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On a competitive system with ideal free dispersal

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Abstract

In this article we study the long term behavior of the competitive system

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot \left[\alpha(x)\nabla \dfrac{u}{m}\right] + u(m(x) - u - bv) \ \text{ in } \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial t} = \nabla \cdot [\beta(x)\nabla v] + v(m(x) - cu - v) \ \text{ in } \Omega,\ t > 0, \\ \nabla \dfrac{u}{m} \cdot \hat{n} = \nabla v \cdot \hat{n} = 0 \ \text{ on } \partial\Omega,\ t > 0, \end{cases}$$

which supports for the first species an *ideal free distribution*, that is a positive steady state which matches the per-capita growth rate. Previous results have stated that when $b = c = 1$ the ideal free distribution is an evolutionarily stable and neighborhood invader strategy, that is the species with density v always goes extinct. Thus, of particular interest will be to study the interplay between the inter-specific competition coefficients b, c and the diffusion coefficients $\alpha(x)$ and $\beta(x)$ on the critical values for stability of semi-trivial steady states, and the structure of bifurcation branches of positive equilibria arising from these equilibria. We will also show that under certain regimes the system sustains multiple positive steady states.

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1. Introduction

The effect of dispersal on species interaction is an important topic in spatial ecology. In many cases, patterns of dispersal leading to an ideal free distribution (IFD) are evolutionary stable [5–8,10]. Here an ideal free distribution is a positive state which matches the local per-capita growth rate, resulting in a situation whereby the species in the equation has fitness equal to zero and exhibits no net movement. In particular, for two competitors that are ecologically identical a competitor that can attain an IFD can exclude one that can not. However, as we will show in this article, if the competition is not symmetric the outcome depends on both the dispersal strategies and the asymmetry of interaction. See [14] for a related example.

We will consider a situation where the strength of interactions is allowed to vary, and one species uses an ideal free strategy and the other uses a fickian-type diffusion. More precisely, we consider the competition system

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot \left[\alpha(x)\nabla \dfrac{u}{m}\right] + u(m(x) - u - bv) \ \text{ in } \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [\beta(x)\nabla v] + v(m(x) - cu - v) \ \text{ in } \Omega,\ t > 0, \\ \nabla \dfrac{u}{m} \cdot \hat{n} = \nabla v \cdot \hat{n} = 0 \ \text{ on } \partial\Omega,\ t > 0. \end{cases} \tag{1.1}$$

The domain Ω is bounded, with $\partial\Omega$ smooth and $\hat{n}$ the outward unit normal. The diffusion coefficients $\alpha(x), \beta(x)$ are smooth and positive in $\bar{\Omega}$. The function $m(x)$, which accounts for the growth rate, is also smooth and positive in $\bar{\Omega}$. The competition coefficients b, c are positive and constant. The initial conditions are assumed to be nonnegative and smooth, that is

$$u(x,0),\ v(x,0) \geq 0 \ \text{ in } \bar{\Omega}. \tag{1.2}$$

In this paper we analyze how the interaction coefficients b and c influence the dynamics of the system (1.1). Previous work shows that when $b = c = 1$, then competitive exclusion holds, and the competitor which follows the ideal free strategy prevails (see [1]). It readily follows from this result and comparison principles that the same conclusion can be drawn for any combination of competition coefficients with $c \geq 1$ and $b \leq 1$. It is of particular interest to ask how and to what extent this advantage derived from ideal free dispersal continues when there is a trade off relative to competitive impact, for example when $b > 1$ but $c < 1$.

To study the dynamics of (1.1) we need to consider the associated steady-state system

$$\begin{cases} Lu + u(m(x) - u - bv) = 0 \ \text{ in } \Omega, \\ Mv + v(m(x) - cu - v) = 0 \ \text{ in } \Omega, \\ \nabla \frac{u}{m} \cdot \hat{n} = \nabla v \cdot \hat{n} = 0 \ \text{ on } \partial\Omega, \end{cases} \tag{1.3}$$

where the operators L and M are defined as:

$$Lu \equiv \nabla \cdot \left[\alpha(x)\nabla \frac{u}{m}\right], \quad Mv \equiv \nabla \cdot [\beta(x)\nabla v].$$

Since $\nabla\left(\frac{m}{m}\right)=0$, $Lm=0$ and so m is a positive equilibrium of

$$\begin{cases} u_t = Lu + u(m(x)-u) \ \text{ in } \Omega,\ t>0, \\ \nabla \dfrac{u}{m}\cdot \hat{n} = 0 \ \text{ on } \partial\Omega,\ t>0, \end{cases}$$

which can be regarded as an ideal free distribution. That such problems admit ideal free dispersal strategies was established in [3,2]. In this case, the dispersal strategy is a form of area restricted search. Another related movement strategy which produces an ideal free distribution as an equilibrium relative to logistic dynamics comes from combining diffusion with advection up the gradient of $\log m$ (as in [6]). In that case, L could be taken as

$$Lu = \mu\nabla\cdot(\nabla u - u\nabla \log m) \ \text{ in } \Omega,$$

subject to the no-flux boundary condition

$$(\nabla u - u\nabla\log m)\cdot\hat{n} = 0 \ \text{ on } \partial\Omega.$$

This system admits two semi-trivial steady-state solutions of (1.1), that is solutions of (1.3) in which one component is positive and the other is zero. Since only the first species admits an ideal free distribution, we have that $(m(x),0)$ is a semi-trivial solution of (1.3), while $(0,\theta)$ is the other one, with $\theta \not\equiv m$. We will see that coexistence and exclusion will depend largely on the stability of these solutions. Specifically, we identify a parameter $b_{cr}>1$ so that in the region $b<b_{cr}$ we have that $(0,\theta)$ is unstable, while if $b>b_{cr}$ it is asymptotically stable. Thus, b_{cr} accounts for the strength of the advantage of the ideal free distribution. Concerning $(m,0)$ we have that it is unstable when $c<1$, and it is asymptotically stable for $c>1$.

We will use stability analysis, bifurcation theory and monotone dynamical systems theory ([13,16]) to understand the set of equilibria of (1.1). We find conditions where we get coexistence, exclusion and multiple equilibria. In what follows we present some relevant features of the model and results obtained.

As mentioned above, a key property of system (1.1) is that it induces a strongly monotone dynamical system, that is if (u_1,v_1) and (u_2,v_2) are two solutions of (1.1) with $u_1(x,0)\ge u_2(x,0)$, $v_1(x,0)\le v_2(x,0)$ for all $x\in\bar\Omega$ and $(u_1(\cdot,0),v_1(\cdot,0))\not\equiv(u_2(\cdot,0),v_2(\cdot,0))$, then $u_1(x,t)>u_2(x,t)$, $v_1(x,t)<v_2(x,t)$ for all $x\in\bar\Omega$ and $t>0$. Using the theory of monotone dynamical systems, we will be able to establish results on coexistence, a priori bounds, and multiplicity of solutions, among other observations.

The stability properties of these steady states are established in the following proposition:

Proposition 1.1. *For all $0<c<1$, the steady state $(m,0)$ of (1.1) is unstable, while it is linearly asymptotically stable for $c>1$.*

There exists a $b_{cr}>1$ such that for all $0<b<b_{cr}$ the steady state $(0,\theta)$ of (1.1) is unstable, while it is linearly asymptotically stable for $b>b_{cr}$.

As we will see in Section 2, with the aid of this proposition we obtain that for $0<c<1$ and $0<b<b_{cr}$ there exists a stable positive steady state solution, and for $c>1$ and $b>b_{cr}$ there exists an unstable positive steady state of (1.1). The values $c=1$ and $b=b_{cr}$ are critical, and bifurcation occurs in both cases. Indeed we have:

Theorem 1.2. *For any $b > 0$, bifurcation of positive solutions of (1.3) from $(m, 0)$ occurs as the parameter c crosses 1. Moreover, the set of positive solutions near $(m, 0)$ is described by a smooth curve $(u(\varepsilon), v(\varepsilon), c(\varepsilon))$ where $u = m + w(\varepsilon)$, $v = v(\varepsilon)$ with*

$$w(\varepsilon) = \varepsilon b\eta + \varepsilon\tilde{w}(\varepsilon); \quad v = \varepsilon + \varepsilon\tilde{v}(\varepsilon) \text{ and } c = 1 + \gamma(\varepsilon),$$

where $\eta < 0$, $\tilde{w}(0) = \tilde{v}(0) = 0$ and $\gamma(0) = 0$.

Analogously, for any $c > 0$, bifurcation of positive solutions of (1.3) from $(0, \theta)$ occurs as b crosses b_{cr}. The set of positive solutions near $(0, \theta)$ is a smooth curve $u = \varepsilon\varphi_0 + \varepsilon\tilde{w}(\varepsilon)$, $v = \theta + \varepsilon\psi_0 + \varepsilon\tilde{z}(\varepsilon)$ for $b = b_{cr} + \delta(\varepsilon)$, with $\tilde{w}(0) = \tilde{z}(0) = 0$, $\delta(0) = 0$, $\varphi_0 > 0$ and $\psi_0 < 0$.

The direction taken by the bifurcation branches, namely the sign of $\gamma(\varepsilon)$ and $\delta(\varepsilon)$ above, is key to determining the stability properties of the bifurcating solutions, due to the principle of exchanged stability. This direction is determined by the value of the parameter b in the case of the bifurcation from $(m, 0)$, and c in the case of $(0, \theta)$. More precisely, we have the following result:

Proposition 1.3. *There exists a $b^* > 1$ such that the bifurcating solutions $(m + w(\varepsilon), v(\varepsilon))$ of (1.1) for $c = 1 + \gamma(\varepsilon)$ as described in Theorem 1.2, are unstable for $b > b^*$, and locally asymptotically stable for $b < b^*$.*

Similarly, there exists $c^* > 0$ such that the bifurcating solutions $(\varepsilon\varphi_0 + \varepsilon\tilde{w}(\varepsilon), \theta + \varepsilon\psi_0 + \varepsilon\tilde{z}(\varepsilon))$ of (1.1) for $b = b_{cr} + \delta(\varepsilon)$ as above, are unstable for $c > c^*$, and locally asymptotically stable for $c < c^*$.

As stated, the coefficients b^* and c^* play an important role in the dynamics of (1.1). Moreover, depending on the relationship between b_{cr} and b^* as well as 1 and c^*, we can possibly have cases where there are two ordered steady states of (1.1) that share the same stability properties: either both unstable, or both locally asymptotically stable and then, by some properties of monotone dynamical systems, another positive equilibrium of (1.1) exists. We explore this situation in Section 5, where we parametrize the diffusion coefficients, to construct such examples in limiting cases.

Theorem 1.4. *Consider $\alpha(x) = \mu\alpha_0(x)$ and $\beta(x) = \nu\beta_0(x)$, where μ, ν are positive parameters. We have the following examples, where multiple positive steady states of (1.1) arise:*

a) *There exists a number $\bar{b}_1 > 0$ such that for $b \in (1, \bar{b}_1)$ we can find μ_0, ν_0, so that for all $0 < \mu < \mu_0$, $\nu > \nu_0$, there is a $c > 0$ for which the corresponding system (1.1) admits two positive steady states, one unstable and one locally asymptotically stable.*
b) *There exists a number $\bar{b}_2 > 0$ such that for $b \in (1, \bar{b}_2)$ there are μ_0, ν_0 so that for all $\mu > \mu_0$, $0 < \nu < \nu_0$, there is a $c > 0$ for which (1.1) admits two positive steady states, one unstable and one locally asymptotically stable.*

Finally, we point out that in certain cases, whenever one of the competition coefficients is large and the other is in a certain range, no positive solution of (1.3) exists. In this situation, competition drives the dynamics. More precisely, we have the following result, which we prove in Section 3.

Theorem 1.5. *There exists $\bar{b}^* > 0$ such that for all $b > \bar{b}^*$ and $0 \le c \le 1$ the system (1.1) does not admit a positive steady state. Similarly, there is $\bar{c}^* > 0$ so that nonexistence also occurs whenever $c > \bar{c}^*$ and $0 \le b \le b_{cr}$.*

In the case when $0 \le c \le 1$ and b large, the global attractor of (1.1) is $(0, \theta)$, while when $0 \le b \le b_{cr}$ and c is large the global attractor is $(m, 0)$.

In Section 6 we discuss the results obtained, providing examples of several configurations regarding the steady state structure of (1.1) in the (b, c) parameter space.

2. Preliminary results

In this section we will state some basic facts that are needed for characterizing coexistence regions. We start by observing that by using the change of variables $U = \frac{u}{m}$ and $V = v$ we have that system (1.1) is equivalent to

$$\begin{cases} \dfrac{\partial U}{\partial t} = \dfrac{1}{m}\nabla \cdot [\alpha(x)\nabla U] + U(m(x) - mU - bV) \ \text{ in } \Omega,\ t > 0, \\ \dfrac{\partial V}{\partial t} = \nabla \cdot [\beta(x)\nabla V] + V(m(x) - cmU - V) \ \text{ in } \Omega,\ t > 0, \\ \nabla U \cdot \hat{n} = \nabla V \cdot \hat{n} = 0 \ \text{ on } \partial\Omega,\ t > 0. \end{cases} \tag{2.4}$$

By standard theory system (2.4) is competitive and the induced semiflow strongly monotone. Using this, we can proceed as in Lemma 5.4 of [9] to conclude that (1.1) is strongly monotone as well.

Lemma 2.1. *Let (u_i, v_i) for $i = 1, 2$ be two solutions of (1.1), with*

$$u_1(x,0) \ge u_2(x,0),\ v_1(x,0) \le v_2(x,0) \ \textit{for all } x \in \bar{\Omega}$$

and $(u_1(\cdot,0), v_1(\cdot,0)) \not\equiv (u_2(\cdot,0), v_2(\cdot,0))$. Then $u_1(x,t) > u_2(x,t)$, $v_1(x,t) < v_2(x,t)$ for all $x \in \bar{\Omega}$ and $t > 0$.

The other important issue is to characterize the linear stability of the two semitrivial steady state solutions of (1.1), namely $(m, 0)$ and $(0, \theta)$, where θ is the unique positive solution of

$$Mv + v(m(x) - v) = 0 \ \text{ in } \Omega, \quad \nabla v \cdot \hat{n} = 0 \ \text{ on } \partial\Omega. \tag{2.5}$$

Indeed, as stated in the following result, characterizing the stability properties $(m, 0)$ and $(0, \theta)$ is key for establishing the existence of positive steady state solutions of (1.1).

Proposition 2.2. *We have that*

(1) if $(m, 0)$ and $(0, \theta)$ are unstable, then there exists a stable positive equilibrium of (1.1);
(2) if $(m, 0)$ and $(0, \theta)$ are stable, then there exists an unstable positive equilibrium of (1.1);
(3) if (1.1) does not admit a positive steady state solution, then one of the semi-trivial steady states is unstable and the other one is globally asymptotically stable.

This lemma can be proved following Theorem 8 of [1]. The following results establish the linear stability of $(m, 0)$ and $(0, \theta)$.

Lemma 2.3. *For all $0 < c < 1$, the steady state $(m, 0)$ of (1.1) is unstable, while it is linearly asymptotically stable for $c > 1$.*

Proof. We proceed as in Lemma 5.5 of [9]. The linearization of (1.1) at the steady state $(m, 0)$ is given by the triangular system

$$\begin{cases} L\varphi - m\varphi - bm\psi = \lambda\varphi \ \text{ in } \Omega, \\ M\psi + m(1-c)\psi = \lambda\psi \ \text{ in } \Omega, \\ \nabla\frac{\varphi}{m}\cdot\hat{n} = \nabla\psi\cdot\hat{n} = 0 \ \text{ on } \partial\Omega. \end{cases} \tag{2.6}$$

If $c < 1$ then the second equation admits a principal eigenvalue $\lambda_0 > 0$ with corresponding eigenfunction $\psi_0 > 0$. In this case, for a fixed $\psi_0 > 0$ the first equation is solvable, with the corresponding $\varphi_0 < 0$. Then $(m, 0)$ is unstable.

When $c > 1$ then the principal eigenvalue of the second equation of (2.6) is negative. Thus, if (2.6) admits an eigenvalue λ with a positive real part, then the corresponding $\psi \equiv 0$, and then φ has to be a solution of

$$L\varphi - m\varphi = \lambda\varphi \ \text{ in } \Omega, \nabla\frac{\varphi}{m}\cdot\hat{n} = 0 \ \text{ on } \partial\Omega.$$

Since the principal eigenvalue of this equation is negative, we conclude that $\varphi \equiv 0$ as well, which contradicts the fact that λ is an eigenvalue. □

Lemma 2.4. *There exists a $b_{cr} > 1$ such that for all $0 < b < b_{cr}$ the steady state $(0, \theta)$ of (1.1) is unstable, while it is linearly asymptotically stable for $b > b_{cr}$.*

Proof. Analogously to the proof of Lemma 2.3 the linearized stability of $(0, \theta)$ is characterized through the sign of the principal eigenvalue of the equation

$$L\varphi + \varphi(m - b\theta) = \lambda\varphi \ \text{ in } \Omega, \ \ \nabla\frac{\varphi}{m}\cdot\hat{n} = 0 \ \text{ on } \partial\Omega, \tag{2.7}$$

namely, $(0, \theta)$ is unstable if the principal eigenvalue of (2.7) is positive and asymptotically stable if it is negative. Now, we have that there exists a unique $b_{cr} > 0$ such that the principal eigenvalue of (2.7) corresponding to $b = b_{cr}$ is 0. To verify that $b_{cr} > 1$, we multiply the equation (2.7) by $\frac{m}{\varphi}$, with φ the corresponding positive eigenfunction, and integrate over Ω obtaining that

$$\int_\Omega m(m - b_{cr}\theta)\,dx = -\int_\Omega \alpha(x)\left|\nabla\frac{\varphi}{m}\right|^2 \frac{m^2}{\varphi^2}\,dx < 0,$$

and hence, $b_{cr} > \frac{\int_\Omega m^2}{\int_\Omega m\theta}$.

Integrating (2.5) with $v = \theta$ yields $\int_\Omega m\theta = \int_\Omega \theta^2$. Consequently,

$$\int_\Omega \theta^2 = \int_\Omega m\theta \le \left(\int_\Omega m^2\right)^{\frac{1}{2}} \left(\int_\Omega \theta^2\right)^{\frac{1}{2}},$$

and then $\int_\Omega \theta^2 \le \int_\Omega m^2$. Hence, $b_{cr} > 1$.

Finally, by comparison the principal eigenvalue of (2.7) is positive when $0 < b < b_{cr}$ and negative if $b > b_{cr}$. This concludes the proof. □

Using a variational formulation of a weighted principal eigenvalue problem, we obtain that b_{cr} can be expressed as:

$$b_{cr} = \sup_{\varphi \in W^{1,2}(\Omega)\setminus\{0\}} \left[\frac{-\int_\Omega \alpha(x)|\nabla\varphi|^2 + \int_\Omega m^2\varphi^2}{\int_\Omega m\theta\varphi^2} \right]. \tag{2.8}$$

This formula will be used later to estimate b_{cr}.

Observe that using Lemma 2.3, Lemma 2.4 and Proposition 2.2, we have the following basic existence result:

Proposition 2.5. *For $0 < b < b_{cr}$ and $0 < c < 1$ the system (1.1) admits a stable positive equilibrium, and for $b > b_{cr}$ and $c > 1$ it admits an unstable positive equilibrium.*

Another important tool for the construction of the regions of existence is the method of upper and lower solutions, which holds since we can work with the equivalent system (2.4).

Lemma 2.6. *Suppose that (u_1, v_1), (u_2, v_2) satisfy $0 \le u_1 \le u_2$ and $v_1 \ge v_2 \ge 0$ in $\bar\Omega$ and*

$$\begin{cases} Lu_1 + u_1(m(x) - u_1 - bv_1) \le 0, \;\; Lu_2 + u_2(m(x) - u_2 - bv_2) \ge 0 \;\; \text{in } \Omega, \\ Mv_1 + v_1(m(x) - cu_1 - v_1) \ge 0, \;\; Mv_2 + v_2(m(x) - cu_2 - v_2) \le 0 \;\; \text{in } \Omega, \\ \nabla\frac{u_1}{m}\cdot\hat n \le 0, \;\; \nabla\frac{u_2}{m}\cdot\hat n \ge 0, \;\; \nabla v_1\cdot\hat n \ge 0, \;\; \nabla v_2\cdot\hat n \le 0 \;\; \text{on } \partial\Omega, \end{cases} \tag{2.9}$$

then there exists a solution (u^*, v^*) of (1.3) with $u_1 \le u^* \le u_2$ and $v_1 \ge v^* \ge v_2$.

As a consequence of this result, and the strong maximum principle, we have the following a priori bound for the steady states of (1.3).

Corollary 2.7. *If (u^*, v^*) is a nonnegative equilibrium of (1.3), then $u^* \le m$ and $v^* \le \theta$. Moreover, if u^* and v^* are positive then $u^* < m$ and $v^* < \theta$.*

Furthermore, we have a comparison lemma for coexistence states.

Lemma 2.8. *If the system (1.3) has a coexistence state for parameters $(b, c) = (\bar b, \bar c)$ with $\bar b < b_{cr}$ and $\bar c > 1$, then (1.3) has a coexistence state for parameters $(b, c) = (\bar b, \tilde c)$ with $\tilde c \in (0, \bar c)$. Also we have a coexistence state for $(b, c) = (\tilde b, \bar c)$ with $\tilde b \in (\bar b, b_{cr})$.*

Recall if $b < b_{cr}, c < 1$ then there exists a coexistence state for the system (1.3) by Proposition 2.2, so we will study the case when $(m, 0)$ and $(0, \theta)$ have different stabilities.

Proof. Let $(\bar{u}, \bar{v})$ be a coexistence state for parameters $(\bar{b}, \bar{c})$, so that for $\tilde{c} \in (0, \bar{c})$ we have that

$$\begin{cases} L\bar{u} + \bar{u}(m(x) - \bar{u} - \bar{b}\bar{v}) = 0 \ \text{ in } \Omega, \\ M\bar{v} + \bar{v}(m(x) - \tilde{c}\bar{u} - \bar{v}) \geq 0 \ \text{ in } \Omega, \end{cases}$$

hence $(\bar{u}, \bar{v})$ is an upper solution of system (1.3) with parameters $(\bar{b}, \tilde{c})$.

On the other hand, since $\bar{b} < b_{cr}$ the problem:

$$L\varphi + \varphi(m - \bar{b}\theta) = \lambda\varphi \ \text{ in } \Omega, \ \ \nabla\frac{\varphi}{m} \cdot \hat{n} = 0 \ \text{ on } \partial\Omega,$$

has a principal eigenvalue $\lambda_0 > 0$ with a respective eigenfunction $\varphi_0 > 0$. If $\varepsilon > 0$ is small enough then $(\varepsilon\varphi_0, \theta)$ satisfies

$$\begin{cases} L(\varepsilon\varphi_0) + \varepsilon\varphi_0(m(x) - \varepsilon\varphi_0 - \bar{b}\theta) = \varepsilon\varphi_0(\lambda_0 - \varepsilon\varphi_0) > 0 \ \text{ in } \Omega, \\ M\theta + \theta(m(x) - \tilde{c}\varepsilon\varphi_0 - \theta) = -\varepsilon\tilde{c}\theta\varphi_0 < 0 \ \text{ in } \Omega, \end{cases}$$

therefore $(\varepsilon\varphi_0, \theta)$ is a lower solution and since $\varepsilon\varphi_0 < \bar{u}$ and $\bar{v} < \theta$ for ε small enough, we conclude that there exists a coexistence state for $(b, c) = (\bar{b}, \tilde{c})$. The proof of the other case is similar. □

We also have the following result.

Lemma 2.9. *If the system (1.3) has a coexistence state for parameters $(b, c) = (\bar{b}, \bar{c})$ with $\bar{b} > b_{cr}$ and $\bar{c} < 1$, then (1.3) has a coexistence state for parameters $(b, c) = (\bar{b}, \tilde{c})$ with $\tilde{c} \in (\bar{c}, 1)$. Also we have a coexistence state for $(b, c) = (\tilde{b}, \bar{c})$ with $\tilde{b} \in (0, \bar{b})$.*

3. Nonexistence of positive steady states

We will prove that if one of the competition coefficients is large then no positive steady states exist for system (1.1), and thus one of the semi-trivial steady states is the global attractor for the system.

Theorem 3.1. *There exists $\bar{b}^* > 0$ such that for all $b > \bar{b}^*$ and $0 \leq c \leq 1$ the system (1.1) does not admit a positive steady state.*

Proof. We will prove the result by contradiction. Suppose that we have a sequence (u_n, v_n) of solutions of (1.3), with $u_n > 0$, $v_n > 0$, corresponding to the parameters $0 \leq c_n \leq 1$ and $b_n \to \infty$. Without loss of generality, we can assume that $c_n \to \bar{c}$, with $0 \leq \bar{c} \leq 1$.

Integrating the first equation of (1.3)

$$\int_{\Omega} u_n(m(x) - u_n - b_n v_n)\, dx = 0, \tag{3.10}$$

so that

$$\int_\Omega u_n v_n\, dx = \frac{1}{b_n} \int_\Omega (m(x)u_n - u_n^2)\, dx.$$

Since by Corollary 2.7 we have that u_n, v_n are bounded, we conclude that $\int_\Omega u_n v_n\, dx \to 0$ as $n \to \infty$ and $u_n v_n \to 0$ in $L^p(\Omega)$ for all $p \geq 1$.

Using the above bound we obtain that, except possibly for a subsequence, there exists $\bar{v} \in W^{2,p}(\Omega)$ such that $v_n \to \bar{v}$. Indeed, we have that v_n satisfies

$$Mv_n + v_n(m(x) - c_n u_n - v_n) = 0 \text{ in } \Omega,\ \nabla v_n \cdot \hat{n} = 0 \text{ on } \partial\Omega,$$

and because v_n is bounded and $u_n v_n \to 0$ in $L^p(\Omega)$, we can use Sobolev's imbedding theorems and elliptic regularity estimates to conclude the convergence of a subsequence of $\{v_n\}$. Moreover, taking the limit in the above equation, we obtain that $\bar{v} \geq 0$ satisfies the equation

$$Mv + v(m - v) = 0 \text{ in } \Omega,\ \nabla v \cdot \hat{n} = 0 \text{ on } \partial\Omega,$$

and thus we have that either $\bar{v} = \theta$ or $\bar{v} = 0$. If $\bar{v} = \theta$, then for n large enough, $m - u_n - b_n v_n < 0$, which contradicts (3.10). Therefore, $\bar{v} = 0$.

Consider now $w_n = \frac{v_n}{||v_n||_\infty}$ and write system (1.3) in terms of u_n and w_n as

$$\begin{cases} Lu_n + u_n(m(x) - u_n - b_n ||v_n||_\infty w_n) = 0 \text{ in } \Omega, \\ Mw_n + w_n(m(x) - c_n u_n - ||v_n||_\infty w_n) = 0 \text{ in } \Omega, \\ \nabla \frac{u_n}{m} \cdot \hat{n} = 0,\ \nabla w_n \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases} \tag{3.11}$$

Without loss of generality, we need to consider two cases:

Case 1 $b_n ||v_n||_\infty \to \infty$ as $n \to \infty$.
Case 2 $b_n ||v_n||_\infty \to d$ as $n \to \infty$, with $d \geq 0$.

If Case 1 holds, because $||v_n||_\infty \to 0$, we can proceed as before to prove that, except possibly for a subsequence, $w_n \to \bar{w}$ in $W^{2,p}(\Omega)$ with $\bar{w}$ solution of

$$Mw + mw = 0 \text{ in } \Omega,\ \nabla w \cdot \hat{n} = 0 \text{ on } \partial\Omega.$$

If we integrate this equation on Ω we obtain that $\bar{w} \equiv 0$, contradicting the fact that $||w_n||_\infty = 1$. Therefore, Case 2 holds.

Observe that since u_n, w_n and $b_n ||v_n||_\infty$ are bounded, we have that u_n is also bounded in $W^{2,p}(\Omega)$, and as before we can conclude that up to a subsequence, $(u_n, w_n) \to (\bar{u}, \bar{w})$ with $0 \leq \bar{u} \leq m$, $\bar{w} \geq 0$ and $\bar{w} \not\equiv 0$, with $(\bar{u}, \bar{w})$ a solution of:

$$\begin{cases} Lu + u(m(x) - u - dw) = 0 \text{ in } \Omega,\ \nabla \dfrac{u}{m} \cdot \hat{n} = 0 \text{ on } \partial\Omega. \\ Mw + w(m(x) - \bar{c}u) = 0 \text{ in } \Omega,\ \nabla w \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases} \tag{3.12}$$

If $\bar{c} < 1$ then $m - \bar{c}\bar{u} > (1-\bar{c})m > 0$, thus we must have that $w \equiv 0$, which is a contradiction. Hence, $\bar{c} = 1$ and since $m - \bar{u} \geq 0$ we can integrate the second equation of (3.12) to get that $\bar{u} = m$ and as a consequence $w = 1$. Replacing $\bar{u}$, $\bar{w}$ in the first equation of (3.12), we obtain that $d = 0$.

We define $\varphi_n = m(x) - u_n$. We already proved that $\varphi_n \geq 0$ and $\varphi_n \to 0$ as $n \to \infty$. If we integrate the first equation of (3.11), we obtain by a simple computation

$$\int_\Omega u_n \varphi_n \, dx = b_n ||v_n||_\infty \int_\Omega u_n w_n \, dx,$$

whence we deduce that for n large

$$\int_\Omega \varphi_n \, dx \geq b_n ||v_n||_\infty |\Omega| \delta, \tag{3.13}$$

where $\delta = \min_{\bar{\Omega}} m(x) / \max_{\bar{\Omega}} m(x)$.

Integrating the second equation of (3.11) we find that

$$\int_\Omega w_n((1-c_n)m + c_n\varphi_n - ||v_n||_\infty w_n) \, dx = 0,$$

whence

$$\int_\Omega c_n w_n \varphi_n \, dx \leq \int_\Omega w_n((1-c_n)m + c_n\varphi_n) \, dx = ||v_n||_\infty \int_\Omega w_n^2 \, dx.$$

Because $c_n \to 1$, $w_n \to 1$, we can deduce from the last inequality that

$$\frac{1}{2} \int_\Omega \varphi_n \, dx \leq \int_\Omega c_n w_n \varphi_n \, dx \leq 2||v_n||_\infty |\Omega|, \tag{3.14}$$

for n large enough. Finally, combining (3.13) and (3.14) we obtain

$$b_n ||v_n||_\infty \leq \frac{4||v_n||_\infty}{\delta},$$

which contradicts $b_n \to \infty$. $\square$

We have a similar result when c is large.

Theorem 3.2. *There exists $\bar{c}^* > 0$ such that for all $c > \bar{c}^*$ and $0 \leq b \leq b_{cr}$ the system (1.1) does not admit a positive steady state.*

Proof. Suppose that we have a sequence (u_n, v_n) of positive solutions of (1.3) with respective parameters b_n, c_n such that $0 \leq b_n \leq b_{cr}$ and $c_n \to \infty$. Without loss of generality, we can suppose that $b_n \to \bar{b}$, with $0 \leq \bar{b} \leq b_{cr}$.

By using the same technique as in the proof of the previous theorem, we conclude the result for $\bar{b} < b_{cr}$. Suppose now that $\bar{b} = b_{cr}$, so that by the same idea we get $(u_n, v_n) \to (0, \theta)$ in $W^{2,p}(\Omega)$ and $c_n||u_n||_\infty \to 0$ as $n \to \infty$.

Consider $\varphi_n = \frac{u_n}{||u_n||_\infty}$, so that by Sobolev's embeddings and elliptic regularity we get $\varphi_n \to \bar{\varphi}$ in $W^{2,p}(\Omega)$, which is solution of the problem:

$$L\bar{\varphi} + \bar{\varphi}(m(x) - b_{cr}\theta) = 0 \text{ in } \Omega,\ \nabla\frac{\bar{\varphi}}{m} \cdot \hat{n} = 0 \text{ on } \partial\Omega,$$

and $\bar{\varphi} > 0$ by the maximum principle. On the other hand consider $w_n = v_n - \theta$, so that $w_n \le 0$ and satisfies:

$$\begin{cases} Mw_n + w_n(m - 2\theta) = w_n^2 + c_n||u_n||_\infty w_n\varphi_n + c_n||u_n||_\infty \theta\varphi_n \text{ in } \Omega \\ \nabla w_n \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

By elliptic estimates, there exists $C > 0$ independent of n, such that

$$||w_n||_{2,p} \le C(||w_n^2||_p + c_n||u_n||_\infty||w_n\varphi_n||_p + c_n||u_n||_\infty||\theta\varphi_n||_p)$$

As $w_n \to 0$ we conclude that $\xi_n = \frac{w_n}{c_n||u_n||_\infty}$ is uniformly bounded. Now write system (1.3) in terms of φ_n and ξ_n as

$$\begin{cases} L\varphi_n + \varphi_n(m(x) - b_{cr}) = (b_n - b_{cr})\theta\varphi_n + b_n c_n||u_n||_\infty\xi_n + ||u_n||_\infty\varphi_n^2 \text{ in } \Omega, \\ M\xi_n + \xi_n(m - 2\theta) = w_n\xi_n + w_n\varphi_n + \theta\varphi_n \text{ in } \Omega, \\ \nabla\frac{\varphi_n}{m} \cdot \hat{n} = 0,\ \nabla\xi_n \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

We get that, except possibly for a subsequence, $\xi_n \to \bar{\xi}$ since ξ_n is uniformly bounded. The function $\bar{\xi}$ is solution of the problem:

$$M\bar{\xi} + \bar{\xi}(m(x) - 2\theta) = \theta\bar{\varphi} \text{ in } \Omega,\ \nabla\bar{\xi} \cdot \hat{n} = 0 \text{ on } \partial\Omega,$$

and $\bar{\xi} < 0$ by the maximum principle.

If we multiply the equation of φ_n by $\frac{\bar{\varphi}}{m}$ and the equation of $\bar{\varphi}$ by $\frac{\varphi_n}{m}$, we get by integrating and subtracting that:

$$(b_n - b_{cr})\int_\Omega \frac{\varphi_n\bar{\varphi}\theta}{m} = -||u_n||_\infty\left(c_n b_n\int_\Omega \frac{\xi_n\varphi_n\bar{\varphi}}{m} + \int_\Omega \frac{\varphi_n^2\bar{\varphi}}{m}\right)$$

In this equality, the left-hand side is non-positive since $b_n \le b_{cr}$, and for n large enough the right-hand side is strictly positive, which is a contradiction. □

4. Bifurcating solutions from the semitrivial steady states

In this section we are going to characterize the positive solutions of (1.3) which bifurcate from the semitrivial solutions $(m(x), 0)$ and $(0, \theta)$. For this we will apply the Crandall–Rabinowitz Theorem directly to system (1.1) in order to obtain the bifurcating solutions, and to characterize their stability. We can do this, since we can make the change of variables $U = \frac{u}{m}$ and $V = v$ to obtain the equivalent system (2.4) which has regular Neumann boundary conditions, but is not in divergence form.

4.1. Local bifurcating solutions from $(m(x), 0)$

By Lemma 2.3, bifurcation of positive steady states from $(m(x), 0)$ can only occur when $c = 1$. We start by fixing $b > 0$ and setting the following:

$$\begin{aligned} &X = \{(w, v) \in W^{2,p}(\Omega) \times W^{2,p}(\Omega) \ / \ \nabla \tfrac{w}{m} \cdot \hat{n} = \nabla v \cdot \hat{n} = 0 \ \text{ on } \partial\Omega\}, \\ &Y = L^p(\Omega) \times L^p(\Omega), \end{aligned} \tag{4.15}$$

with $p > N$ and the map $F : X \times \mathbb{R} \to Y$ given by

$$F(u, v, c) = \begin{pmatrix} Lu + u(m - u - bv) \\ Mv + v(m - cu - v) \end{pmatrix}. \tag{4.16}$$

By definition, (u, v) is a solution of (1.3) if and only if $F(u, v, c) = 0$. Observe that $F(m, 0, c) = 0$.

To apply the Crandall–Rabinowitz local bifurcation result, we need to study $\mathrm{Ker}\big(D_{(u,v)}F(m, 0, 1)\big)$ and $\mathrm{Range}\big(D_{(u,v)}F(m, 0, 1)\big)$, which are characterized in the next lemma.

Lemma 4.1. *We have that*

$$\begin{aligned} &\mathrm{Ker}\big(D_{(u,v)}F(m, 0, 1)\big) = \langle (b\eta, 1) \rangle \ \textit{and} \\ &\mathrm{Range}\big(D_{(u,v)}F(m, 0, 1)\big) = \left\{(f, g) \in Y \ / \ \textstyle\int_\Omega g\, dx = 0\right\}, \end{aligned} \tag{4.17}$$

where $\eta < 0$ is the unique solution of

$$L\eta - m\eta = m \ \textit{in } \Omega, \quad \nabla \frac{\eta}{m} \cdot \hat{n} = 0 \ \textit{ on } \partial\Omega. \tag{4.18}$$

Proof. To simplify notation, set $\mathcal{L}_0 = D_{(u,v)}F(m, 0, 1)$. After some standard computations, we obtain that

$$\mathcal{L}_0(\varphi, \psi) = \begin{pmatrix} L\varphi + m(-\varphi - b\psi) \\ M\psi \end{pmatrix}, \tag{4.19}$$

thus, if $(\varphi, \psi) \in \mathrm{Ker}\,(\mathcal{L}_0)$ then ψ is constant and $L\varphi - m\varphi = bm\psi$, whence the characterization of $\mathrm{Ker}\,(\mathcal{L}_0)$ given in (4.17) follows.

To obtain Range $(\mathcal{L}_0)$ we need to find all $(f, g) \in Y$, such that there is $(\varphi, \psi) \in X$ for which

$$L\varphi + m(-\varphi - b\psi) = f, \text{ and } M\psi = g.$$

The second equation above is solvable if and only if $\int_\Omega g = 0$, and since $L - m$ is invertible the first equation has a unique solution once we have determined ψ. Hence, Range $(\mathcal{L}_0) = \left\{(f, g) \in Y \;/\; \int_\Omega g = 0\right\}$, which concludes the proof. □

Proposition 4.2. *There exists a neighborhood U of $((m, 0), 1)$ in $X \times \mathbb{R}$ such that the only solutions of (1.3) in U are $\{(m, 0)\} \times \mathbb{R}$ or along a smooth curve $\Gamma = \{(u(\varepsilon), v(\varepsilon), c(\varepsilon)) : \varepsilon \in (-\varepsilon_0, \varepsilon_0)\}$ for some $\varepsilon_0 > 0$ where $u = m + w(\varepsilon)$, $v = v(\varepsilon)$ with*

$$w(\varepsilon) = \varepsilon b\eta + \varepsilon\tilde{w}(\varepsilon), \quad v = \varepsilon + \varepsilon\tilde{v}(\varepsilon) \text{ and } c = 1 + \gamma(\varepsilon),$$

and $\tilde{w}(0) = \tilde{v}(0) = 0$ and $\gamma(0) = 0$.

Proof. Since

$$\operatorname{Ker}\left(D_{(u,v)}F(m, 0, 1)\right) = \langle (b\eta, 1)\rangle,$$

to apply the Crandall–Rabinowitz Theorem we just need to check that

$$D^2_{((u,v),c)}F(m, 0, 1)(b\eta, 1) \notin \operatorname{Range}\left(D_{(u,v)}F(m, 0, 1)\right).$$

After a simple computation, we obtain that $D^2_{((u,v),c)}F(m, 0, 1)(b\eta, 1) = (0, -m)$, and since $\int_\Omega -m(x) < 0$ we obtain the desired result. □

We define the positive and negative branch given respectively by:

$$\begin{aligned} \Gamma^+ &= \{(u(\varepsilon), v(\varepsilon), c(\varepsilon)) : \varepsilon \in (0, \varepsilon_0)\} \\ \Gamma^- &= \{(u(\varepsilon), v(\varepsilon), c(\varepsilon)) : \varepsilon \in (-\varepsilon_0, 0)\} \end{aligned} \tag{4.20}$$

As we are interested in positive solutions, from now we will only focus in the positive branch Γ^+.

The following proposition establishes the stability properties of the bifurcating solutions of (1.3).

Proposition 4.3. *Set*

$$b^* = \frac{|\Omega|}{\int_\Omega -\eta\, dx}, \tag{4.21}$$

where η is defined in (4.18). The bifurcating positive solutions $(m + w(\varepsilon), v(\varepsilon))$ of (1.3) for $c = 1 + \gamma(\varepsilon)$ as given in Proposition 4.2, are unstable for $b > b^*$, and locally asymptotically stable for $b < b^*$. Also $b^* > 1$.

Proof. By the principle of exchanged stability, we just need to obtain the direction of the bifurcation branch according to the parameter γ. From this result and Lemma 2.3, we will have that the positive bifurcating solutions are unstable whenever for $\varepsilon > 0$ we have $\gamma(\varepsilon) > 0$, and locally asymptotically stable when for $\varepsilon > 0$ it holds that $\gamma(\varepsilon) < 0$. Replacing $v(\varepsilon) = \varepsilon + \varepsilon\tilde{v}(\varepsilon)$ and $u = m + \varepsilon b\eta + \varepsilon\tilde{w}(\varepsilon)$ in the corresponding equation of (1.3), and then dividing by ε we obtain:

$$M\tilde{v}(\varepsilon) + [-\gamma(\varepsilon)m - (1+\gamma(\varepsilon))(\varepsilon b\eta + \tilde{w}(\varepsilon)) - \varepsilon - \varepsilon\tilde{v}(\varepsilon)](1+\tilde{v}(\varepsilon)) = 0 \text{ in } \Omega.$$

Replacing $\tilde{v} = \bar{v}_1 + \varepsilon\bar{v}(\varepsilon)$, $\tilde{w} = \bar{w}_1 + \varepsilon\bar{w}(\varepsilon)$ and $\gamma(\varepsilon) = \varepsilon\gamma_1 + \varepsilon\bar{\gamma}(\varepsilon)$ in the equation above, and considering the highest order term we have that

$$M\bar{v}_1 + [-\gamma_1 m - b\eta - 1] = 0 \text{ in } \Omega.$$

Since $\frac{\partial\bar{v}_1}{\partial\hat{n}} = 0$ on $\partial\Omega$, we can integrate the equation above to obtain that

$$\int_\Omega \gamma_1 m - b\eta - 1\, dx = 0,$$

whence

$$\gamma_1 = -\frac{\int_\Omega (b\eta + 1)\, dx}{\int_\Omega m\, dx}.$$

Thus, if we set b^* as in (4.21) we have that: if $b > b^*$, $\gamma_1 > 0$ and then $c = 1 + \gamma(\varepsilon) > 1$, while if $b < b^*$, $\gamma_1 < 0$ and then $c = 1 + \gamma(\varepsilon) < 1$, for all $\varepsilon > 0$, as claimed.

Finally, let us prove that $b^* > 1$. Observe that multiplying the equation (4.18) by $\frac{\eta}{m}$ and integrating over Ω, we obtain

$$-\int_\Omega \alpha(x)\left|\nabla\frac{\eta}{m}\right|^2 dx - \int_\Omega \eta^2\, dx = \int_\Omega \eta\, dx,$$

thus $\int_\Omega \eta^2\, dx < \int_\Omega -\eta\, dx$, whence $\int_\Omega \eta^2\, dx < \left(\int_\Omega \eta^2\, dx\right)^{\frac{1}{2}} |\Omega|^{\frac{1}{2}}$, and then

$$\int_\Omega \eta^2\, dx < |\Omega|.$$

On the other hand,

$$b^* = \frac{|\Omega|}{\int_\Omega -\eta\, dx} > \frac{|\Omega|}{\left(\int_\Omega \eta^2\, dx\right)^{\frac{1}{2}} |\Omega|^{\frac{1}{2}}},$$

and using the previous inequality, we conclude that $b^* > \frac{|\Omega|^{\frac{1}{2}}}{\left(\int_\Omega \eta^2\, dx\right)^{\frac{1}{2}}} > 1$. □

4.2. Local bifurcating solutions from $(0, \theta)$

To study the bifurcation branch from $(0, \theta)$ we proceed as above. By Lemma 2.4 such bifurcation of positive steady states can only occur when $b = b_{cr}$. We set some new variables

$$v = \theta + z, b = b_{cr} + \delta, \text{ with } z \sim 0, \; \delta \sim 0. \tag{4.22}$$

We define X and Y as in (4.15), and the map $G : X \times \mathbb{R} \to Y$ as

$$G(u, z, \delta) = \begin{pmatrix} Lu + u(m - u - (b_{cr} + \delta)(\theta + z)) \\ Mz + \theta(-z - cu) + z(m - \theta - z - cu) \end{pmatrix}. \tag{4.23}$$

By definition, (u, v) is a solution of (1.3) if and only if $G(u, z, \delta) = 0$ with z, δ as in (4.22). As before, to establish the existence of a bifurcating branch we need to characterize $\mathrm{Ker}\left(D_{(u,z)}G(0, 0, 0)\right)$ and $\mathrm{Range}\left(D_{(u,z)}G(0, 0, 0)\right)$.

Lemma 4.4. *We have that*

$$\begin{aligned} &\mathrm{Ker}\left(D_{(u,z)}G(0, 0, 0)\right) = \langle(\varphi_0, \psi_0)\rangle \;\; \textit{and} \\ &\mathrm{Range}\left(D_{(u,z)}G(0, 0, 0)\right) = \left\{(f, g) \in Y \;/\; \textstyle\int_\Omega \frac{\varphi_0}{m} f \, dx = 0\right\}, \end{aligned} \tag{4.24}$$

where $\varphi_0 > 0$ *is a positive solution of*

$$L\varphi_0 + (m - b_{cr}\theta)\varphi_0 = 0 \textit{ in } \Omega, \;\; \nabla \frac{\varphi_0}{m} \cdot \hat{n} = 0 \;\textit{ on } \partial\Omega, \tag{4.25}$$

and $\psi_0 < 0$ *is the unique solution of*

$$M\psi_0 + \psi_0(m - 2\theta) = c\theta\varphi_0 \textit{ in } \Omega, \;\; \nabla\psi_0 \cdot \hat{n} = 0 \;\textit{ on } \partial\Omega. \tag{4.26}$$

Proof. After some straightforward computation we have that

$$D_{(u,z)}G(0, 0, \delta)(\varphi, \psi) = \begin{pmatrix} L\varphi + \varphi(m - (b_{cr} + \delta)\theta) \\ M\psi + (m - 2\theta)\psi - c\theta\varphi \end{pmatrix}. \tag{4.27}$$

Since the equation

$$M\psi + (m - 2\theta)\psi = f \text{ in } \Omega, \;\; \nabla\psi \cdot \hat{n} = 0 \;\text{ on } \partial\Omega,$$

is solvable for any $f \in C^{0,\mu}(\bar{\Omega})$, we have that (4.24) follows, with φ_0, ψ_0 defined as in (4.25), (4.26). □

Observe that we can write $\psi_0 = c\xi$ where

$$M\xi + \xi(m - 2\theta) = \theta\varphi_0 \text{ in } \Omega, \;\; \nabla\xi \cdot \hat{n} = 0 \;\text{ on } \partial\Omega. \tag{4.28}$$

Proposition 4.5. *There exists a neighborhood U of $((0,\theta), b_{cr})$ in $X \times \mathbb{R}$, such that only positive solutions of (1.3) in U are $\{(0,\theta)\} \times \mathbb{R}$ or along a smooth curve $\Gamma = \{u(\varepsilon), v(\varepsilon), b(\varepsilon)) : \varepsilon \in (-\varepsilon_0, \varepsilon_0)\}$ for some $\varepsilon_0 > 0$ with $u = \varepsilon\varphi_0 + \varepsilon\tilde{w}(\varepsilon)$, $v = \theta + \varepsilon\psi_0 + \varepsilon\tilde{z}(\varepsilon)$, $b = b_{cr} + \delta(\varepsilon)$, with $\tilde{w}(0) = \tilde{z}(0) = 0$ and $\delta(0) = 0$.*

Proof. By Lemma 4.4 to apply the Crandall–Rabinowitz Theorem we just need to check that

$$D^2_{((w,v),\delta)} G(0,0,0)(\varphi_0, \psi_0) \notin \text{Range}\left(D_{(w,v)} G(0,0,0)\right).$$

After a simple computation, we obtain that

$$D^2_{((w,v),\delta)} G(0,0,0)(\varphi_0, \psi_0) = (-\varphi_0\theta, 0),$$

and $(-\varphi_0\theta, 0) \notin \text{Range}\left(D_{(w,v)} G(0,0,0)\right)$ since

$$\int_\Omega \frac{\varphi_0}{m}(-\varphi_0\theta)\, dx = \int_\Omega -\frac{\varphi_0^2\theta}{m}\, dx < 0. \quad \square$$

Proposition 4.6. *Set*

$$c^* = -\frac{\int_\Omega \frac{\varphi_0^3}{m}\, dx}{b_{cr} \int_\Omega \frac{\varphi_0^2 \xi}{m}\, dx}, \tag{4.29}$$

where φ_0 and ξ are as defined in (4.25) and (4.28) respectively. The bifurcating solutions $(\varepsilon\varphi_0 + \varepsilon\tilde{w}(\varepsilon), \theta + \varepsilon\psi_0 + \varepsilon\tilde{z}(\varepsilon))$ of (1.1) for $b = b_{cr} + \delta(\varepsilon)$ as given in Proposition 4.5, are unstable for $c > c^*$, and locally asymptotically stable for $c < c^*$.

Proof. As in the proof of Proposition 4.3, we just need to obtain the direction of the bifurcation branch according to the parameter δ. From Lemma 2.4 we will have that the positive bifurcating solutions are unstable whenever for $\varepsilon > 0$ we have $\delta(\varepsilon) > 0$, and locally asymptotically stable when for $\varepsilon > 0$ it holds that $\delta(\varepsilon) < 0$. To determine the sign of $\delta(\varepsilon)$ we consider a first order expansion of $\delta(\varepsilon)$, $\tilde{w}(\varepsilon)$ and $\tilde{z}(\varepsilon)$:

$$\delta(\varepsilon) = \varepsilon\delta_1 + \varepsilon\hat{\delta}(\varepsilon), \;\; \tilde{w}(\varepsilon) = \varepsilon w_1 + \varepsilon\hat{w}(\varepsilon), \;\; \tilde{z}(\varepsilon) = \varepsilon z_1 + \varepsilon\hat{z}(\varepsilon),$$

with $\hat{\delta}(0) = 0$, $\hat{w}(0) = 0$ and $\hat{z}(0) = 0$. Setting $u = \varepsilon\varphi_0 + \varepsilon^2(w_1 + \hat{w}(\varepsilon))$, $v = \theta + \varepsilon\psi_0 + \varepsilon^2(z_1 + \hat{z}(\varepsilon))$ and $b = b_{cr} + \varepsilon(\delta_1 + \hat{\delta}(\varepsilon))$ in (1.3), and then computing the ε^2 terms, we obtain that (w_1, z_1) satisfy:

$$\begin{cases} Lw_1 + w_1(m - b_{cr}\theta) = \varphi_0(\varphi_0 + \delta_1\theta + b_{cr}\psi_0) \text{ in } \Omega, \\ Mz_1 + z_1(m - 2\theta) - c\theta w_1 = \psi_0(\psi_0 + c\varphi_0) \text{ in } \Omega, \\ \nabla\frac{w_1}{m} \cdot \hat{n} = \nabla z_1 \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases} \tag{4.30}$$

Thus, using (4.27) we can write this system as

$$D_{(u,z)}G(0,0,0)(w_1,z_1)=\begin{pmatrix}\varphi_0(\varphi_0+\delta_1\theta+b_{cr}\psi_0)\\ \psi_0(\psi_0+c\varphi_0)\end{pmatrix},$$

so, the right hand side of the above equation must belong to the range of $D_{(u,z)}G(0,0,0)$, which using (4.24) is equivalent to having δ_1 satisfy

$$\int_\Omega \frac{\varphi_0}{m}(\varphi_0(\varphi_0+\delta_1\theta+b_{cr}\psi_0)\,dx=0,$$

so that by replacing ψ_0 with $c\xi$ we obtain that

$$\delta_1\int_\Omega \frac{\varphi_0^2\theta}{m}\,dx=-\left(\int_\Omega \frac{\varphi_0^3}{m}\,dx+cb_{cr}\int_\Omega \frac{\varphi_0^2\xi}{m}\,dx\right).$$

Since $\int_\Omega \frac{\varphi_0^3}{m}\,dx>0$ and $\int_\Omega \varphi_0^2\xi\,dx<0$ there exists a unique c^* given by (4.29) for which δ_1 changes sign. Indeed, for $c>c^*$ we have that $\delta_1>0$ and then $\delta(\varepsilon)>0$ for $\varepsilon>0$, while for $c<c^*$ we have that $\delta_1>0$ and so $\delta(\varepsilon)<0$ for $\varepsilon>0$. This concludes the proof. □

4.3. Global bifurcation

Now, we will prove a result concerning the continuation of the local bifurcation branch from $(m,0)$.

For this section consider $V=\{(u,v,c)\in X\times\mathbb{R}\colon u>0, c>0\}$ and $b>0$ fixed. From [8] section 6, we have the following proposition. The best current version of the underlying global bifurcation theory can be found in [15].

Proposition 4.7. *Let Γ^+,Γ^- be the two branches of solutions defined in (4.20). Then Γ^+ and Γ^- are contained in $\mathcal{C}$, where $\mathcal{C}$ is a connected component of $\bar{S}$ with $S=\{(u,v,c)\in V\colon F(u,v,c)=0, (u,v)\neq(m,0)\}$. Let $\mathcal{C}^+$ be the connected component of $\mathcal{C}\backslash\Gamma^-$ containing Γ^+. Then $\mathcal{C}^+$ satisfies one of the following options:*

(i) It is not compact in V.
(ii) It contains a point $(m,0,c)$ with $c\neq 1$.
(iii) It contains a point (u,v,c) where $(u,v)\neq(m,0)$ and $(u,v)\in Z$, where Z is any complementary space of $\langle(b\eta,1)\rangle$.

We must determine which of the options holds for $\mathcal{C}^+$. First, we need the following lemmas.

Lemma 4.8. *For all c we have that $(0,0,c)\notin\bar{S}$.*

Proof. Suppose there exists a sequence (u_n,v_n,c_n) in V converging to $(0,0,c)$ in $X\times\mathbb{R}$, so that for n large enough we have $u_n(m-u_n-bv_n)>0$. On the other hand, by integrating the first equation of (1.3) we get that $\int_\Omega u_n(m-u_n-bv_n)=0$, which is a contradiction. □

Lemma 4.9. *Let* $(u, v, c) \in \mathcal{C}^+$ *be such that* $\min_{\bar{\Omega}} v = 0$*, then* $(u, v) = (m, 0)$*.*

Proof. The function v satisfies:

$$\begin{cases} Mv + v(m - u - cv) = 0 \text{ in } \Omega, \\ \nabla v \cdot \hat{n} = 0 \ \text{ on } \partial\Omega. \end{cases}$$

By maximum principle we conclude $v \equiv 0$ and u satisfies:

$$\begin{cases} Lu - (m - u)u = 0 \text{ in } \Omega, \\ \nabla \frac{u}{m} \cdot \hat{n} = 0 \ \text{ on } \partial\Omega. \end{cases}$$

As $u \geq 0$ we conclude that $u = m$ or $u = 0$. By Lemma 4.8 we get $u = m$. □

Proposition 4.10. *The connected component* $\mathcal{C}^+$ *is not compact in* V*. Moreover, if* $(u, v, c) \in \mathcal{C}^+$ *then* $v \geq 0$*.*

Proof. By Proposition 4.7 we must rule out the options (ii) and (iii).

In $X \times \mathbb{R}$ consider the sets A, B given by:

$$A = \{(u, v, c) \in \overline{\mathcal{C}^+} : \min_{\bar{\Omega}} v > 0\}, \ B = \{(u, v, c) \in \overline{\mathcal{C}^+} : \min_{\bar{\Omega}} v < 0\}$$

As bifurcation of positive steady states from $(m(x), 0)$ only occurs when $c = 1$, we conclude that $\bar{A} = A \cup \{(m, 0, 1)\}$ and $\bar{B}$ contains B plus possible solutions of the form $(m, 0, c)$ with $c \neq 1$ by Lemma 4.9. If both $\bar{A}$, $\bar{B}$ were non-empty then $\overline{\mathcal{C}^+}$ would be the union of two disjoint closed sets, contradicting the connectedness of $\overline{\mathcal{C}^+}$. As $\bar{A}$ contains Γ^+, we conclude that $\bar{B}$ is empty. This rules out option (ii) and proves positivity in the variable v.

In order to rule out (iii), choose as complement of $\langle (b\eta, 1) \rangle$ the space given by $Z = \{(u, v) \in X : \int_\Omega v = 0\}$ and suppose we have a solution (u, v, c) as asserted in (iii). In particular, we have that $\min_{\bar{\Omega}} v \leq 0$. Take $(u_0, v_0, c_0) \in \Gamma^+$ so that $\min_{\bar{\Omega}} v_0 > 0$, then by the intermediate value theorem we get that there exists $(u_1, v_1, c_1) \in \mathcal{C}^+$ such that $\min_{\bar{\Omega}} v_1 = 0$, so by Lemma 4.9 we get $(u_1, v_1) = (m, 0)$. Notice that $c_1 \neq 1$ because $\mathcal{C}^+ \setminus \{(m, 0, 1)\}$ is connected, as the only solutions in $\mathcal{C}^+$ close enough to $(m, 0, 1)$ are in Γ^+ and we can restrict to $\mathcal{C}^+ \setminus \{(m, 0, 1)\}$. Therefore we conclude that option (iii) implies option (ii) that was ruled out. □

By Corollary 2.7 the set of positive steady states is uniformly bounded in X. Using Sobolev embeddings and elliptic regularity, we conclude that non-compactness of $\mathcal{C}^+$ in V means that $u \to 0$, $c \to 0$ or $c \to \infty$. We must determine which of the cases occurs in terms of parameter b.

We start by studying the case when $u \to 0$:

Lemma 4.11. *Let* (u_n, v_n, c_n) *be a sequence in* $\mathcal{C}^+$ *such that* $u_n \to 0$ *in* $W^{2,p}(\Omega)$ *and* c_n *is bounded, then* $v_n \to \theta$ *in* $W^{2,p}(\Omega)$ *and* $b = b_{cr}$*.*

Proof. Without loss of generality we can assume c_n converges to some $\bar{c}$. Consider $\varphi_n = \frac{u_n}{||u_n||_\infty}$ and write system (1.3) in terms of φ_n and v_n as:

$$\begin{cases} L\varphi_n + \varphi_n(m(x) - u_n - bv_n) = 0 \text{ in } \Omega, \\ Mv_n + v_n(m(x) - c_n u_n - v_n) = 0 \ \text{ in } \Omega, \\ \nabla \frac{\varphi_n}{m} \cdot \hat{n} = 0, \ \nabla v_n \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

By Sobolev embeddings and elliptic regularity we can assume there exists $(\bar{\varphi}, \bar{v}) \in X$ such that $(\varphi_n, v_n) \to (\bar{\varphi}, \bar{v})$. Note that $\bar{v}$ satisfies:

$$\begin{cases} M\bar{v} + \bar{v}(m(x) - \bar{v}) = 0 \text{ in } \Omega, \\ \nabla \bar{v} \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

By Lemma 4.8 we get $\bar{v} = \theta$, so $\bar{\varphi}$ satisfies:

$$\begin{cases} L\bar{\varphi} + \bar{\varphi}(m(x) - b\theta) = 0 \text{ in } \Omega, \\ \nabla \frac{\bar{\varphi}}{m} \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases} \tag{4.31}$$

We conclude that $\bar{\varphi}$ is a positive eigenfunction of problem (2.7) where the corresponding eigenvalue equals zero. This implies $b = b_{cr}$. □

Proposition 4.12. *Consider $b = b_{cr}$ and suppose there exists a sequence (u_n, v_n, c_n) in $\mathcal{C}^+$ such that $u_n \to 0$. Then $v_n \to \theta$ and $c_n \to c^*$, where c^* is the value defined in (4.29).*

Proof. By Theorem 3.2 we get the sequence c_n must be bounded and without loss of generality we can suppose $c_n \to \bar{c}$, for some $\bar{c} \geq 0$. Let $\varphi_n = \frac{u_n}{||u_n||_\infty}$. Using the same arguments as in the proof of Lemma 4.11 we get $(\varphi_n, v_n) \to (\bar{\varphi}, \theta)$ in X, where $\bar{\varphi}$ is solution of (4.31) with $\bar{b} = b_{cr}$ and $||\bar{\varphi}||_\infty = 1$.

Now define w_n so that $v_n = \theta + w_n$, so that the equation of φ_n may be written as:

$$\begin{cases} L\varphi_n + \varphi_n(m(x) - b_{cr}\theta)\varphi_n = u_n\varphi_n + b_{cr}w_n\varphi_n \text{ in } \Omega, \\ \nabla \frac{\varphi_n}{m} \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

If we multiply this equation by $\frac{\bar{\varphi}}{m}$ and equation (4.31) by $\frac{\varphi_n}{m}$, we get by subtracting and integration by parts that:

$$\int_\Omega \frac{u_n \varphi_n \bar{\varphi}}{m} dx + b_{cr} \int_\Omega \frac{w_n \varphi_n \bar{\varphi}}{m} dx = 0. \tag{4.32}$$

Next, we rewrite the equation of v_n in terms of w_n as:

$$\begin{cases} Mw_n + (m - 2\theta)w_n = w_n^2 + c_n u_n \theta + c_n u_n w_n \text{ in } \Omega, \\ \nabla w_n \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

Then there exists $C > 0$, independent of n such that

$$||w_n||_{2,p} \leq C(||w_n^2||_p + c_n||u_n\theta||_p + c_n||u_n w_n||_p).$$

Using this estimate and the fact that $(u_n, w_n) \to (0, 0)$ in X, we get $\psi_n = \frac{w_n}{||u_n||_\infty}$ is bounded uniformly. Also ψ_n satisfies the equation:

$$\begin{cases} M\psi_n + (m - 2\theta)\psi_n = \psi_n w_n + c_n \varphi_n \theta + c_n u_n \psi_n \text{ in } \Omega, \\ \nabla \psi_n \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

By Sobolev embeddings and elliptic regularity argument we can suppose that $\psi_n \to \bar{\psi}$ in $W^{2,p}(\Omega)$, where $\bar{\psi}$ is solution of the problem:

$$\begin{cases} M\bar{\psi} + (m - 2\theta)\bar{\psi} = \bar{c}\bar{\varphi}\theta \text{ in } \Omega, \\ \nabla \bar{\psi} \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

Therefore $\bar{\psi} = \bar{c}\xi$, where $\xi < 0$ is solution of the equation (4.28). Finally, dividing equality (4.32) by $||u_n||_\infty$ and taking limit we get:

$$\int_\Omega \frac{\bar{\varphi}^3}{m} dx + b_{cr}\bar{c} \int_\Omega \frac{\xi\bar{\varphi}^2}{m} dx = 0.$$

So we obtain $\bar{c} = c^*$ as defined in (4.29). $\square$

Now, we must study the case when $c \to 0$.

Proposition 4.13. *Suppose there exists a sequence (u_n, v_n, c_n) in $\mathcal{C}^+$ such that $c_n \to 0$. Then $b < b_{cr}$, $v_n \to \theta$ and $u_n \to \bar{u}$ where $\bar{u}$ is the unique positive solution of:*

$$\begin{cases} L\bar{u} + (m - b\theta - \bar{u})\bar{u} = 0 \textit{ in } \Omega, \\ \nabla \frac{\bar{u}}{m} \cdot \hat{n} = 0 \textit{ on } \partial\Omega. \end{cases} \tag{4.33}$$

Proof. By Sobolev embeddings and elliptic regularity we can suppose that $(u_n, v_n) \to (\bar{u}, \bar{v})$ in X, with $(\bar{u}, \bar{v})$ satisfying that:

$$\begin{cases} L\bar{u} + \bar{u}(m - \bar{u} - b\bar{v}) = 0 \text{ in } \Omega, \\ M\bar{v} + \bar{v}(m - \bar{v}) = 0 = 0 \ \text{ in } \Omega, \\ \nabla \frac{\bar{u}}{m} \cdot \hat{n} = 0, \ \nabla \bar{v} \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

From the second equation of this system we get $\bar{v} = 0$ or $\bar{v} = \theta$. If $\bar{v} = 0$ we have $\bar{u} = m$ by Lemma 4.8, so this implies that $(m, 0, 0) \in \mathcal{C}^+$, which contradicts that option (ii) in Proposition 4.7 does not hold. Therefore, we have $\bar{v} = \theta$.

Observe that equation (4.33) has a positive solution if and only if $b < b_{cr}$. If $\bar{u} = 0$ then $b = b_{cr}$ by Lemma 4.11 and $c_n \to c^*$ by Proposition 4.12, which is a contradiction. Therefore $\bar{u}$ must be a non-trivial solution and necessarily $b < b_{cr}$. $\square$

Finally we study the case when $c \to \infty$.

Proposition 4.14. *Suppose there exists a sequence (u_n, v_n, c_n) in $\mathcal{C}^+$ such that $c_n \to \infty$, then $b > b_{cr}$ and $u_n \to 0$.*

Proof. By Theorem 3.2 we get that $b > b_{cr}$. On the other hand, (u_n, v_n) satisfies the system:

$$\begin{cases} Lu_n + u_n(m(x) - u_n - bv_n) = 0 \text{ in } \Omega, \\ Mv_n + v_n(m(x) - c_n u_n - v_n) = 0 \ \text{ in } \Omega, \\ \nabla \frac{u_n}{m} \cdot \hat{n} = 0, \ \nabla v_n \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases}$$

We get by integrating the second equation that $\int_\Omega u_n v_n \to 0$. Using Sobolev embeddings and regularity theory we can suppose that $u_n \to \bar{u}$ in $W^{2,p}(\Omega)$, where $\bar{u}$ is solution of the equation:

$$\begin{cases} L\bar{u} + \bar{u}(m(x) - \bar{u}) = 0 \text{ in } \Omega, \\ \nabla \frac{\bar{u}}{m} \cdot \hat{n} = 0, \text{ on } \partial\Omega. \end{cases}$$

Then we have $\bar{u} = 0$ or $\bar{u} = m$. If $\bar{u} = m$, then for n large enough we have that $v_n(m - c_n u_n - v_n) < 0$ and on the other hand, by integrating the equation of v_n we get $\int_\Omega v_n(m - c_n u_n - v_n) = 0$, which is a contradiction and therefore $\bar{u} = 0$. □

Respecting the convergence of v_n, we have following result:

Proposition 4.15. *Under the same hypothesis of previous proposition, the sequence $c_n u_n$ is uniformly bounded. Consider $\varphi_n = \frac{u_n}{||u_n||_\infty}$ and $d \in \mathbb{R}$ a limit point of $c_n||u_n||_\infty$. Then $d > 0$ and the sequence (φ_n, v_n) has a limit point $(\bar{\varphi}, \bar{v})$ in X, which satisfies the system:*

$$\begin{cases} L\bar{\varphi} + \bar{\varphi}(m(x) - b\bar{v}) = 0 \textit{ in } \Omega, \\ M\bar{v} + \bar{v}(m(x) - \bar{v} - d\bar{\varphi}) = 0 \ \textit{ in } \Omega, \\ \nabla \frac{\bar{\varphi}}{m} \cdot \hat{n} = 0, \ \nabla \bar{v} \cdot \hat{n} = 0 \textit{ on } \partial\Omega. \end{cases} \tag{4.34}$$

Proof. Observe that (φ_n, v_n) satisfies the system:

$$\begin{cases} L\varphi_n + \varphi_n(m(x) - ||u_n||_\infty \varphi_n - bv_n) = 0 \text{ in } \Omega, \\ Mv_n + v_n(m(x) - v_n - c_n||u_n||_\infty \varphi_n) = 0 \ \text{ in } \Omega, \\ \nabla \frac{\varphi_n}{m} \cdot \hat{n} = 0, \ \nabla v_n \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases} \tag{4.35}$$

By Sobolev embeddings and elliptic regularity we observe that up to a subsequence $\varphi_n \to \bar{\varphi}$ in $W^{2,p}(\Omega)$. Suppose that $c_n||u_n||_\infty \to \infty$ then by integrating the equation of v_n, we get that $\int_\Omega \varphi_n v_n \to 0$. This implies that $L\bar{\varphi} + m\bar{\varphi} = 0$ and $\int_\Omega m\bar{\varphi} = 0$, which is a contradiction because $\bar{\varphi} \geq 0$ and $||\bar{\varphi}||_\infty = 1$. Hence, the sequence $c_n u_n$ is uniformly bounded and v_n has a limit point $\bar{v}$ in $W^{2,p}(\Omega)$.

Let d be a limit point of the $c_n||u_n||_\infty$, then $(\bar{\varphi}, \bar{v})$ satisfies the system (4.34). If $d = 0$ we get by Lemma 4.8 that $\bar{v} = \theta$ since $u_n \to 0$. Then by the equation of $\bar{\varphi}$ we get $b = b_{cr}$, which is a contradiction and therefore $d > 0$. □

In the case when $c \to \infty$, we might have more than one limit for the sequence v_n.

From the results of this section, we have proved the following theorem:

Theorem 4.16. *For the connected component $\mathcal{C}^+$, the following assertions hold:*

(i) $b = b_{cr}$ *if and only if the case* $u \to 0$ *holds and* c *remains bounded in* $\mathcal{C}^+$*. In this case* $\overline{\mathcal{C}^+} = \mathcal{C}^+ \cup \{(0, \theta, c^*)\}$*, in other words* $(m, 0, 1)$ *connects with the equilibrium* $(0, \theta, c)$ *only at* $c = c^*$.
(ii) $b < b_{cr}$ *if and only if the case* $c \to 0$ *holds. In this case* $\overline{\mathcal{C}^+} = \mathcal{C}^+ \cup \{(\bar{u}, \theta, 0)\}$*, where* $\bar{u}$ *is the unique positive solution of equation* (4.33).
(iii) $b > b_{cr}$ *if and only if the case* $c \to \infty$ *holds. In this case we have also the case* $u \to 0$.

For the parameter c fixed, we have the corresponding results for the global bifurcation from $(0, \theta, b_{cr})$, by studying the functional G defined in (4.23).

Theorem 4.17. *Let* $\mathcal{B}^+$ *be the connected component containing the branch of positive solutions* (u, v, b) *bifurcating from* $(0, \theta, b_{cr})$ *and excluding the negative ones. The following assertions hold:*

(i) $c = 1$ *if and only if the case* $v \to 0$ *holds and* b *remains bounded in* $\mathcal{B}^+$*. In this case* $\overline{\mathcal{B}^+} = \mathcal{B}^+ \cup \{(m, 0, b^*)\}$ *with* b^* *defined in* (4.21)*. In other words* $(0, \theta, b_{cr})$ *connects with the equilibrium* $(m, 0, b)$ *only at* $b = b^*$.
(ii) $c < 1$ *if and only if the case* $b \to 0$ *holds. In this case* $\overline{\mathcal{B}^+} = \mathcal{B}^+ \cup \{(m, \bar{v}, 0)\}$*, where* $\bar{v}$ *is the unique positive solution of the problem.*

$$\begin{cases} M\bar{v} + ((1-c)m - \bar{v})\bar{v} = 0 \text{ in } \Omega, \\ \nabla \bar{v} \cdot \hat{n} = 0 \text{ on } \partial\Omega. \end{cases} \tag{4.36}$$

(iii) $c > 1$ *if and only if the case* $b \to \infty$ *holds. In this case we have also the case* $v \to 0$.

5. Existence of multiple positive steady states

The key to providing examples for which equation (1.1) exhibits at least two positive steady state solutions is to construct bifurcating solutions from $(m, 0)$ which are unstable or locally asymptotically stable, in parameter regions where $(0, \theta)$ shares the same stability properties. Since these solutions are ordered we can conclude the existence of a third steady state lying strictly between those, using a similar result as Proposition 2.2. To achieve this, it is key to estimate b^* and b_{cr}, which we will be able to do in certain situations. We consider $\alpha(x) = \mu\alpha_0(x)$ and $\beta(x) = \nu\beta_0(x)$, where μ, ν are positive parameters, yielding

$$Lu = \mu\nabla \cdot \alpha_0(x)\nabla \frac{u}{m} \text{ and } Mv = \nu\nabla \cdot \beta_0(x)\nabla v.$$

We define $\theta(\nu)$ and $\eta(\mu)$ as the corresponding solutions of (2.5) and (4.18) respectively. The coefficient $b^*(\mu)$ defined in (4.21) is given by

$$b^*(\mu) = -\frac{|\Omega|}{\int_\Omega \eta(\mu)\, dx} \tag{5.37}$$

while the coefficient $b_{cr}(\mu,\nu)$ can be written as

$$b_{cr}(\mu,\nu)=\sup_{\varphi\in W^{1,2}(\Omega)\setminus\{0\}}\left[\frac{-\mu\int_\Omega \alpha_0(x)|\nabla\varphi|^2\,dx+\int_\Omega m^2\varphi^2\,dx}{\int_\Omega m\theta(\nu)\varphi^2\,dx}\right]. \tag{5.38}$$

5.1. Existence of multiple solutions when $\mu\sim 0$ and $\nu\sim\infty$

In this subsection we will study $b^*(\mu)$ and $b_{cr}(\mu,\nu)$ in this case. For that we need to state the behavior of $\theta(\nu)$ and $\eta(\mu)$.

Lemma 5.1. *Let $\eta(\mu)$ be the solution of*

$$\mu\nabla\cdot\alpha_0(x)\nabla\frac{\eta}{m}-m\eta=m,\ \text{in }\Omega,\ \nabla\frac{\eta}{m}\cdot\hat{n}=0\ \text{on }\partial\Omega. \tag{5.39}$$

Then $\eta(\mu)\to -1$ uniformly as $\mu\to 0$.

The lemma can be proved using some standard comparison arguments by constructing appropriate sub-super solutions. As a direct corollary of this lemma, we obtain the behavior of $b^*(\mu)$.

Corollary 5.2. *We have that* $\lim_{\mu\to 0} b^*(\mu)=1$.

Next, we establish the behavior of $\theta(\nu)$ as the diffusion coefficient $\nu\to\infty$.

Lemma 5.3. *We have that $\theta(\nu)\to\frac{1}{|\Omega|}\int_\Omega m(x)\,dx$ in $C^{2,\lambda}(\bar{\Omega})$ as $\nu\to\infty$.*

Proof. We have that $\theta(\nu)$ satisfies

$$\nu\nabla\cdot\beta_0(x)\nabla\theta(\nu)+\theta(\nu)(m(x)-\theta(\nu))=0\ \text{ in }\Omega,\quad \nabla\theta(\nu)\cdot\hat{n}=0\ \text{ on }\partial\Omega. \tag{5.40}$$

By the maximum principle we have that $||\theta(\nu)||_\infty\le\max_{x\in\bar{\Omega}}m(x)$. Then, multiplying (5.40) by $\theta(\nu)$ and integrating in Ω we get

$$\int_\Omega \beta_0(x)|\nabla\theta(\nu)|^2\,dx\to 0 \text{ as } \nu\to\infty.$$

Then, there exists a constant C such that, except possibly for a subsequence $\theta(\nu)\to C$ in $W^{1,2}(\bar{\Omega})$. By elliptic regularity estimates and Sobolev imbedding theorem, we also have that the convergence is in $C^{2,\lambda}(\bar{\Omega})$. Integrating (5.40) we have that

$$\int_\Omega (m-\theta(\nu))\theta(\nu)\,dx=0. \tag{5.41}$$

Thus taking the limit we get that $\int_\Omega (m-C)C\,dx = 0$, so either $C=0$ or $C = \frac{1}{|\Omega|}\int_\Omega m(x)\,dx$. The case $C=0$ cannot happen since in this case

$$(m-\theta(\nu))\theta(\nu) > 0 \text{ for all large } \nu,$$

contradicting (5.41). Hence we have the desired limit. □

The following lemma is a well known result that will be useful to study $b_{cr}(\mu,\nu)$ in the limiting cases.

Lemma 5.4. *For $f \in L^\infty(\Omega)$ we have that*

$$\sup_{\varphi\in L^2(\Omega)} \frac{\int_\Omega f\varphi^2\,dx}{\int_\Omega \varphi^2\,dx} = ||f||_\infty.$$

The next result gives the limiting behavior of $b_{cr}(\mu,\nu)$ as $\mu\to 0$ and $\nu\to\infty$.

Proposition 5.5.

$$b_{cr}(\mu,\nu) \to ||m||_\infty \frac{|\Omega|}{\int_\Omega m(x)\,dx},$$

as $\mu\to 0$ and $\nu\to\infty$.

Proof. For $V\in C(\bar{\Omega})$, $V>0$ define

$$J_\mu(V) = \sup_{\varphi\in W^{1,2}(\Omega)\setminus\{0\}} \left[\frac{-\mu\int_\Omega \alpha_0(x)|\nabla\varphi|^2\,dx + \int_\Omega m^2\varphi^2\,dx}{\int_\Omega mV\varphi^2\,dx}\right]. \tag{5.42}$$

Observe that $J_\mu(V)$ increases as μ decreases to 0, then

$$\begin{aligned}\lim\nolimits_{\mu\downarrow 0} J_\mu(V) &= \sup_{\varphi\in W^{1,2}(\Omega)\setminus\{0\}} \frac{\int_\Omega m^2\varphi^2\,dx}{\int_\Omega mV\varphi^2\,dx} = \sup_{\varphi\in L^2(\Omega)\setminus\{0\}} \frac{\int_\Omega m^2\varphi^2\,dx}{\int_\Omega mV\varphi^2\,dx}\\ &= \sup_{\varphi\in L^2(\Omega)\setminus\{0\}} \frac{\int_\Omega \frac{m}{V}\varphi^2\,dx}{\int_\Omega \varphi^2\,dx} = \left|\left|\frac{m}{V}\right|\right|_\infty = J_0(V),\end{aligned}$$

where in the last equality we have used Lemma 5.4. By Dini's theorem, we have that if K is a compact subset of $C_+(\bar{\Omega})$ then $J_\mu(V)\to J_0(V)$ as $\mu\downarrow 0$ uniformly in K. Hence, since by Lemma 5.3 we have that $\theta(\nu)\to \frac{1}{|\Omega|}\int_\Omega m(x)\,dx$ uniformly as $\nu\to\infty$, we obtain:

$$\lim_{\mu\to 0\ \nu\to\infty} b_{cr}(\mu,\nu) = J_0\left(\frac{\int_\Omega m\,dx}{|\Omega|}\right) = \left|\left|\frac{m|\Omega|}{\int_\Omega m\,dx}\right|\right|_\infty = ||m||_\infty \frac{|\Omega|}{\int_\Omega m\,dx},$$

concluding the proof. □

Note that since m is positive and nonconstant

$$b_{cr}(0,\infty) \equiv ||m||_\infty \frac{|\Omega|}{\int_\Omega m(x)\,dx} > 1,$$

hence $b_{cr}(\mu,\nu) > 1$ uniformly for μ small and ν large.

Theorem 5.6. *Set $b \in (1, b_{cr}(0,\infty))$. There exists μ_0, ν_0 such that for all $0 < \mu < \mu_0$, $\nu > \nu_0$, there exists c for which the corresponding system (1.1) admits two positive steady states, one unstable and one locally asymptotically stable.*

Proof. Observe that for such b, it holds that $b^*(\mu) < b < b_{cr}(\mu,\nu)$ for μ small and ν large enough. For such b, μ and ν fixed we have that by Proposition 4.3, the bifurcating solutions $u(\varepsilon) = m + w(\varepsilon)$, $v = v(\varepsilon)$ for $c = 1 + \gamma(\varepsilon)$ given in Proposition 4.2, are unstable. On the other hand, because $b < b_{cr}(\mu,\nu)$ the solution $(0,\theta(\nu))$ is unstable as stated in Lemma 2.4. Then, we have an ordered pair of steady states $(0,\theta(\nu)) < (u(\varepsilon), v(\varepsilon))$ of (1.1) which are unstable. By Theorem 10.2 and Corollary 7.6 in [12] we conclude that for $c = 1 + \gamma(\varepsilon)$ the system (1.1) has an stable equilibria $(\tilde{u},\tilde{v})$ which satisfies $(0,\theta(\nu)) < (\tilde{u},\tilde{v}) < (u(\varepsilon), v(\varepsilon))$. □

5.2. *Existence of multiple solutions when $\nu \sim 0$ and $\mu \sim \infty$*

As before, to establish the existence of two positive steady states for (1.1) we need to study $b^*(\mu)$ and $b_{cr}(\mu,\nu)$.

Lemma 5.7. *We have the following limits:*

a) $\eta(\mu) \to -m\frac{\int_\Omega m\,dx}{\int_\Omega m^2\,dx}$ *uniformly as* $\mu \to \infty$.
b) $\theta(\nu) \to m$ *uniformly as* $\nu \to 0$.

The proof of this lemma is standard and will be omitted. As a corollary we obtain the behavior of $b^*(\mu)$.

Corollary 5.8.

$$\lim_{\mu\to\infty} b^*(\mu) = \frac{|\Omega|\int_\Omega m^2\,dx}{\left(\int_\Omega m\,dx\right)^2}$$

Observe that

$$b^*(\infty) \equiv \frac{|\Omega|\int_\Omega m^2\,dx}{\left(\int_\Omega m\,dx\right)^2} > 1. \tag{5.43}$$

Now we estimate $b_{cr}(\mu,\nu)$.

Proposition 5.9. *As $\mu \to \infty$ and $\nu \to 0$ we have that $b_{cr}(\mu,\nu) \to 1$.*

Proof. Set $\varphi_{\mu,\nu}$ to be a principal eigenfunction associated to b_{cr}, that is a positive solution of

$$\mu\nabla\cdot\alpha_0(x)\nabla\frac{\varphi_{\mu,\nu}}{m}+\varphi_{\mu,\nu}(m(x)-b_{cr}\theta(\nu))=0 \text{ in } \Omega, \quad \nabla\frac{\varphi_{\mu,\nu}}{m}\cdot\hat{n}=0 \text{ on } \partial\Omega, \tag{5.44}$$

satisfying $||\varphi_{\mu,\nu}||_\infty=1$.

Now, observe that by Lemma 5.4 we have

$$b_{cr}(\mu,\nu)\le \sup_{\varphi\in W^{1,2}(\Omega)\setminus\{0\}}\frac{\int_\Omega m^2\varphi^2\,dx}{\int_\Omega m\theta(\nu)\varphi^2\,dx}=\left|\left|\frac{m}{\theta(\nu)}\right|\right|_\infty,$$

and by Lemma 5.7 we obtain that $b_{cr}(\mu,\nu)$ is bounded independent of μ and ν.

Proceeding as in Lemma 5.3, and using Lemma 5.7 and the boundedness of $b_{cr}(\mu,\nu)$, we can show that $\varphi_{\mu,\nu}$ converges uniformly, up to a subsequence, to a constant C as $\mu\to\infty$ and $\nu\to 0$. Since $||\varphi_{\mu,\nu}||_\infty=1$ we have that $C=1$.

Finally, we integrate (5.44) in Ω to obtain

$$\int_\Omega \varphi_{\mu,\nu}(m-b_{cr}(\mu,\nu)\theta(\nu))\,dx=0,$$

and by Lemma 5.7 we have that $\theta(\nu)\to m$ as $\nu\to 0$ from which we conclude that $b_{cr}(\mu,\nu)\to 1$ as $\mu\to\infty$ and $\nu\to 0$. □

Theorem 5.10. *Set $b\in(1,b^*(\infty))$, with $b^*(\infty)$ defined in (5.43). There exists μ_0, ν_0 such that for all $\mu>\mu_0$, $0<\nu<\nu_0$, there exists c for which the corresponding system (1.1) admits two positive steady states, one unstable and one locally asymptotically stable.*

Proof. We proceed as in the proof of Theorem 5.6. By Corollary 5.8 and Proposition 5.9, it holds that $b_{cr}(\mu,\nu)<b<b^*(\mu)$ for μ large and ν small enough. For such b, μ and ν fixed we have that by Proposition 4.3, the bifurcating solutions $u(\varepsilon)=m+w(\varepsilon)$, $v=v(\varepsilon)$ for $c=1+\gamma(\varepsilon)$ given in Proposition 4.2, are locally asymptotically stable. On the other hand, because $b<b_{cr}(\mu,\nu)$ the solution $(0,\theta(\nu))$ is also locally asymptotically stable as stated in Proposition 2.4. Then, we have an ordered pair of steady states $(0,\theta(\nu))<(u(\varepsilon),v(\varepsilon))$ of (1.1) which are stable. By Theorem 4 in [11] we conclude that $c=1+\gamma(\varepsilon)$ the system (1.1) has an unstable equilibria $(\tilde{u},\tilde{v})$ which satisfies $(u(\varepsilon),v(\varepsilon))<(\tilde{u},\tilde{v})<(0,\theta(\nu))$. □

6. Concluding observations

In (1.1) with $b=c=1$, ideal free dispersal holds an evolutionary advantage over fickian dispersal, being both an evolutionary stable strategy and a neighborhood invader strategy. Allowing b and c to take in arbitrary positive values enables us to explore how and to what extent this advantage, which is based on the ability to match resources, broadly translates into an ecological advantage.

There are two aspects that are both rather immediate and striking. First of all, competitive exclusion of a fickian disperser by an ideal free disperser continues to hold whenever $c\ge 1$ and $b\le 1$. This feature follows from having the result hold when $b=c=1$ and comparison principles. The second aspect concerns invasibility of the semi-trivial equilibria $(m(x), 0)$ and $(0, \theta(x))$. Here $(m(x), 0)$ can be regarded as an ideal free distribution where as $(0, \theta(x))$ can not. Both these equilibria are invasible under weak competition. Here, when $0 < b < 1$, the ideal free disperser can increase if it is introduced at low densities when the fickian disperser is at its spatially varying carrying capacity $\theta(x)$. Likewise, when $0 < c < 1$, the fickian disperser can increase when it is introduced at low densities whenever the ideal free disperser perfectly matches resources at its spatially varying carrying capacity $m(x)$.

Once the competitive impact of the ideal free disperser on the fickian disperser becomes strong (i.e. $c > 1$), the ideal free dispersal strategy is no longer invasible by the fickian dispersal. On the other hand, the ideal free dispersal strategy can invade the fickian dispersal strategy for values of b up to some critical value $b_{cr} > 1$, so that it can invade in the presence of strong competition up to some extent. One consequence here is that (1.1) exhibits permanence or uniform persistence when $0 < b < b_{cr}$ and $0 < c < 1$. In particular, a monotone dynamical system approach may be employed to conclude that (1.1) exhibits a global attracting order interval, i.e. is compressive [4].

When $c > 1$ and $b > b_{cr}$, both semi-trivial equilibria for (1.1) are locally asymptotically stable, and it follows that (1.1) must have an componentwise positive equilibrium. On the other hand, when the competitive impact of the fickian disperser allows invasion by the ideal free disperser (actually when $b \in [0, b_{cr}]$), a componentwise positive equilibrium is not possible once $c \geq \bar{c}^*$, with $\bar{c}^* > 1$, and thus $(m(x), 0)$ is globally asymptotically stable. Likewise $(0, \theta(x))$ is global asymptotically stable for $0 \leq c \leq 1$ when $b \geq \bar{b}^* > b_{cr} > 1$.

As noted in Section 4, bifurcation from the semi-trivial steady state $(m(x), 0)$ to componentwise positive steady states of (1.1) occurs along the line $c = 1$, while bifurcation from the steady state $(0, \theta(x))$ to componentwise positive steady states of (1.1) happens when $b = b_{cr}$. These bifurcations create the possibility of multiple positive equilibria for (1.1). For b small, bifurcation from $(m(x), 0)$ is in the decreasing direction with respect to the c parameter and the resulting positive equilibria are stable as solutions of (1.1), whereas for large values of b, the direction is increasing with respect to c and the resulting equilibria are unstable as solutions of (1.1). The value of b (i.e. b^*) where the direction of bifurcation switches depends on the operator L and the function m but is independent of M and θ, while the value b_{cr} depends on L, m and θ (and hence by extension M). As observed, $b^* > 1$ and clearly $b^* < \bar{b}^*$. But, as we show in Theorems 5.6 and 5.10, we can have $b^* < b_{cr}$ or $b^* > b_{cr}$. Corresponding results can be obtained for the bifurcation from $(0, \theta(x))$. However, in this case c^* depends on L, M, m, θ and b_{cr} and we have not been able to determine the value of c^* relative to 1. In particular, we do not know whether we can have cases where $c^* < 1$ and other cases where $c^* > 1$.

So let us suppose that $1 < b^* < b_{cr}$. Then for values of $b \in (b^*, b_{cr})$, the bifurcation from $(m(x), 0)$ to componentwise positive steady states of (1.1) tracks initially in c in the increasing direction with the corresponding positive steady states unstable as solutions of (1.1). These positive steady states continue as long as c remains positive. There are no such steady states for this value of b for $c \geq \bar{c}^*$. Consequently the continuum of positive steady states $\mathcal{C}^+$, extend upwards in c to some maximum value $c_{max}(b) < \bar{c}^*$, exhibits a saddle node bifurcation and extends downward in c to $c = 0$. Consequently, (1.1) has at least two steady states for this value of b when $c \in (1, c_{max}(b))$. We have that (1.1) is permanent for $c \in (0, 1)$ and that the componentwise positive steady states approach $(\bar{u}, \theta)$ as $c \to 0$, where $\bar{u}$ is the unique solution of (4.33). Note that $\bar{u} \to 0$ as $b \uparrow b_{cr}$. The track of this continuum of componentwise positive steady states is illustrated in Fig. 1.

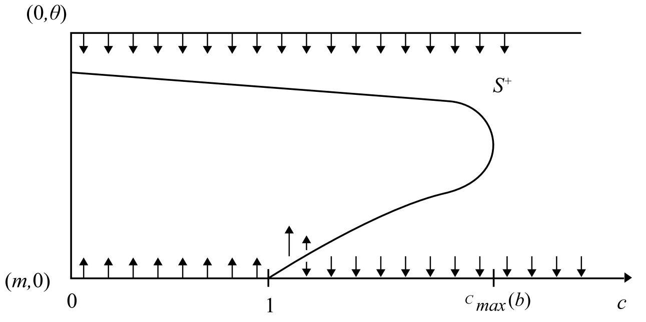

Fig. 1. The curve S^+ accounts for $\{(||u||_\infty, c) : (u, v, c) \in \mathcal{C}^+\}$ with $\mathcal{C}^+$ defined in Proposition 4.7.

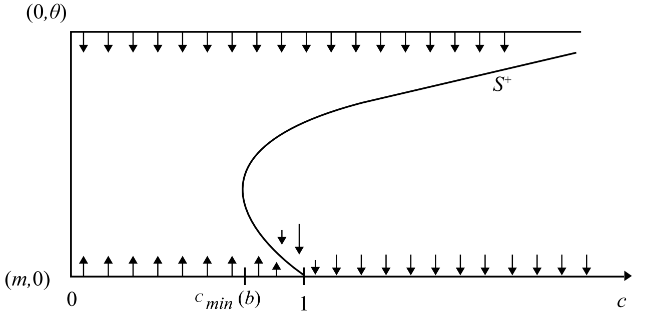

Fig. 2. The curve S^+ accounts for $\{(||u||_\infty, c) : (u, v, c) \in \mathcal{C}^+\}$ with $\mathcal{C}^+$ defined in Proposition 4.7.

If $b^* > b_{cr}$, bifurcation from $(m(x), 0)$ to componentwise positive steady states of (1.1) is initially decreasing in c for values of $b \in (b_{cr}, b^*)$ and positive steady states are locally asymptotically stable as solutions of (1.1). The continuum $\mathcal{C}^+$ cannot exit the region of componentwise positive solutions through values of c that approach 0, since $b > b_{cr}$. So there must be $c_{min}(b) \in (0, 1)$ where there is a saddle node bifurcation in terms of c, and the continuum continues through increasing values of c as $c \to \infty$. This guarantees multiple componentwise positive equilibria for $c \in (c_{min}(b), 1)$. The track of this continuum of positive steady states is illustrated in Fig. 2.

Analogous results hold relative to bifurcation from $(0, \theta(x))$ to componentwise positive steady states of (1.1) when either $c^* > 1$ or $c^* < 1$. As noted, we can not determine whether one or both of these alternatives are possible. However for the sake of argument, assume that $1 < b^* < b_{cr}$ and $c^* > 1$ in this case, Fig. 3 gives a schematic overview of our results in terms of the $bc-$plane in Fig. 3.

In region (I) there is stable coexistence via pairwise invasibility, while in (III) there is unstable coexistence via stability of both semi-trivial equilibria. In regions (II) and (IV) one of the semi-trivial steady states, $(0, \theta(x))$ and $(m(x), 0)$ respectively, is globally asymptotically stable via competitive overmatch of the non-ideal free disperser or the ideal free disperser. In (V) we have that $(m(x), 0)$ is globally asymptotically stable (advantage of ideal free dispersal). In the region (A) multiple componentwise equilibria occur.

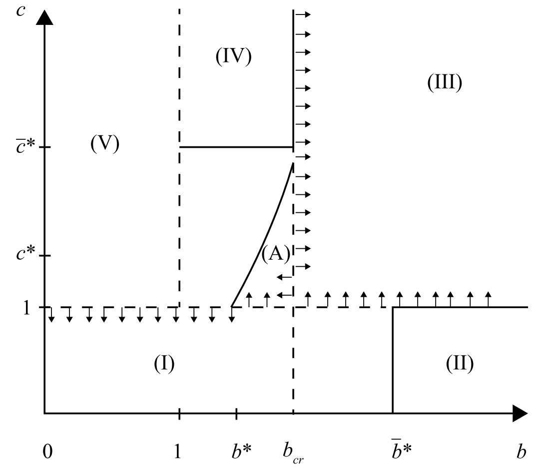

Fig. 3. Schematic in (b, c) parameter space of steady states of (1.1) in the case where $1 < b < b_{cr}$ and $1 < c^*$. Vertical arrows indicate direction of bifurcation from $(m(x), 0)$ at $c = 1$ and horizontal arrows indicate direction of bifurcation from $(0, \theta(x))$ at b_{cr}. Multiple componentwise positive equilibria occur in region (A).

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