscr{C}_0^+$. Lemma 5.4 asserts that we necessarily have $c_2^0 < c_2 < c_2^{\max}(c_1)$. Hence c_2 remains in a fixed bounded subset of $\mathbb{R}$. Besides, the proof of Lemma 5.4 also asserts that (R, U, V) necessarily belong to a fixed compact subset of X^3. Hence situation (ii) cannot occur.
This ends the proof. □

The above proposition asserts that $\mathscr{C}_0^+$ necessarily leaves the positive cone. The following lemma provides information on the points where $\mathscr{C}_0^+$ leaves the positive cone.

Lemma 5.7 *Take $c_1 > c_1^0$. Let $(c_2, R, U, V) \in \mathbb{R} \times (X_+)^3$ be the limit, in $\mathbb{R} \times X^3$, of a sequence of positive solutions $(c_2^k, R_k, U_k, V_k) \in \mathbb{R} \times (X_+^*)^3$ to (5.1). Then, we have*

$$\lambda_1(A_1 - c_1 f_1(R)) = \lambda_1(A_2 - c_2 f_2(R)) = 0.$$

Proof of Lemma 5.7 For all $k \geq 0$, the function $\psi_k = U_k \|U_k\|_X^{-1} > 0$ verifies $A_1\psi_k - c_1 f_1(R_k)\psi_k = 0$. Passing to the strong limit and using elliptic regularization provides a $\psi \geq 0$, limit of the ψ_k's, with $\|\psi\|_X = 1$ and $A_1\psi - c_1 f_1(R)\psi = 0$. Hence, Lemma 2.2 provides $\psi > 0$ and $\lambda_1(A_1 - c_1 f_1(R)) = 0$. The proof for $\lambda_1(A_2 - c_2 f_2(R))$ is similar. □

The maximum principle now implies the following proposition which end the proof of Theorem 2.15.

Proposition 5.8 *Take $c_1 > c_1^0$.*
Then, there exists $c_2^{**}(c_1) > c_2^0$, such that

$$\mathscr{C}_0^+ \text{ joins } (c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0) \\ \text{ to } (c_2^{**}(c_1), R_v^*(c_2^{**}(c_1)), 0, V^*(c_2^{**}(c_1))).$$

Proof of Proposition 5.8 In the neighbourhood of $(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)$, we anyhow have $\dot{\mathscr{C}}_0^+ \subset \mathbb{R} \times (X_+^*)^3$.
On the other hand, by Proposition 5.6, there exists $(\widehat{c_2}, \widehat{R}, \widehat{U}, \widehat{V})$ in the set $\dot{\mathscr{C}}_0^+ \cap (\mathbb{R} \times \partial(X_+^*)^3)$, which is the limit of a sequence of solutions (c_2^k, R_k, U_k, V_k) lying in $\dot{\mathscr{C}}_0^+ \cap (\mathbb{R} \times (X_+^*)^3)$. In particular, $(\widehat{R}, \widehat{U}, \widehat{V}) \in (X_+)^3$ satisfies (5.1), hence for some $x \in \overline{\Omega}$, we have $\widehat{R}(x)\widehat{U}(x)\widehat{V}(x) = 0$.
The maximum principle and the Hopf lemma then assert that $\widehat{R}$ (resp. $\widehat{U}$, resp. $\widehat{V}$) cannot reach its minimal value 0 in $\overline{\Omega}$ unless it is constant. In the case when $\widehat{R} \equiv 0$, we recover $I = 0$, which is impossible. It follows that either $\widehat{U} \equiv 0$ or $\widehat{V} \equiv 0$. If $\widehat{U} = \widehat{V} \equiv 0$, then $(\widehat{c_2}, \widehat{U}, \widehat{V}, \widehat{R})$ is the trivial solution. By Lemma 5.7, this implies that c_1 is an eigenvalue of $A_1\phi - c_1 f_1(S)\phi = 0$, hence that $c_1 = c_1^0$. This contradicts $c_1 > c_1^0$. Now, suppose $\widehat{V} \equiv 0$ and $\widehat{U} > 0$. Uniqueness of the semi-trivial solution provides $\widehat{U} = U^*(c_1)$ and $\widehat{R} = R_u^*(c_1)$. By Lemma 5.7, there exists $\psi > 0$ satisfying $A_2\psi - \widehat{c_2} f_2(R_u^*(c_1))\psi = 0$. Lemma 5.3 then provides the necessary relation $\widehat{c_2} = c_2^*(c_1)$ which is again a contradiction. Eventually, the only possibility is $\widehat{V} > 0$, $\widehat{R} > 0$ and $\widehat{U} \equiv 0$. Hence $(c_1, \widehat{c_2}, \widehat{U}, \widehat{V}, \widehat{R}) \in \mathscr{C}_v$. □

5.3 Coexistence domain: Proof of Theorem 2.17

Theorem 2.15 states that two families of coexistence solutions may be obtained, namely the first one is constructed by freezing $c_1 > c_1^0$ and seeing c_2 as a bifurcation parameter to bifurcate from the semi-trivial $(c_2^*(c_1), R_u^*(c_1), U^*(c_1), 0)$ where $c_2^*(c_1) > c_2^0$, while the second one is constructed by freezing $c_2 > c_2^0$ and seeing c_1 as a bifurcation parameter to bifurcate from the semi-trivial $(c_1^*(c_2), R_v^*(c_1), 0, V^*(c_2))$ where $c_1^*(c_2) > c_1^0$. This construction leads to defining the quantities $c_2^{**}(c_1) > c_2^0$ and $c_1^{**}(c_2) > c_1^0$. Note that the three situations $c_2^{**}(c_1) > c_2^*(c_1)$, $c_2^{**}(c_1) < c_2^*(c_1)$, $c_2^{**}(c_1) = c_2^*(c_1)$ may very well occur, and similarly for $c_1^{**}(c_2)$ and $c_1^*(c_2)$.

Let us now exhibit some properties of the $c_i^*(c_j)$'s and $c_i^{**}(c_j)$'s.

Lemma 5.9 *For each $c_1 > c_1^0$ and $c_2 > c_2^0$, we define*

$$\mu(c_1, c_2) := \lambda_1(A_1 - c_1 f_1(R_v^*(c_2))), \quad \nu(c_1, c_2) := \lambda_1(A_2 - c_2 f_2(R_u^*(c_1))).$$

We have the relation (where $\operatorname{sgn}(s) = +1$ *if* $s > 0$, $= -1$ *if* $s < 0$ *and* $= 0$ *if* $s = 0$*)*

$$\begin{aligned}\operatorname{sgn}(\mu(c_1, c_2)) &= \operatorname{sgn}(c_1^*(c_2) - c_1) = -\operatorname{sgn}(c_2^{**}(c_1) - c_2),\\ \operatorname{sgn}(\nu(c_1, c_2)) &= \operatorname{sgn}(c_2^*(c_1) - c_2) = -\operatorname{sgn}(c_1^{**}(c_2) - c_1).\end{aligned}$$

Proof of Lemma 5.9 We show the result for μ. The proof for ν is similar.
Take $c_2 > c_2^0$. The definition of $c_1^*(c_2)$ readily provides $\mu(c_1^*(c_2), c_2) = \lambda_1(A_1 - c_1^*(c_2) f_1(R_v^*(c_2))) = 0$. On the other hand, Lemma 2.2 states that the map $c_1 \mapsto \mu(c_1, c_2)$ is increasing so that $\operatorname{sgn}(\mu(c_1, c_2)) = \operatorname{sgn}(c_1^*(c_2) - c_1)$.
Take $c_1 > c_1^0$. The definition of the point $(c_2^{**}(c_1), R_v^*(c_2^{**}(c_1)), 0, V^*(c_2^{**}(c_1)))$, together with Lemma 5.7, provide $\mu(c_1, c_2^{**}(c_1)) = \lambda_1(A_1 - c_1 f_1(R_v^*(c_2^{**}(c_1)))) = 0$. By Theorem 2.12, the map $c_2 \mapsto R_v^*(c_2)$ is decreasing, hence by Lemma 2.1, the map $c_2 \mapsto \mu(c_1, c_2)$ is increasing.
This shows $\operatorname{sgn}(\mu(c_1, c_2)) = -\operatorname{sgn}(c_2^{**}(c_1) - c_2)$. □

With this lemma at hand, we may now prove the

Proposition 5.10 *Let be $\{i, j\} = \{1, 2\}$. For all $c_j > c_j^0$, the scalar $c_i^{**}(c_j)$ is characterized by* [20]

$$c_i^*(c_j^{**}(c_i)) = c_i.$$

Proof of Proposition 5.10 Take $c_1 > c_1^0$. Set $d_2 = c_2^{**}(c_1)$, a quantity that is characterized by the fact that $\lambda_1(A_1 - c_1 f_1(R_v^*(d_2))) = 0$, according to the previous lemma. Now the quantity $d_1 := c_1^*(d_2)$ is in turn characterized by the relation $\lambda_1(A_1 - d_1 f_1(R_v^*(d_2))) = 0$, and the previous relation shows $d_1 = c_1$. This establishes $c_1^*(c_2^{**}(c_1)) = c_1$. The proof of the relation $c_2^*(c_1^{**}(c_2)) = c_2$ is the same. □

[20] That is, $c_i^{**} = (c_i^*)^{-1}$.

At this level of the analysis, one may define the three open sets

$$\begin{aligned}
\Theta_+ &= \{(c_1, c_2) \in (c_1^0, +\infty) \times (c_2^0, +\infty), c_1 > c_2^*(c_1), c_2 > c_1^*(c_2)\},\\
\Theta_- &= \{(c_1, c_2) \in (c_1^0, +\infty) \times (c_2^0, +\infty), c_1 < c_2^*(c_1), c_2 < c_1^*(c_2)\}.\\
\Theta &= \Theta_- \cup \Theta_+.
\end{aligned}$$

It is clear that whenever $(c_1, c_2) \in \Theta$, a coexistence solution may be exhibited to (5.1). Note however that these sets may be void. Note as well that our construction *anyhow* exhibits coexistence solutions for *some* values of (c_1, c_2), obtained by fixing c_1 and letting c_2 vary, say: in that respect the set Θ may not exhaust all values of (c_1, c_2) for which a coexistence solution may be exhibited.

The following Proposition is another consequence of the above lemma and end the Proof of Theorem 2.17.

Proposition 5.11 *(i) The function* $c_1 \mapsto c_2^*(c_1)$ *is continuous and increasing from* $(c_1^0, +\infty)$ *to* $(c_2^0, +\infty)$. *The similar statement holds for* $c_2 \mapsto c_1^*(c_2)$.
(ii) We have $\lim_{c_1 \to \infty} c_2^*(c_1) = +\infty$ *and* $\lim_{c_2 \to \infty} c_1^*(c_2) = +\infty$.
(iii) We have $\lim_{c_1 \to c_1^0} c_2^*(c_1) = c_2^0$ *and* $\lim_{c_2 \to c_2^0} c_1^*(c_2) = c_1^0$.

Proof of Proposition 5.11 We only prove the properties concerning the map $c_2 \mapsto c_1^*(c_2)$.

Take $c_2 > c_2^0$. We have $\lambda_1(A_1 - c_1^*(c_2) f_1(R_v^*(c_2))) = 0$. On the other hand, Theorem 2.12 asserts that the function $c_2 \mapsto R_v^*(c_2)$ is continuous and decreasing. Hence, from Lemma 2.1 we deduce that $c_1 \mapsto c_2^*(c_1)$ is continuous and increasing.

Now, we have that $R_v^*(c_2)$ tends uniformly to 0 when $c_2 \to \infty$. If $c_1^*(c_2)$ remains bounded as $c_2 \to \infty$, then $\lambda_1(A_1 - c_1^*(c_2) f_1(R_v^*(c_2))) = 0 \to \lambda_1(A_1) > 0$ as $c_2 \to \infty$, which is impossible. Therefore, we necessarily have $c_1^*(c_2) \to \infty$ as $c_2 \to \infty$.

Similarly, as $R_v^*(c_2)$ tends uniformly to S as $c_2 \to c_2^0$, Lemma 5.3 provides the relation $\lim_{c_2 \to c_2^0} c_1^*(c_2) = c_1^0$. □

6 Interpretations, and ecological aspects

For later convenience we define

$$\widetilde{\Theta_+} = \{(c_1, c_2) \in (c_1^0, +\infty) \times (c_2^0, +\infty), c_i^*(c_j) \le c_i \le c_i^{**}(c_j), i \ne j\},$$

$\widetilde{\Theta_-}$ by reversing the inequalities and $\widetilde{\Theta} = \widetilde{\Theta_-} \cup \widetilde{\Theta_+}$.

6.1 A conjecture

Conjecture

(i) If $(c_1, c_2) \notin \widetilde{\Theta}$, then there cannot exist $(R, U, V) \in (X_+^*)^3$ solution to (5.1).
(ii) We have $\Theta_- = \emptyset$, or, in other words, $c_i^*(c_j) \le c_i^{**}(c_j)$ whenever $i \ne j$.

This conjecture is motivated by our numerical simulations and the study of the slow diffusion asymptotics (see Ducrot and Madec 2012 and Sect. 6.4). It states that the set $\widetilde{\Theta}$ actually characterizes those values of (c_1, c_2) for which a coexistence solution may be exhibited. It also states that species i survives if and only if $c_i \geq c_i^*(c_j)$. In other words, species i survives if and only if $\lambda_1(A_i - c_i f_i(R^*(c_j))) \geq 0$.

6.2 Two ecological properties

Lemma 5.3 readily provides the following result.

Proposition 6.1 (dependence of the coexistence solutions on the diffusion rates).

Take a_0 and a_1 in $(0, +\infty)$, and consider the system (5.1) as a function of the diffusion rate a_2.

Then, the map $a_2 \mapsto c_2^*(c_1)(a_2)$ is nondecreasing.

Moreover, if $x \mapsto m_2(x) - f_2(x, R_u^*(c_1)(x))$ is not a constant function, then $a_2 \mapsto c_2^*(c_1)(a_2)$ is increasing.

Provided the above conjecture holds, this assertion implies that as the diffusion rate of a given species increases, its ability to survive decreases.

Proposition 6.2 (rôle of the heterogeneity).

(i) If $(c_1, c_2) \in \Theta$, we necessarily have that $R_u^*(c_1) - R_v^*(c_2)$ is neither positive nor negative.

(ii) If $R_u^*(c_1) = R_v^*(c_2)$, then, for all $i, j = 1, 2,\ i \neq j$, we have $c_i^*(c_j) = c_i^{**}(c_j) = c_i$ and $\{(c_1, c_2, R_u^*, (1-t)U^*, tV^*), t \in [0, 1]\} \in \{c_1, c_2\} \times X_+^3$ is a family of solutions joining $\mathscr{C}_u$ to $\mathscr{C}_v$.

In other words, the coexistence domain Θ is embedded in the set of (c_1, c_2)'s such that $R_u^*(c_1) - R_v^*(c_2)$ is neither positive nor negative. This point highlights the importance of the spatial heterogeneity in the coexistence process (see also the next subsection).

Proof of Proposition 6.2 If $(c_1, c_2) \in \Theta$, then $\mu(c_1, c_2)\nu(c_1, c_2) > 0$. On the other hand, we know that $\lambda_1(A_1 - c_1 f_1(R_u^*(c_1))) = 0$ and $\lambda_1(A_2 - c_2 f_2(R_v^*(c_2))) = 0$. Hence, if $R_u^*(c_1) \geq R_v^*(c_2)$, then $\mu(c_1, c_2) = \lambda_1(A_1 - c_1 f_1(R_v^*(c_2))) > 0$. Therefore, $\nu(c_1, c_2) = \lambda_1(A_2 - c_2 f_2(R_u^*(c_1))) > 0$ as well. Hence $\lambda_1(A_2 - c_2 f_2(R_v^*(c_2))) > 0$, which is impossible. The same arguments shows that $R_v^*(c_2) \geq R_u^*(c_1)$ is impossible.

Now, if $R_u^*(c_1) = R_v^*(c_2) := R$, then $\mu(c_1, c_2) = \nu(c_1, c_2) = 0$, hence $c_i = c_i^*(c_j) = c_i^{**}(c_j)$. One gets $A_0 R + c_1 f_1(R)U = A_0 R + c_2 f_2(R)V$ thus, for all $t \in [0, 1]$, we have $A_0 R + (1-t)c_1 f_1(R)U^* + tc_1 f_1(R)V^* = I$. Since $A_1 U^* = c_1 f_1(R)U^*$ and $A_2 V^* = c_2 f_2(R)V^*$, we see that $\{(c_1, c_2, R_u^*, (1-t)U^*, tV^*), t \in [0, 1]\}$ is a family of solutions. □

6.3 Two degenerate cases

In the homogeneous case where the functions $I(x)$, $f_i(x)$, $m_i(x)$, $a_i(x)$ do not depend on x, and when Neumann boundary conditions are retained, we have that $R_u^*(c_1)(x)$

and $R_v^*(c_2)(x)$ are constant functions. Hence, by Proposition 6.2, the coexistence is possible only if $R_u^*(c_2) = R_u^*(c_1)$, which induces a degenerate solution. Moreover, the fact that $R_u^*(c_1)$ and $R_v^*(c_2)$ decrease imply that meas$\{(c_1, c_2) \in (c_1^0, +\infty) \times (c_2^0, +\infty), R_u^*(c_2) = R_u^*(c_1)\} = 0$. In that degenerate case we have the

Proposition 6.3 (The homogeneous case) *Assume the problem is homogeneous, i.e. I, m_i and f_i do not depend on x. Assume Neumann boundary conditions are retained. Then we have*

$$c_i^0 = \inf \left\{ c_i > 0,\ f_i^{-1}(m_i/c_i) \text{ exists and is smaller than } \frac{I}{m_0} \right\}.$$

For $i = 1, 2$ and $c_i > c_i^0$ denote

$$R_i^*(c_i) = f_i^{-1}(m_i/c_i), \quad \text{and} \quad U_i^*(c_i) = (I - m_i R_i^*(c_i))/m_0.$$

The only semi-trivial solutions are $(R_1^*(c_1), U_1^*(c_1), 0)$ and $(R_2^*(c_2), 0, U_2^*(c_2))$ and we have

$$\Theta = \emptyset \text{ and } \widetilde{\Theta} = \{(c_1, c_2) \in (c_1^0, +\infty) \times (c_2^0, +\infty) \text{ s.t. } R_1^*(c_1) = R_2^*(c_2) < S\}$$

Moreover, for all $(c_1, c_2) \in \widetilde{\Theta}$, there exists a family of solutions $\{(R_1^*(c_1), tU_1^*(c_1), (1-t)U_2^*(c_2)), t \in [0, 1]\}$.

Another critical case appears when the two species possess heterogeneous but proportional diffusion rates, mortality rate, and consumption rate, namely

Proposition 6.4 (Case of similar species) *Suppose that $f_1 = f_2$ and $A_2 = \alpha A_1$ for some constant $\alpha \in \mathbb{R}_+^*$.*

Then, for all $(c_1, c_2) \in \Theta$, we have the four relations

$$R_u^*(c_1) = R_v^*(c_2/\alpha), \quad \Theta = \emptyset, \quad \widetilde{\Theta} = \{(c_1, \alpha c_1), c_1 \geq c_1^0\}, \quad c_2^*(c_1) = \alpha c_1.$$

Moreover, the system has a coexistence solution $(R, U, V) \in (X_+^*)^3$ if and only if $(c_1, c_2) \in \widetilde{\Theta}$. In that case $\mathscr{C} = \{(R_u^*, tU^*, \frac{1}{\alpha}(1-t)U^*), t \in (0, 1)\}$ is a family of solutions and each coexistence solution satisfies $(R, U, V) \in \mathscr{C}$.

Proof of Proposition 6.4 The system defining $(R_u^*(c_1), U^*(c_1))$ is

$$A_1 U^*(c_1) - c_1 f_1(R_u^*(c_1)) U^*(c_1) = 0, \quad A_0 R_u^*(c_1) + A_1 U^*(c_1) = 0,$$

while the system defining $(R_v^*(c_2), V^*(c_2))$ is in the present case

$$\alpha A_1 V^*(c_2) - c_2 f_1(R_v^*(c_2)) V^*(c_1) = 0, \quad A_0 R_v^*(c_2) + \alpha A_1 V^*(c_2) = 0.$$

The uniqueness result of Proposition 4.4 provides $V^*(c_2) = \dfrac{1}{\alpha} U^*(\dfrac{c_2}{\alpha})$, and $R_v^*(c_2) = R_u^*(\frac{c_2}{\alpha})$. Now, since $c_2^*(c_1)$ is defined as the unique value of the parameter c_2 such that $0 = \lambda_1(A_2 - c_2 f_2(R_u^*(c_1))) = \lambda_1(A_1 - (c_2/\alpha) f_1(R_u^*(c_1)))$, it comes $c_2^*(c_1) = \alpha c_1$. This together with the analogous relation for $c_1^*(c_2)$ provides $\Theta = \emptyset$ and $\widetilde{\Theta} = \{(c_1, \alpha c_1);\ c_1 > c_1^0\}$.

Take now (c_1, c_2) such that (R, U, V) is an associated coexistence solution. We have

$$\lambda_1(A_1 - \frac{c_2}{\alpha} f_1(R)) = \lambda_1(A_1 - c_1 f_1(R)) = 0,$$

and monotone dependence of the above λ_1's with the parameters c_1 and c_2 implies $c_2 = \alpha c_1$. Besides, summing the last two equations of (1.2) leads to

$$\begin{cases} A_0 R + c_1 f_1(R)(U + \alpha V) = I, \\ (A_1 - c_1 f_1(R))(U + \alpha V) = 0, \end{cases}$$

so that uniqueness provides $U + \alpha V = U^*(c_1)$, and $R = R_u^*(c_1)$. On top of that, coming back to the equation satisfied by U, it appears that there exists $t \in \mathbb{R}_+$ such that $U = tU^*(c_1)$, and then $\alpha V = (1 - t)U^*(c_1)$. This ends the proof. □

6.4 Influence of the diffusion rates on the coexistence domain

Let $d > 0$, we consider the system

$$\begin{cases} (m_0 - d a_0 \Delta) R + c_1 f_1(R) U + c_2 f_2(R) V = I, \\ (m_1 - d a_1 \Delta) U - c_1 f_1(R) U = 0, \\ (m_2 - d a_2 \Delta) U - c_2 f_2(R) V = 0, \end{cases} \tag{6.1}$$

with Neumann boundary condition.[21] Remark in passing that, if Assumption 2 is true for a given $d > 0$, then it remains true for each $d > 0$. In this case, Theorem 2.17 shows that there exists $\Theta^d \subset \mathbb{R}_+^2$ such that, for each $(c_1, c_2) \in \Theta^d$, the system (6.1) admits a coexistence solution.

Let us start by the case of small diffusion, that it $d \to 0$. Formally, if $d = 0$ then the system (6.1) consists in a family of independent systems parametrized by $x \in \overline{\Omega}$. Each system is described by the critical quantity: $R_i^*(c_i)(x) = f_i^{-1}(x, \cdot)(m_i(x)/c_i)$ when this is well-defined, $R_i^*(c_i)(x) = +\infty$ otherwise $(i = 1, 2)$.

The set $\Theta^0 := \{(c_1, c_2)$ s.t., $R_1^*(c_1) - R_2^*(c_2)$ is neither positive nor negative$\}$ is the set of (c_1, c_2)'s for which both species are dominant on at least one point $x \in \Omega$. This completes the description of the case $d = 0$. When $d \ll 1$ at variance, it is shown[22] in Ducrot and Madec (2012) that (6.1) has positive solutions if and only if $(c_1, c_2) \in \Theta^0$. In other words, we have in $\Theta^d \to \Theta^0$ as $d \to 0$ in a strong sense.

[21] This is the only place in this text where Neumann—and not Robin—boundary conditions are required.

[22] This point needs and additional assumption on the functions f_i, an assumption which is verified in practice by most "standard" consumption functions f_i.

In the opposite direction, when $d \to +\infty$, it can be shown using classical methods inspired by Conway et al. (1978), that solutions to (6.1) converge to the solutions of the so-called aggregated system

$$\begin{cases} \widetilde{m_0} r + c_1 \widetilde{f_1}(r) u + c_2 \widetilde{f_2}(r) v = \widetilde{I} \\ (\widetilde{m_1} - c_1 \widetilde{f_1}(r)) u = 0 \\ (\widetilde{m_2} - c_2 \widetilde{f_2}(r)) v = 0 \end{cases} \tag{6.2}$$

where $\widetilde{m_i} = \frac{1}{|\Omega|} \int_\Omega m_i(x)\, dx$, $\widetilde{f_i}(r) = \frac{1}{|\Omega|} \int_\Omega f_i(x, r)\, dx$, $\widetilde{I} = \frac{1}{|\Omega|} \int_\Omega I(x)\, dx$, and the unknown r, u, v now are scalars (independent of x). System (6.2) is a homogeneous chemostat system. Define for convenience the quantity $r_i^*(c_i)$ as $r_i^*(c_i) = \widetilde{f_i}^{-1}(m_i/c_i)$ if this is well-defined, and $r_i^*(c_i) = +\infty$ else. Denote $\Theta^\infty = \{(c_1, c_2) \text{ s.t. } r_1^*(c_1) = r_2^*(c_2) < +\infty\}$. As is easily seen on the equations, system (6.2) does posses positive solution if and only if $(c_1, c_2) \in \Theta^\infty$. It turns out that for each $(c_1, c_2) \notin \Theta^\infty$, there exists $d_0 > 0$ such that $\forall d > d_0$, we have $(c_1, c_2) \notin \Theta^d$. In this sense, the coexistence domain Θ^d tends to the *curve* Θ^∞ when $d \to +\infty$ in a strong sense.

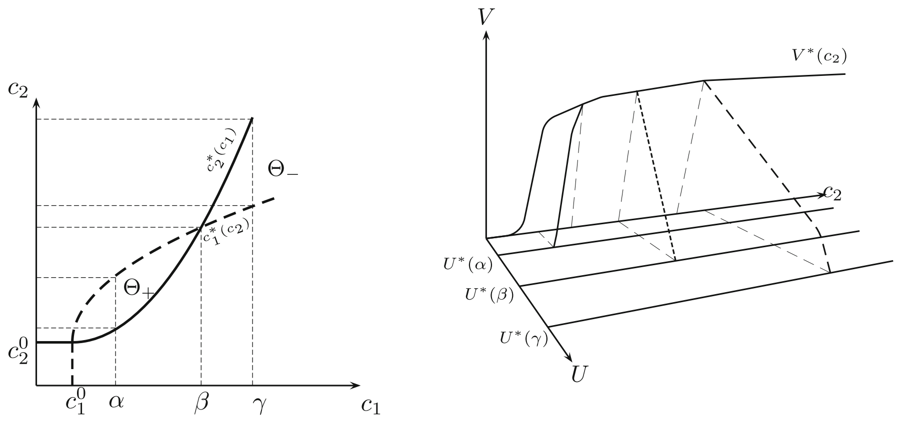
The result of this section can be summarized as follows. As the diffusion rates decrease, the local phenomena are the only important phenomena and the coexistence region is determined by the points where one or the other species dominates. As the diffusion rates increase, the aggregation phenomena leads to system that is close to homogeneous in space, and the coexistence domain shrinks to a curve. Hence, as the diffusion rates goes from 0 to ∞, the coexistence domain describes the transition from local phenomena to aggregated phenomena.

7 Conclusion and perspectives

This study examines a model where two species compete for a single resource, in a spatially heterogeneous domain. Our system differs from the classical unstirred chemostat system (Dung et al. 1999; Hsu et al. 1994; Hsu and Waltman 1993; Smith and Waltman 1995; Wu 2000) in that the reaction terms do depend on space, and, more importantly, we allow the diffusion rates to depend on the species under consideration. This point leads to a new mathematical difficulty. Namely, the conservation law which links the resource R with the two species U and V, written $A_0 R + A_1 U + A_2 V = I$ in the core of the paper, becomes a *nonlocal* equation (as compared to the previously quoted papers where the analogous equation is local). We circumvent this difficulty by introducing Assumption 2 (supplemented with Assumption (1.6) in the case of Robin boundary conditions).

We show that coexistence occurs when the consumption parameters (c_1, c_2) lie in a subdomain $\Theta \subset \mathbb{R}_+^2$. In addition, we study the set Θ by using a characterisation of Θ that relies on the two functions $c_1^*(c_2)$ and $c_2^*(c_1)$ defined in the text.

We may extend this study in several directions. Firstly, our numerical observations indicate that the coexistence solution are non-degenerate, except in the particular case when the two functions $c_1^*(.)$ and $c_2^*(.)$ coincide. *When the coexistence solution is non-degenerate*, it turns out that our construction can be extended to three species,



(a) Coexistence domain **(b)** Bifurcation curves

Fig. 2 Coexistence domain and bifurcation solutions. **a** a possible coexistence domain Θ. The *full curve* represents $(c_1, c_2^*(c_1))$ and the *dashed one* represents $(c_1^*(c_2), c_2)$. For any $t > c_1^0$, the line $c_1 = t$ intersects these two curves at $(t, c_2^*(t))$ resp. $(t, c_2^{**}(t))$, as implied by the very definition of the two quantities $c_2^*(c_1)$ and $c_2^{**}(c_1)$. **b** some bifurcating solutions corresponding to three values α, β and γ of the parameter $c_1 > c_1^0$. The retained values are here assumed to satisfy $c_2^*(\alpha) < c_2^{**}(\alpha)$, resp. $c_2^*(\beta) = c_2^{**}(\beta)$, resp. $c_2^*(\gamma) > c_2^{**}(\gamma)$. For each $c_1 > c_1^0$, there is a coexistence solution joining $(R, U^*(c_1), 0)$ and $(R, 0, V^*(c_1))$

and by iteration, to N species for any value of N. It would therefore be a key step to actually prove that the coexistence solutions necessarily are non-degenerate, unless $c_1^*(.)$ and $c_2^*(.)$ coincide. Note in passing that Propositions 6.3 and 6.4 give two examples of situations where $c_1^*(.)$ and $c_2^*(.)$ do coincide, and a complete description of the coexistence phenomena is provided in these situations.

Secondly, we defined Θ as the union of two subdomain Θ_- and Θ_+. If $(c_1, c_2) \in \Theta_-$ then $c_i^* > c_i^{**}$ and the bifurcation occurs "to the left" (see Fig. 2). We conjecture that $\Theta_- = \emptyset$ in any case. In fact, to rephrase our conjecture, if $(c_1, c_2) \in \Theta_-$, then both species are "not invasive" in the sense that

$$\lambda_1(A_1 - c_1 f_1(R_v^*(c_2))) < 0, \quad \text{and} \quad \lambda_1(A_2 - c_2 f_2(R_u^*(c_1))) < 0.$$

Note that Hsu and Waltman (1993) formulate a similar conjecture. Namely, they conjecture that a necessary condition for two species to coexist is that both species are "invasive" in the sense that $\lambda_1(A_1 - c_1 f_1(R_v^*(c_2))) \geq 0$ and $\lambda_1(A_2 - c_2 f_2(R_u^*(c_1))) \geq 0$. This implies in particular that both semi-trivial solution are not stable (for the time-dependent problem). Note that even if the latter result is proved, it is not clear that the coexistence solution itself is stable. Indeed, Hofbauer and So (1994) show that there exists gradostats (i.e. similar models with a discrete spatial structuration) for which an unstable coexistence solution may be exhibited. A more precise description of Θ would be a first step to understand the situation.

Thirdly, we conjecture that if $(c_1, c_2) \notin \widetilde{\Theta}$, then no coexistence solution can be found. Would this result be proved, we could use Θ as a geometric indicator of the possibility of coexistence in a given system. Numerical investigations on the relation between Θ, spatial heterogeneity, and the biodiversity, will be published soon.

Finally, our proof uses basically Assumption 2, an assumption that allows us to extend the analysis of the (known) case where all diffusion operators coincide. It is to be noted, however, that a global bifurcation argument proves the existence of semi-trivial solutions *without* using Assumption 2. This assumption is only needed to obtain uniqueness and non-degeneracy of the so-obtained semi-trivial solutions. A natural question is: can one extend our construction to situations where Assumption 2 is not verified?

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