

CHAPTER 3

Analytical properties of the model

We first recall the definition of the model:

$$\begin{aligned}
 (M) \quad & \partial_t u = -\mu_f u + m_1 \frac{uv}{1+uv} - \mu_b uv, \\
 & \partial_t v = d_1 \Delta v - \mu_l v + m_2 \frac{uv}{1+uv} - \mu_b uv - vw, \quad (x, t) \in \Omega \times \mathbb{R}_{\geq 0} \\
 & \partial_t w = d_2 \Delta w - \mu_e w + m_3 \frac{uv}{1+uv}.
 \end{aligned}$$

$$\begin{aligned}
 u &: \Omega \times \mathbb{R}_{>0} \rightarrow \mathbb{R}_{>0}, \\
 v &: \Omega \times \mathbb{R}_{>0} \rightarrow \mathbb{R}_{>0}, \\
 w &: \Omega \times \mathbb{R}_{>0} \rightarrow \mathbb{R}_{>0}
 \end{aligned}$$

Solutions are sought on a bounded domain $\Omega = (0, L) \subset \mathbb{R}$, (we choose $L = 1$ for now), supplemented with Neumann boundary conditions $\partial_\nu v = 0$ and $\partial_\nu w = 0$ on $\partial\Omega$ with initial data $u_0, v_0, w_0 \in L^\infty(\Omega, \mathbb{R})$. The operator $\Delta = \Delta_\nu^\Omega$ is the Laplacian on Ω with Neumann boundary condition, the quantities $\mu_f, \mu_b, \mu_l, \mu_e, m_1, m_2, m_3$ are parameters of the model. For convenience, we also introduce the notation

$$(3.1) \quad f(u, v, w) = -\mu_f u + m_1 \frac{uv}{1+uv} - \mu_b uv,$$

$$(3.2) \quad g(u, v, w) = -\mu_l v + m_2 \frac{uv}{1+uv} - \mu_b uv - vw,$$

$$(3.3) \quad h(u, v, w) = -\mu_e w + m_3 \frac{uv}{1+uv}.$$

Where $\mathbf{f} := (f, g, h)$ denotes the vector field generated by the reaction term in (M). Our goal for this chapter is to investigate on the properties of this model.

1. Existence of solutions

1.1. Existence of local solutions. To show there exists local-in-time solution, we introduce a few notions from operator semigroup theory. The aim of this section is not to provide a robust, rigorous introduction to the theory but rather hand out some key ideas on how to prove the existence of such solutions. We start by considering system (M) in the form

$$\begin{aligned}
 (AC) \quad & \partial_t \mathbf{u} = \mathcal{A}[\mathbf{u}] + \mathbf{f}(\mathbf{u}), \\
 & \mathbf{u}(0) = \mathbf{u}_0.
 \end{aligned}$$

The problem is now called *abstract Cauchy problem*, where the operator $\mathcal{A} := D\Delta$ is defined for $D := \text{diag}(0, d_1, d_2)$, with real diffusion coefficients $d_1, d_2 > 0$. The operator \mathcal{A} has domain

$$\mathcal{D}(\mathcal{A}) := \{(u, v, w) \in L^\infty(\Omega) \times (H^2(\Omega))^2 : \partial_\nu v = 0, \partial_\nu w = 0 \text{ on } \partial\Omega\}.$$

This way of writing is more suited to the presentation of the following results. Before we state the main theorem, we need a few definitions, starting with what is a semigroup of operators.

DEFINITION 1. *Let X be a Banach space. A one parameter family $T(t)$, $0 \leq t < \infty$, of bounded linear operators from X into X is a semigroup of bounded linear operators on X if*

- (i) $T(0) = I$
- (ii) $T(t + s) = T(t)T(s)$ for every $t, s \geq 0$ semigroup property

We can ask $T(t)$ to have slightly more structure by adding the constraint

$$\lim_{t \downarrow 0} T(t)x = x, \quad \forall x \in X.$$

When this relation holds, then $T(t)$ is called C_0 -semigroup (read strongly continuous semigroup). A famous example of such family is the shift operator:

$$S(t) : \mathcal{C}(\mathbb{R}) \rightarrow \mathcal{C}(\mathbb{R}), \quad S(t)[f] = f(\cdot + t),$$

for functions $f : L^2(\mathbb{R}) \rightarrow L^2(\mathbb{R})$. It is quite clear that $S(0)[f] = f(\cdot + 0) = f$, and that for any $s, t \geq 0$, we have

$$S(t + s)[f] = f((\cdot + s) + t) = S(t)[f(\cdot + s)] = S(t)S(s)[f].$$

So the semigroup property is satisfied.

Remark: When defined on the L^2 space, $S(t)$ is a C_0 -semigroup, but it is not when defined on L^∞ . To see why, take the function $f(x) = \mathbb{1}_{[0,1]}(x)$ and see that $\|S(t)f - f\|_\infty = 1$ for all $t \neq 0$.

For a semigroup of operators $(T(t))_{t \geq 0}$, one can define the operator $(A, \mathcal{D}(A))$ as

$$\mathcal{D}(A) = \left\{ x \in X : \lim_{t \downarrow 0} \frac{T(t)x - x}{t} \text{ exists} \right\}, \quad Ax = \lim_{t \downarrow 0} \frac{T(t)x - x}{t}, \quad \text{for } x \in \mathcal{D}(A).$$

This operator is called *infinitesimal generator* of the semigroup $T(t)$ with domain $\mathcal{D}(A)$ and we say that A generates $T(t)$. The reader quickly realises that A is nothing but the right derivative of T at the origin. Echoing back to the shift operator, one has that for $f \in L^2(\mathbb{R})$ differentiable,

$$A = \lim_{t \downarrow 0} \frac{S(t)[f](x) - f(x)}{t} = \lim_{t \downarrow 0} \frac{f(x + t) - f(x)}{t} = f'(x),$$

which the right derivative of the function itself. We omit the computation of the domain $\mathcal{D}(A)$ since these computations are technical and involve some results that require more detail than we want to give in this section.

The way we presented things is by first introducing a semigroup $(T(t))_{t \geq 0}$ and then its infinitesimal generator A . In a general setting, knowledge on the family $T(t)$ is helpful to

deduce properties on A , but one could also look at it the other way and deduce properties on $T(t)$ based on properties of A . For that we introduce the notion of sectoriality

DEFINITION 2. *We call a linear operator A in a Banach space X a sectorial operator if it is a closed, densely defined operator such that, for some ϕ in $(0, \pi/2)$ and some $M \geq 1$ and real a , the sector*

$$S_{a,\phi} := \{\lambda : \phi \leq |\arg(\lambda - a)| \leq \pi, \lambda \neq a\},$$

is contained in the resolvent set of A and that $\|(\lambda - A)^{-1}\| \leq M|\lambda - a|^{-1}$ for all $\lambda \in S_{a,\phi}$.

Knowing that an operator is sectorial gives crucial cues on the behavior of its spectrum and is used (among others) to prove the asymptotic stability of steady states of the linearized problem¹ under relatively weak assumptions. In our case, we also have

LEMMA 1. *Any sectorial operator generates a C_0 -semigroup.*

This is a technical lemma whose proof can be found in [K.J. Engel], and it is of prime importance to the next theorem from [AnnaThesis]

THEOREM 1. *There exists for each $x \in X$ a unique weak solution \mathbf{u} of (AC) on $[0, T]$ satisfying $\mathbf{u}(0) = \mathbf{u}_0$ if and only if A is the infinitesimal generator of a C_0 -semigroup $T(t)$ of bounded linear operators on X . In this case, \mathbf{u} is given by*

$$\mathbf{u}(\cdot, t) = T(t)\mathbf{u}_0 + \int_0^t T(t-s)[\mathbf{f}(\mathbf{u}(\cdot, s))]ds.$$

Remark: By weak solution we mean that, if A^* is the dual operator of A , for every $\mathbf{v}^* \in \mathcal{D}(A^*)$, the duality bracket $\langle \mathbf{u}, \mathbf{v}^* \rangle$ is absolutely continuous on $[0, T]$ and

$$\partial_t \langle \mathbf{u}, \mathbf{v}^* \rangle = \langle \mathbf{u}, A^* \mathbf{v}^* \rangle + \langle \mathbf{f}(\mathbf{u}), \mathbf{v}^* \rangle, \quad a.e. \text{ on } [0, T]$$

Remark: The integral in the theorem is defined for Banach-valued functions, so we have to use the definition in the sense of Bochner.

To conclude this section, we use the fact that the operator $\mathcal{A} := D\Delta$ in (AC) is sectorial (proof in [AnnaThesis]), and therefore there exists a unique weak solution of the problem. This unique solution can be extended into a classical solution using the notion of mild solutions and $E_{\infty,0,T}$ -mild solutions combined with a theorem from [Rothe] under weak regularity assumptions.

1.2. Existence of global solutions. Now is the time for us to build global solutions to system (M) by building upon local solutions. For that, we introduce elements of the theory of invariant regions established by Smoller in the 70's, (and thoroughly developed in [21]) in the context of general semilinear parabolic equations of the type

$$(3.4) \quad \begin{cases} \partial_t \mathbf{v} = \varepsilon D(\mathbf{v}, x) \Delta \mathbf{v} + \sum_{j=1}^n M^j(\mathbf{v}, x) \partial_j \mathbf{v} + \boldsymbol{\phi}(\mathbf{v}, t), & (x \in \Omega, t \geq 0) \\ \mathbf{v}(x, 0) = \mathbf{v}_0(x). \end{cases}$$

¹the problem $\partial_t \mathbf{u} = \mathcal{A}[\mathbf{u}] + \mathbf{Jac}_{\mathbf{f}}(x)\mathbf{u}$

In this direction, we introduce said invariant regions together with the notion of invariant rectangles for such equations.

DEFINITION 3. A closed subset $\Sigma \subset \mathbb{R}^n$ is called a (positively) invariant region for the local solution of (3.4) if any solution $\mathbf{v}(x, t)$, having all of its boundary and initial values in Σ , satisfies $\mathbf{v}(x, t) \in \Sigma$ for all $x \in \Omega$ and for all $t \geq 0$.

It is a good sanity-check to verify that our system indeed fits this category of problems. To see that, we take the domain-rescaling parameter $\varepsilon = 1$, the matrix of diffusion terms $D = \text{diag}(0, d_1, d_2)$ with constant, positive entries d_1, d_2 , set all matrices M^j equal to zero and, finally, $\phi(\cdot, t) = \mathbf{f}(\cdot)$ to land back on our system.

In the general case, most invariant regions, Σ , are defined by an intersection of $(n - 1)$ -dimensional hypersurfaces (half spaces) which are sets of points satisfying some constraints $G_i \leq 0$, $i = 1, \dots, m$. In other words, regions of the form

$$(3.5) \quad \Sigma = \bigcap_{i=1}^m \{G_i \leq 0\},$$

where every $G_i = G_i(u, v, w)$ are smooth, real-valued functions defined on a domain $\text{Dom}(G_i) \supset \text{im}(\mathbf{u})$ such that ∇G_i never vanishes. In the special case where Σ is invariant and generated by linear constraints ($G_i(\mathbf{v}) = \mathbf{v} - \alpha$, for some $\alpha \in \mathbb{R}$), Σ is referred to as an invariant rectangle. Additionally, in the special case where D, M^j are diagonal matrices (this applies to us), it is shown that any invariant region must be a rectangular region, and this under weak assumptions [ref].

The case of rectangular regions is particularly easy to deal with since it is only needed to show that the gradient of the active constraint G_i points inwards Σ . With symbols, if $v \in \partial\Sigma$ denotes a point on the boundary of Σ i.e., there is an index i for which $G_i(v) = 0$, then

$$\nabla G_i(v) \cdot \mathbf{f} \leq 0.$$

To ensure the proper introduction of this new notion, we propose to accompany it with a geometric interpretation of invariant regions. Visually speaking, if Σ is an invariant region and u a solution of (3.4), then we can show that if u touches the edge of Σ , the solution immediately bounces back inside the region. In other words, the solution is trapped inside the rectangle, see figure 1.2.

THEOREM 2 (Existence of an invariant rectangle). *There exists three positive reals A_u, A_v, A_w , large enough, such that the region*

$$\Sigma = \{(u, v, w) \in \mathbb{R}^3 \mid 0 \leq u \leq A_u, \quad 0 \leq v \leq A_v, \quad 0 \leq w \leq A_w, \},$$

is an invariant rectangle of (M)

PROOF. We start by writing

$$\Sigma = \Sigma_0 \cap \Sigma_A =: \bigcap_i \left(\underbrace{\{G_\kappa \leq 0\}}_{\Sigma_0} \cap \underbrace{\{H_\kappa \leq 0\}}_{\Sigma_A} \right), \quad \kappa = u, v, w.$$

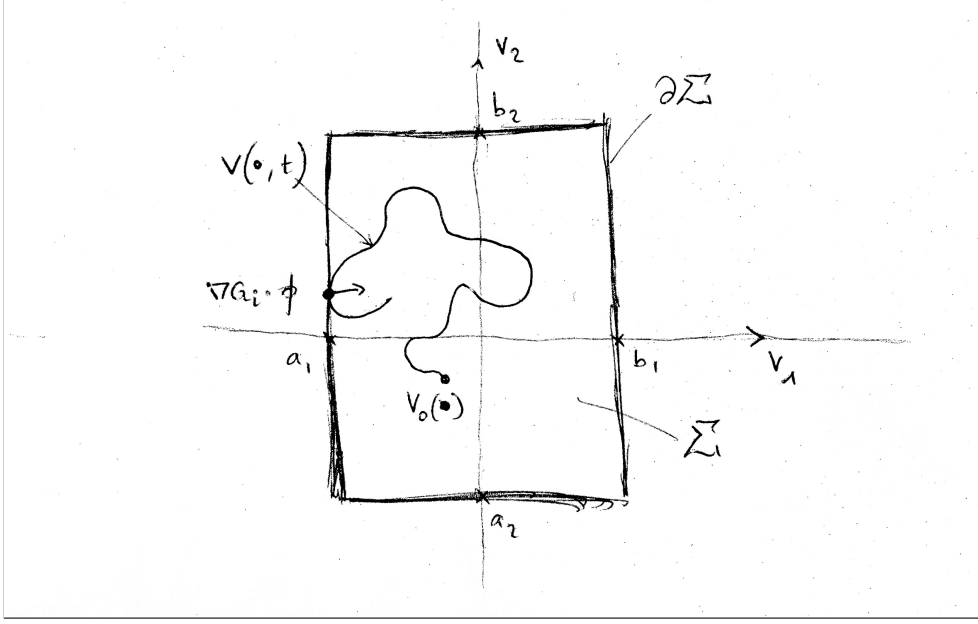


FIGURE 2. Schematic representation of an invariant rectangle Σ in the two-dimensional case. At initial time, the solution sits at the point $v_0(\cdot)$ and starts travelling as t grows. For some time $t > 0$, the solution represented by the point $v(\cdot, t)$ eventually touches the border of Σ and bounces back to the interior of the region.

The rectangular region where each G_i and H_i are prescribing the constraints on Σ defined as follows

$$G_u(u, v, w) = -u$$

$$H_u(u, v, w) = u - A_u$$

$$G_v(u, v, w) = -v$$

$$H_v(u, v, w) = v - A_v$$

$$G_w(u, v, w) = -w$$

$$H_w(u, v, w) = w - A_w$$

Each G_i and H_i is obviously smooth. Now let

$$\partial\Sigma := \left\{ (u, v, w) \in \Sigma : \exists i, \quad G_i(u, v, w) = 0 \quad \text{or} \quad H_i(u, v, w) = 0 \right\},$$

be the boundary of Σ , we consider a point $(u, v, w) \in \partial\Sigma$ and proceed case-by-base. Let X denote such a point. If $u = 0$, then

$$(\nabla G_u \cdot \mathbf{f})(X)|_{u=0} = u \left(\mu_f + \mu_b v - m_1 \frac{v}{1 + uv} \right) \Big|_{u=0} = 0.$$

The case $v = 0$ is similar in a way that

$$(\nabla G_v \cdot \mathbf{f})(X)|_{v=0} = v \left(\mu_l + \mu_b u + w - m_2 \frac{u}{1 + uv} \right) \Big|_{v=0} = 0.$$

Finally, since $X \in \partial \Sigma_0$, it holds that $u, v \geq 0$, meaning that if $w = 0$, then

$$(\nabla G_w \cdot \mathbf{f})(X)|_{w=0} = -m_3 \frac{uv}{1 + uv} < 0.$$

We proceed in similar fashion to take care of $\partial \Sigma_A$. First, we notice that

$$\begin{aligned} f(u, v, w) &= -\mu_f u + m_1 \frac{uv}{1 + uv} - \mu_b uv \\ &\leq m_1 - \min(\mu_f, \mu_b) u (1 + v). \end{aligned}$$

Using the fact that $X \in \Sigma$, we deduce $1 + v \geq 1$ and therefore we get rid of it in the product, leaving us with

$$f(u, v, w) \leq m_1 - \min(\mu_f, \mu_b) u.$$

In other words, we can find $A_u \in \mathbb{R}_{>0}$ satisfying $A_u > m_1 / \min(\mu_f, \mu_b)$. This implies $(\nabla H_u \cdot \mathbf{f})(X)|_{u=A_u} = f(A_u, v, w) \leq 0$. The same logic applies to show

$$g(u, v, w) \leq m_2 - \min(\mu_f, \mu_b, 1) v.$$

Thus, by picking $A_v \geq m_2 / \min(\mu_f, \mu_b, 1)$, we get $(\nabla H_v \cdot \mathbf{f})(X)|_{v=A_v} \leq 0$. Finally, we show that

$$h(u, v, w) \leq m_3 - \mu_e w,$$

and take $A_w \geq m_3 / \mu_e$ to obtain $(\nabla H_w \cdot \mathbf{f})(X)|_{w=A_w} \leq 0$. This concludes the proof. \square

We have thus showed the existence of an invariant rectangle. This provides an upper bound for each quantity and we finally use theorem 14.9, [21] to deduce the existence of the solution to (M) for all $t > 0$ provided we take initial data u_0 continuous, bounded with values $u_0(x) \in \Sigma$ for $x \in \Omega$. Meaning that we can guarantee the existence of a global solution under reasonable assumptions on our model.

Remark: We actually used two assumptions under the hood for this result (that are verified in our case but worth mentioning nonetheless). The first one is that the system we work with is \mathbf{f} -stable, in the sense of [Smoller1994], which allows the proof to be valid even though the gradient vanishes on $\partial \Sigma$ as soon as one quantity is zero. The second one is that the Banach space in which our solutions u, v, w live in is *admissible*, still in the sense of [Smoller1994], which allows us to use the theorem in the first place.

2. Finding steady states of the model

Finding steady states of the model was, by far, the most exploratory part of this work, and we were not able to formulate satisfying results regarding steady states of the system for an arbitrary choice of parameters.

That being said, we were able to obtain some estimates and analytical formulas for the location of steady-state. We recall that steady states of (M) are the points (functions) $\bar{\mathbf{u}} := (\bar{u}, \bar{v}, \bar{w})$ such that $\partial_t \bar{\mathbf{u}} = 0$. Using equations of (M), we find that such points must obey the relation

$$(3.6) \quad -\mu_f \bar{u} + m_1 \frac{\bar{u}\bar{v}}{1 + \bar{u}\bar{v}} - \mu_b \bar{u}\bar{v} = 0,$$

$$(3.7) \quad d_1 \Delta \bar{v} - \mu_l \bar{v} + m_2 \frac{\bar{u}\bar{v}}{1 + \bar{u}\bar{v}} - \mu_b \bar{u}\bar{v} - \bar{v}\bar{w} = 0,$$

$$(3.8) \quad d_2 \Delta \bar{w} - \mu_e \bar{w} + m_3 \frac{\bar{u}\bar{v}}{1 + \bar{u}\bar{v}} = 0.$$

From this expression, it is quite clear that the trivial solution $\bar{\mathbf{u}} = (0, 0, 0)$ will always be a steady state of (M). Let us look for more interesting ones by assuming $\bar{\mathbf{u}}$ has only nonzero coordinates, which allows us to divide by \bar{u} in (3.6). After some algebraic manipulations, we find

$$\bar{u} = \underbrace{\frac{m_1}{\mu_f + \mu_b \bar{v}} - \frac{1}{\bar{v}}}_{=: \mathcal{R}(\bar{v})},$$

and

$$(3.9) \quad d_1 \Delta \bar{v} = -m_2 \frac{\mathcal{R}(\bar{v})\bar{v}}{1 + \mathcal{R}(\bar{v})\bar{v}} + \mu_l \bar{v} + \mu_b \mathcal{R}(\bar{v})\bar{v} - \bar{v}\bar{w},$$

$$(3.10) \quad d_2 \Delta \bar{w} = -m_3 \frac{\mathcal{R}(\bar{v})\bar{v}}{1 + \mathcal{R}(\bar{v})\bar{v}} + \mu_e \bar{w},$$

which we rewrite as

$$(3.11) \quad d_1 \Delta \bar{v} = -m_2 \left(1 - \frac{\mu_f + \mu_b \bar{v}}{m_1 \bar{v}} \right) + \mu_l \bar{v} + \mu_b \left(\frac{m_1 \bar{v}}{\mu_f + \mu_b \bar{v}} - 1 \right) - \bar{v}\bar{w},$$

$$(3.12) \quad d_2 \Delta \bar{w} = -m_3 \left(1 - \frac{\mu_f + \mu_b \bar{v}}{m_1 \bar{v}} \right) + \mu_e \bar{w}.$$

So finding steady states of (M) boils down to finding the solution of a system of elliptic partial differential equations with highly nonlinear terms. Put differently, we need to find another angle of attack... A possible solution is to look for constant (spatially homogeneous) steady states instead. Not only they are the one we are interested in when dealing with Turing instability (more on that in the next chapter), they are also slightly easier to find than their nonconstant (spatially nonhomogeneous) counterpart .

Limiting our scope to spatially homogeneous steady states only, the Laplace operator vanishes (constant functions are harmonic), therefore, the previous system reduces to

$$(3.13) \quad m_2 \left(1 - \frac{\mu_f + \mu_b \bar{v}}{m_1 \bar{v}} \right) = \mu_l \bar{v} + \mu_b \left(\frac{m_1 \bar{v}}{\mu_f + \mu_b \bar{v}} - 1 \right) - \bar{v} \bar{w},$$

$$(3.14) \quad m_3 \left(1 - \frac{\mu_f + \mu_b \bar{v}}{m_1 \bar{v}} \right) = \mu_e \bar{w},$$

which is already much friendlier. A quick division by μ_e in (3.14) allows to express \bar{w} as a function of \bar{v} . This allows us to formulate the following result

LEMMA 2. *Let $\mathcal{P} : x \mapsto Ax^3 + Bx^2 + Cx + D$ be the third order polynomial with coefficients given by*

$$\begin{aligned} A &= -\mu_l \mu_b - \frac{m_3 \mu_b}{\mu_e} + \frac{m_3 \mu_b^2}{m_1 \mu_e}, \\ B &= -\mu_l \mu_f + m_2 \mu_b - \frac{m_2 \mu_b^2}{m_1} + \mu_b^2 - m_1 \mu_b - \frac{m_3 \mu_f}{\mu_e} + \frac{2 \mu_f \mu_b m_3}{\mu_e m_1}, \\ C &= m_2 \mu_f - \frac{2 \mu_f \mu_b m_2}{m_1} + \mu_f \mu_b + \frac{m_3 \mu_f^2}{\mu_e m_1}, \\ D &= -\frac{m_2 \mu_f^2}{m_1}. \end{aligned}$$

Then, the following statements are equivalent

- (i) V is a real root of \mathcal{P}
- (ii) The point $\left(\frac{m_1}{\mu_f + \mu_b V} - \frac{1}{V}, V, \frac{m_3}{\mu_e} - \frac{m_3(\mu_f + \mu_b V)}{\mu_e m_1 V} \right)$ is a constant steady state of (M)

Remark: Although \mathcal{P} may have several real roots, we only care about those yielding positive values of $(\bar{u}, \bar{v}, \bar{w})$, because not only we have proved global existence for nonnegative initial data, we also showed that solution with positive initial condition will stay positive for all times, and we do not particularly care about negative solutions for reasons of biological realism. Since solutions represent concentrations of molecules, having negative values would go against every known physical laws.

From the expression of steady state, one can derive a lower bound on \bar{v} to guarantee the positivity of the steady state, that is

PROPOSITION 1. *Assume that the choice of parameters is such that $\mu_b < m_1$ (this is biologically relevant when looking at the nature of both parameters). Let $S_{\mathcal{P}}$ denote the set of real roots of \mathcal{P} from lemma 2, if*

$$\sup_{V \in S_{\mathcal{P}}} V < \frac{\mu_f}{m_1 - \mu_b},$$

then the origin is the only steady state with only nonnegative coordinates.

PROOF. The proof is a direct computation. Take any root $V \in S_{\mathcal{P}}$, by definition V is real and nonzero, then the condition that the steady state has only nonnegative coordinates is (using (ii) in lemma 2):

$$\begin{aligned} \frac{m_1}{\mu_f + \mu_b V} - \frac{1}{V} &\geq 0, \\ V &\geq 0, \\ \frac{m_3}{\mu_e} \left(1 - \frac{\mu_f + \mu_b V}{m_1 V} \right) &\geq 0 \end{aligned}$$

The first and third equations are redundant and provide the same estimate, i.e., the steady state has only nonnegative entries if and only iff

$$V \geq 0 \quad \text{and} \quad V \geq \frac{\mu_f}{m_1 - \mu_b}$$

The condition $V \geq 0$ becomes redundant as well, and we deduce by contraposition that $V < \mu_f(m_1 - \mu_b)^{-1}$ implies that at least one coordinate is negative. We conclude by taking the supremum on both sides. \square

Another way to see those constant steady states is to see each equation $f = 0, g = 0, h = 0$ as the algebraic equation of a hypersurface. This way, steady states become the intersection points between those three manifolds, which enables some visual intuition about the location of these equilibria, see figure 2).

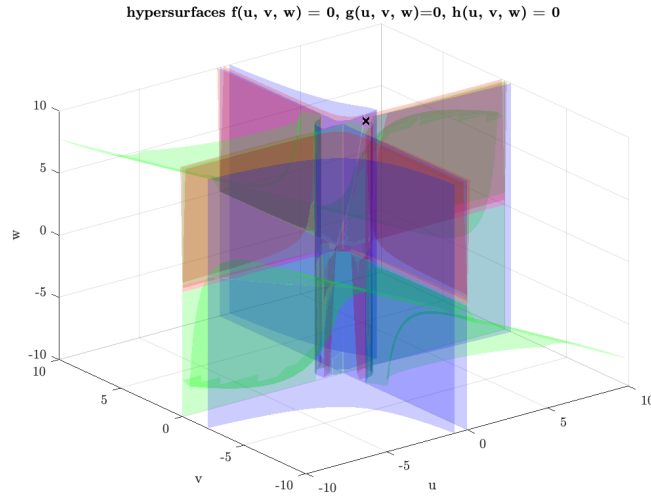


FIGURE 3. Three-dimensional plot of algebraic hypersurfaces associated to the equations $f \equiv 0$ (blue), $g \equiv 0$ (green) and $h \equiv 0$ (red). Parameters values are fixed and each curve is plotted on $[-10, 10]$. The black cross highlight the only steady state with only (strictly) positive coordinates, i.e., the intersections of these hypersurfaces in the positive quadrant.

To summarize, we showed that there exists local solutions using classical results from the theory of semigroups of operators and spectral analysis. We then bridged from local to global solutions with invariant rectangles to prove that these solutions, provided we use biologically relevant initial data (all nonnegative quantities), will stay nonnegative and bounded over time. Lastly, being unable to find spatially nonhomogeneous steady-states, we showed that the origin was always an equilibrium of (M) and derived a set of conditions to obtain the existence of other nonnegative constant steady-states under a biologically meaningful assumption on the parameters.