EVOLUTION OF CROSS-DIFFUSION AND SELF-DIFFUSION

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Abstract. This paper is concerned with the evolution of certain type density-dependent dispersal strategy in the context of two competing species with identical population dynamics and same random dispersal rates. Such density-dependent movement, often referred as cross-diffusion and self-diffusion, assumes that the movement rate of each species depends on the density of both species and that the transition probability from one place to its neighborhood depends solely upon the arrival spot (independent of the departure spot). Our results suggest that for one-dimensional homogeneous habitat, if the gradients of two cross- and self-diffusion coefficients have the same direction, the species with the smaller gradient will win, i.e., the dispersal strategy with the smaller gradient of cross- and self-diffusion coefficient will evolve. In particular, it suggests that the species with constant cross- and self-diffusion coefficient may have competitive advantage over species with non-constant cross- and self-diffusion coefficient. However, if the two gradients have opposite directions, neither of the two dispersal strategies wins as these two species can coexist.

Keywords: Density-dependent dispersal; Competition; Coexistence

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1. Introduction

Dispersal is probably one of the most common yet fascinating features that we often witness in this world: birds fly across continents to breed, herds run over wild lands in searching for food, etc. How did they adopt their dispersal behaviors? How would these behaviors change in the future? The evolution of dispersal is of keen biological interest and importance and has been investigated extensively for decades in biological literatures (see, e.g., [1, 10, 11, 14, 15, 16, 22, 30, 34, 36, 39, 40, 41]). One of the major mathematical modeling approaches is to use reaction-diffusion models (see, e.g., [2, 4, 5, 6, 7, 9, 18, 19, 21, 28]). While substantial progress has been made via this mathematical approach in understanding random spatial movement of species, much less is known on the role of population density dependent dispersal in the evolution of dispersal. In reality, species do not always move randomly. Instead, they can often sense local environment and may adopt different dispersal strategies under different circumstances. This paper is concerned about certain kind of density-dependent dispersal strategies.

To be more specific, we are interested in how cross-diffusion and self-diffusion can affect the dynamics of two competing species. Cross-diffusion and self-diffusion models are originally

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proposed by Shigesada et al. [37] to model the spatial segregation of two competing species. The main feature of such model is that the movement rate of each species depend on the density of both species, and one key underlying biological assumption is that the transition probability from one place to its neighborhood depends solely upon the arrival spot and is independent of the departure spot. The goal of [37] was to show that if random diffusion alone can not give arise to spatial segregation of two competing species, such nonlinear dispersal strategy may be able to do so. For later work on competition models with cross- and/or self-diffusion, see [8, 20, 23, 25, 26, 27, 29, 31, 32, 33] and references therein.

While we will use the cross-diffusion and self-diffusion model in this paper, our motivations are different. Our goal here is to understand how density-dependent dispersal strategies will evolve in spatially homogeneous environment. Following [37] we consider the following strongly coupled parabolic system

$$\begin{cases} u_t &= \Delta[D_1(x,u,v)u] + (1-u-v)u, \quad x \in \Omega, \ t > 0, \\ v_t &= \Delta[D_2(x,u,v)v] + (1-u-v)v, \quad x \in \Omega, \ t > 0, \\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \quad x \in \partial\Omega, \ t > 0, \end{cases} \tag{1.1}$$

where $u(x,t), v(x,t)$ are the densities of two competing species, and $D_i(x,u,v)$ $(i = 1,2)$ are their density-dependent dispersal rates ([37]), respectively. We assume that Ω is a domain in R^N with smooth boundary $\partial\Omega$, and ν is the outward unit normal vector on $\partial\Omega$. The boundary conditions in (1.1) means that there is no individuals crossing the boundary. In [37], $D_i(x,u,v)$ assumes the form of $d_i + \rho_{i1}u + \rho_{i2}v$, $i = 1,2$. Throughout this paper we consider the case $d_1 = d_2, \rho_{i1} = \rho_{i2}$, $i = 1,2$. More precisely, we assume that

$$D_i(x,u,v) = \mu\left[1 + (\gamma + \tau\rho_i(x))(u+v)\right], \quad i = 1,2,$$

where the parameter μ is positive and can be regarded as the random dispersal rate; γ, τ are two non-negative constants, and they together with functions $\rho_i(x)$ measure the degree of density-dependence in the movement of the species. We shall focus on the situation when τ is small, i.e., the two species are almost identical and their cross-diffusion and self-diffusion coefficients are all close to the same constant γ. The biological motivation behind is that we envision that some mutation occurs and both species are adopting biased movement strategies which avoid the crowding of the whole population. One natural question is: *what kind of $\rho_i(x)$ can convey some competitive advantage?*

For notational convenience, we will refer $\rho_i(x)$ as cross- and self-diffusion coefficients throughout this paper. Also for technical reasons, we assume that $\rho_i(x)$, $i = 1,2$, are nonnegative smooth functions and that they satisfy the boundary condition

$$\frac{\partial \rho_1}{\partial \nu} = \frac{\partial \rho_2}{\partial \nu} = 0, \quad x \in \partial\Omega. \tag{1.2}$$

We first consider the case when one of ρ_i is a constant function.

Theorem 1.1. *Suppose that at least one of ρ_1, ρ_2 is constant. Then, for every $\mu > 0$, there exists τ_0 such that for every $0 < \tau < \tau_0$, the system (1.1) does not admit any nonconstant positive steady state.*

If both ρ_1 and ρ_2 are constants, then (1.1) has a continuum family of constant positive steady states, which are all neutrally stable and as a whole may be the global attractor of system (1.1). Also, both semi-trivial steady state are neutrally stable. Therefore, if both species adopt cross-diffusion and self-diffusion strategy with constant coefficient, neither one wins or loses.

If ρ_1 is non-constant and ρ_2 is a constant, we can further show that the semi-trivial steady state $(u, 0)$ is locally unstable and $(0, v)$ is neutrally stable for τ small. We conjecture that for this case, $(0, v)$ is the global attractor. If this were the case, biologically this would mean that the species with non-constant cross- and self-diffusion coefficient always loses and thus constant cross- and self-diffusion will evolve.

What happens if both ρ_1 and ρ_2 are non-constant? It turns out this case is much more delicate and there may or may not exist any stable positive steady state. Thus, we are going to be looking for positive solutions of

$$\begin{cases} \mu\Delta[(1+(\gamma+\tau\rho_1)(u+v))u]+(1-u-v)u=0, & x\in\Omega,\\ \mu\Delta[(1+(\gamma+\tau\rho_2)(u+v))v]+(1-u-v)v=0, & x\in\Omega,\\ \frac{\partial u}{\partial\nu}=\frac{\partial u}{\partial\nu}=0,\ x\in\partial\Omega. \end{cases} \tag{1.3}$$

We first state some abstract results for coexistence of two species and then give some more explicit conditions under which coexistence of two species is possible or impossible. For small positive τ, the conditions for existence/nonexistence of coexistence states can be expressed in terms of two functions $G(\mu)$ and $H(\mu)$. Define $T_\mu : W_n^{2,p} \to L^p(\Omega)$ as

$$T_\mu f = -\mu(1+2\gamma)\Delta f + f, \tag{1.4}$$

where $W_n^{2,p}(\Omega) = \{y \in W^{2,p}(\Omega)\ :\ \frac{\partial y}{\partial\nu} = 0 \text{ on } \partial\Omega\}$, $p > N$. We define

$$H(\mu)=\int_\Omega T_\mu^{-1}(\Delta\rho_1)(\rho_2-\rho_1),\quad G(\mu)=\int_\Omega T_\mu^{-1}(\Delta\rho_2)(\rho_1-\rho_2). \tag{1.5}$$

Using Fourier series expansion, it is easy to prove that if $g \in W^{2,p}(\Omega)$ is nonconstant then $\int_\Omega(T_\mu^{-1}\Delta g)g < 0$. Therefore, if $\rho_1-\rho_2$ is nonconstant we have that $G(\mu)+H(\mu) > 0$ for every μ. Thus, given any μ, at least one of $G(\mu)$ and $H(\mu)$ is strictly positive.

Theorem 1.2. *Suppose that* $\nabla(\rho_1-\rho_2) \not\equiv 0$.

1. *If* $G(\mu)H(\mu) < 0$, *system* (1.3) *has no positive solutions provided that* $\tau > 0$ *is small. Furthermore, if* $G(\mu) > 0 > H(\mu)$, *the semi-trivial steady state* $(u, 0)$ *is stable and* $(0, v)$ *is unstable; the stability is switched if* $G(\mu) < 0 < H(\mu)$.
2. *If* $G(\mu)H(\mu) > 0$, *system* (1.3) *has a unique positive solution, which is also locally stable, provided that* $\tau > 0$ *is small. Furthermore, both semi-trivial steady states are unstable.*

We conjecture that if $G(\mu)H(\mu) < 0$ and τ is positive small, one of the two semi-trivial states is globally asymptotically stable; if $G(\mu)H(\mu) > 0$ and τ is positive small, the unique positive steady state is globally asymptotically stable.

As applications of Theorem 1.2, we have

Corollary 1.1. *Suppose that* $\Omega = (0,1)$, ρ_1, ρ_2 *and* $\rho_1 - \rho_2$ *are non-constant functions.*

(1) *If* $\rho_1'(x) \geq \rho_2'(x) \geq 0$ *or* $\rho_1'(x) \leq \rho_2'(x) \leq 0$ *for all* $x \in (0,1)$, *then for any* $\mu > 0$, *there exists* τ_1 *such that* (1.3) *has no positive solution provided that* $0 < \tau < \tau_1$. *Furthermore, the semi-trivial steady state* $(u, 0)$ *is locally unstable and* $(0, v)$ *is stable.*

(2) *If* $\rho_1'(x) \geq 0 \geq \rho_2'(x)$ *or* $\rho_1'(x) \leq 0 \leq \rho_2'(x)$ *for all* $x \in (0,1)$, *then for any* $\mu > 0$, *there exists* τ_2 *for which the system* (1.3) *admits a unique positive solution, which is also locally stable provided that* $0 < \tau < \tau_2$.

Part (1) suggests that the semi-trivial steady state $(0, v)$ may be globally asymptotically stable, which biologically would mean that if the gradients of cross- and self-diffusion coefficients have the same direction, then the one with the *smaller* gradient will evolve. This is also consistent with our discussions following Theorem 1.1, where we conjecture that the species with constant cross- and self-diffusion coefficient always wins.

Part (2) implies that if the two gradients have opposite directions, these two species can coexist. Intuitively, one would reason that neutral competitions often lead to competitive exclusion since similar species will likely compete for similar resources. So it is rather interesting to see from our model that two similar competing species can coexist under fairly general conditions. Recently there have been some studies on the dynamics of two similar competing species in various contexts. For example, in [17, 13, 3] the two species are identical except their intrinsic growth rates; in [24], the two species are identical except their inter-specific competition coefficients. While the general analytical approach adopted in this paper shares some similarity with those in previous works, both mathematical results and technical details are rather different, so are biological motivations, interpretations (of mathematical results) and predictions.

The paper is organized as follows: Theorem 1.1 follows from Propositions 2.2 and 3.3, which are established in Sects. 2 and 3, respectively; Theorem 1.2 follows from Theorem 3.1 (existence part), Propositions 4.1 and 4.2 and Theorem 4.1 (stability part). In fact, Theorem 3.1 gives a global bifurcation diagram for positive steady states of (1.1) and is more general than what is stated in Theorem 1.2. Finally, Corollary 1.1 follows from Theorem 1.2 and Corollaries 3.3 and 3.4.

2. ASYMPTOTIC BEHAVIOR OF SOLUTIONS AS $\tau \to 0$

In our first statement we will prove that any positive solution of (1.3) converges to $(s, 1-s)$, with $s \in [0,1]$ as $\tau \to 0$.

Proposition 2.1. *Suppose that for every* τ *sufficiently small system* (1.3) *admits a positive solution* (u_τ, v_τ). *Then, after passing to a subsequence if necessary, we have that* $(u_\tau, v_\tau) \to (s, 1-s)$ *in* $C^{2,\gamma}(\overline{\Omega})$, *as* $\tau \to 0$, *for some* $s \in [0,1]$.

Proof. We set $\varphi_\tau = u_\tau[1 + (\gamma + \tau\rho_1)(u_\tau + v_\tau)]$, $\psi_\tau = v_\tau[1 + (\gamma + \tau\rho_2)(u_\tau + v_\tau)]$, which satisfy the equation

$$\begin{cases} \mu\Delta\varphi_\tau + u_\tau(1 - u_\tau - v_\tau) &= 0 \text{ in } \Omega, \quad \frac{\partial\varphi_\tau}{\partial\nu} = 0 \text{ on } \partial\Omega, \\ \\ \mu\Delta\psi_\tau + v_\tau(1 - u_\tau - v_\tau) &= 0 \text{ in } \Omega, \quad \frac{\partial\psi_\tau}{\partial\nu} = 0 \text{ on } \partial\Omega. \end{cases} \tag{2.6}$$

Using the maximum principle [35] it is easy to prove that there exists a constant $C>0$ such that $||\varphi_\tau||_\infty, ||\psi_\tau||_\infty \leq 1+\gamma+C\tau$, $||u_\tau||_\infty, ||v_\tau||_\infty \leq 1+C\tau$. Hence, by elliptic regularity and Sobolev embedding theorems [12], after passing to a subsequence if necessary, $(\varphi_\tau,\psi_\tau) \to (\varphi^*,\psi^*)$, with $\varphi^*,\psi^* \geq 0$, in $W^{1,p}(\Omega)$ as $\tau \to 0$, for any $p>1$.

Observe that $(\varphi_\tau,\psi_\tau) = F(u_\tau, v_\tau, x)$ with $F : (-\tau, 1+2C\tau) \times (-\tau, 1+2C\tau) \times \Omega \to V$, for V an open subset of $(-\tau, 1+\gamma+2C\tau) \times (-\tau, 1+\gamma+2C\tau)$, and $F(\cdot,\cdot,x)$ a smooth diffeomorphism. Therefore, $(u_\tau, v_\tau) \to (u^*, v^*)$, with $u^*, v^* \geq 0$, in $W^{1,p}(\Omega)$ as $\tau \to 0$. Observe that by definition $\varphi^* = u^*(1+\gamma(u^*+v^*))$, $\psi^* = v^*(1+\gamma(u^*+v^*))$.

Using equation (2.6) we obtain that $(\varphi_\tau,\psi_\tau) \to (\varphi^*,\psi^*)$ in $C^{2,\gamma}(\bar\Omega)$ and consequently $(u_\tau, v_\tau) \to (u^*, v^*)$ in $C^{2,\gamma}(\bar\Omega)$. Observe that $u^*+v^* \geq 0$ satisfies the equation

$$\Delta[(1+\gamma w)w] + w(1-w) = 0 \text{ in } \Omega, \quad \frac{\partial w}{\partial \nu} = 0 \text{ on } \partial\Omega,$$

which has only the nonnegative solutions $w \equiv 0$ and $w \equiv 1$. Therefore, either $u^*+v^*=1$ or $u^*+v^*=0$.

Suppose that $u^*+v^*=0$, i.e, $u^*=v^*=0$. In this case we define $\hat\varphi_\tau = \varphi_\tau/m_\tau$, $\hat\psi_\tau = \psi_\tau/m_\tau$ for $m_\tau = ||\varphi_\tau+\psi_\tau||_\infty$. It is easy to see that $(\hat\varphi_\tau, \hat\psi_\tau)$ converges, except possibly for a subsequence, to a nontrivial nonnegative solution $(\hat\varphi, \hat\psi)$ of

$$\begin{cases} \mu\Delta\hat\varphi + \hat\varphi &= 0 \text{ in } \Omega, \quad \frac{\partial\hat\varphi}{\partial\nu} = 0 \text{ on } \partial\Omega, \\ \\ \mu\Delta\hat\psi + \hat\psi &= 0 \text{ in } \Omega, \quad \frac{\partial\hat\psi}{\partial\nu} = 0 \text{ on } \partial\Omega. \end{cases}$$

which is a contradiction.

Hence, $u^*_\tau + v^*_\tau = 1$ and since

$$\Delta u^* = \Delta v^* = 0 \text{ in } \Omega, \quad \frac{\partial u^*}{\partial\nu} = \frac{\partial v^*}{\partial\nu} = 0 \text{ on } \partial\Omega,$$

we have that $(u_\tau, v_\tau) \to (s, 1-s)$ in $C^{2,\gamma}(\overline{\Omega})$ with $s \in [0,1]$. □

The next result states that if τ is small enough and ρ_1, ρ_2 are constants, then (1.3) does not admit any nonconstant positive solution.

Proposition 2.2. *Suppose that $\rho_1, \rho_2 \geq 0$ are constants. For every $\mu>0$, there exists τ_3 such that if $0<\tau<\tau_3$ system (1.3) does not admit nonconstant positive solutions.*

Proof. We proceed by contradiction. Suppose that we have a sequence (u_τ, v_τ) of nonconstant positive solutions, with $\tau \to 0$. Then, we can write $u_\tau = \overline{u}_\tau + y_\tau$, $v_\tau = \overline{v}_\tau + z_\tau$, with $\int_\Omega y_\tau = \int_\Omega z_\tau = 0$, $||y_\tau||_\infty + ||z_\tau||_\infty \neq 0$ and $(y_\tau, z_\tau) \to (0,0)$ in $C^{2,\gamma}(\overline{\Omega})$. After considering a subsequence if necessary, we have that $(\overline{u}_\tau, \overline{v}_\tau) \to (s, 1-s)$ as $\tau \to 0$, with $s \in [0,1]$.

Set

$$(\hat y_\tau, \hat z_\tau) = \frac{1}{||y_\tau||_\infty + ||z_\tau||_\infty}(y_\tau, z_\tau),$$

which, by some simple computations, satisfy

$$\begin{cases} \mu(1+\gamma)\Delta\hat{y}_\tau + \mu\gamma s\Delta(\hat{y}_\tau+\hat{z}_\tau) + s(-\hat{y}_\tau-\hat{z}_\tau) = f_\tau \text{ in } \Omega, \\ \\ \mu(1+\gamma)\Delta\hat{z}_\tau + \mu\gamma(1-s)\Delta(\hat{y}_\tau+\hat{z}_\tau) + (1-s)(-\hat{y}_\tau-\hat{z}_\tau) = g_\tau \text{ in } \Omega, \\ \\ \frac{\partial y_\tau}{\partial\nu} = \frac{\partial y_\tau}{\partial\nu} = 0 \text{ on } \partial\Omega, \end{cases} \tag{2.7}$$

where $||f_\tau||_{2,p}, ||g_\tau||_{2,p} \leq o(1)(||\hat{y}_\tau||_{2,p} + ||\hat{v}_\tau||_{2,p})$ since

$$\bar{u}_\tau(1-\bar{u}_\tau-\bar{v}_\tau) = \frac{1}{|\Omega|}\int_\Omega y_\tau(y_\tau+z_\tau) \text{ and } \bar{v}_\tau(1-\bar{u}_\tau-\bar{v}_\tau) = \frac{1}{|\Omega|}\int_\Omega z_\tau(y_\tau+z_\tau).$$

For any $s \in [0,1]$ the linear operator $L : W_n^{2,p}(\Omega) \to L^p(\Omega)$, defined as

$$L_{\mu,s}\begin{pmatrix} y \\ z \end{pmatrix} = \begin{pmatrix} \mu(1+\gamma)\Delta y + \mu\gamma s\Delta(y+z) - s(y+z) \\ \mu(1+\gamma)\Delta z + \mu\gamma(1-s)\Delta(y+z) - (1-s)(y+z) \end{pmatrix}, \tag{2.8}$$

satisfies $Ker\,(L) = span\,\{(1,-1)\}$ and $Range\,(L) = \{(1-s,-s)\}^\perp$. Hence, from (2.7) we obtain that

$$||\hat{y}_\tau||_{2,p} + ||\hat{z}_\tau||_{2,p} \leq o(1)(||\hat{y}_\tau||_{2,p} + ||\hat{z}_\tau||_{2,p}),$$

which contradicts $||\hat{y}_\tau||_\infty + ||\hat{z}_\tau||_\infty = 1$. □

3. COEXISTENCE STATES

In this section we will study the existence of positive steady state solutions of (1.1) which are close to the surface

$$\Sigma = \{(\mu, s, 1-s) \ : \ \mu \in [\mu_1,\mu_2], \ s \in [0,1]\},$$

for some $0 < \mu_1 < \mu_2$. Observe that for every $\mu > 0$,

$$\Sigma = \{(s, 1-s) \ : \ s \in [0,1]\}$$

is the set of solutions of (1.3) when $\tau = 0$. Following the proof of Proposition 2.1 we can show that there exists $\tau_3 > 0$ such that for $\mu \in [\mu_1,\mu_2]$ any positive solution of (1.3) is close to Σ provided that $\tau < \tau_3$. We define the spaces

$$\begin{aligned} &X = W_n^{2,p}(\Omega) \times W_n^{2,p}(\Omega), \\ &X_1 = span\{(1,-1)\}, \ X_2 = \{(y,z) \in X \ : \ \textstyle\int_\Omega (y-z) = 0\}, \\ &Y = L^p(\Omega) \times L^p(\Omega), \end{aligned} \tag{3.9}$$

where $p > N$ so that $W^{2,p}(\Omega) \subset C^{1,\gamma}(\overline{\Omega})$. We start with the following result which establishes the existence and expansion of the semitrivial solutions of (1.3).

Proposition 3.1. *Consider the equation*

$$\mu\Delta[(1+(\gamma+\tau\rho(x))u)u] + u(1-u) = 0 \quad \textit{in } \Omega, \quad \frac{\partial u}{\partial\nu} = 0 \quad \textit{on } \partial\Omega, \tag{3.10}$$

with $\mu \in [\mu_1, \mu_2]$, *for* $0 < \mu_1 < \mu_2 < \infty$ *and* $\rho \in C^2(\bar{\Omega})$ *positive satisfying* (1.2). *Then there exists* τ_0 *such that for all* $0 < \tau < \tau_0$ *the equation* (3.10) *admits a unique positive solution* $\theta(\mu, \tau, \rho)$. *Moreover* $\theta(\mu, \tau, \rho)$ *can be expanded as*

$$\theta(\mu, \tau, \rho) = 1 + \tau\omega_1(\mu, \tau, \rho) \quad \textit{with} \quad \omega_1(\mu, 0, \rho) = T_\mu^{-1}(\mu\Delta\rho).$$

Proof. The proof is a direct application of the implicit function theorem using a priori estimates similar to the ones shown in the proof of Proposition 2.2. □

Set $\theta_i(\mu, \tau) := \theta(\mu, \tau, \rho_i)$, $i = 1, 2$. The main result of this section is

Theorem 3.1. *Suppose that* $\nabla(\rho_1 - \rho_2) \not\equiv 0$ *in* Ω.

(1) *If* $GH > 0$ *in* (μ_1, μ_2) *then there exists a neighborhood* U *of* Σ *and* $\delta > 0$ *such that for* $0 < \tau < \delta$, *the set of non-trivial solutions of* (1.3) *consists of the semi-trivial solutions* $(\theta_1(\mu, \tau), 0)$, $(0, \theta_2(\mu, \tau))$ *and* $(u(\mu, \tau), v(\mu, \tau))$ *with* $\mu \in (\mu_1 - \delta, \mu_2 + \delta)$, *where*

$$\begin{aligned} u(\mu, \tau) &= s(\mu, \tau) + \bar{y}(\mu, \tau), && (3.11)\\ v(\mu, \tau) &= (1 - s(\mu, \tau)) + \bar{z}(\mu, \tau). && (3.12)\end{aligned}$$

Here $(\bar{y}(\mu, \tau), \bar{z}(\mu, \tau)) \in X_2$ *are smooth functions and* $s(\mu, \tau)$ *is smooth and satisfies*

$$s(\mu, 0) = \frac{G(\mu)}{G(\mu) + H(\mu)}.$$

(2) *If* $GH < 0$ *in* $[\mu_1, \mu_2]$, *system* (1.3) *has no positive solutions for* $\mu \in [\mu_1, \mu_2]$ *provided that* $\tau > 0$ *is small.*

Proof. For τ small each solution (u, v) of (1.3) near Σ can be written as

$$(u, v) = (s, 1 - s) + (y, z),$$

where $s \in \mathbb{R}$, $(y, z) \in X_2$ in a neighborhood of $(0, 0)$. We define the map $F : X_2 \times (\mu_1 - \delta, \mu_2 + \delta) \times (-\delta, \delta) \times (-\delta, 1 + \delta) \to Y$ by

$$F(y, z, \mu, \tau, s) = L_{\mu,s}\begin{pmatrix} y \\ z \end{pmatrix} + \begin{pmatrix} f_1 \\ f_2 \end{pmatrix}, \tag{3.13}$$

with $L_{\mu,s}$ as in (2.8) and

$$\begin{aligned} f_1 = &\; -y(y + z) + \mu s\tau\Delta\rho_1 + \mu s\tau\Delta[\rho_1(y + z)] + \mu\tau\Delta[\rho_1(y + z)y] + \mu\gamma\Delta[(y + z)y],\\ f_2 = &\; -z(y + z) + \mu(1 - s)\tau\Delta\rho_2 + \mu(1 - s)\tau\Delta[\rho_2(y + z)] + \mu\tau\Delta[\rho_2(y + z)z]\\ &+\mu\gamma\Delta[(y + z)z]. \end{aligned} \tag{3.14}$$

Clearly F is smooth and $u = s + y$, $v = (1 - s) + z$ is a solution of (1.3) if and only if $F(y, z, \mu, \tau, s) = 0$. The two semitrivial equilibria $(\theta_1(\mu, \tau), 0)$, $(0, \theta_2(\mu, \tau))$ of (1.3) can be expressed as

$$\begin{aligned} (\theta_1(\mu, \tau), 0) = &\; (\sigma_1(\mu, \tau), 1 - \sigma_1(\mu, \tau)) + (\eta_1(\mu, \tau), \zeta_1(\mu, \tau)),\\ (0, \theta_2(\mu, \tau)) = &\; (\sigma_2(\mu, \tau), 1 - \sigma_2(\mu, \tau)) + (\eta_2(\mu, \tau), \zeta_2(\mu, \tau)), \end{aligned} \tag{3.15}$$

where $(\eta_i(\mu,\tau),\zeta_i(\mu,\tau)) \in X_2$, $(\eta_i(\mu,0),\zeta_i(\mu,0)) = (0,0)$ for $i = 1,2$ and $\sigma_1(\mu,0) = 1$, $\sigma_2(\mu,0) = 0$. Thus we have that F satisfies

$$\begin{aligned}
&F(0,0,\mu,0,s) = 0,\\
&F(\eta_1(\mu,\tau),\zeta_1(\mu,\tau),\mu,\tau,\sigma_1(\mu,\tau)) = 0,\\
&F(\eta_2(\mu,\tau),\zeta_2(\mu,\tau),\mu,\tau,\sigma_2(\mu,\tau)) = 0.
\end{aligned} \tag{3.16}$$

We define the projection

$$P_s(y,z) = \frac{1}{|\Omega|}\left[(1-s)\int_\Omega y - s\int_\Omega z\right](1,-1),$$

which satisfies $P_s^2 = P_s$, $Range(P_s) = X_1$, $P_sL_{\mu,s} = 0$.

Following the Lyapunov-Schmidt procedure we need to solve

$$P_sF(y,z,\mu,\tau,s) = 0, \tag{3.17}$$

$$(I - P_s)F(y,z,\mu,\tau,s) = 0, \tag{3.18}$$

where I is the identity map.

Observe that $D_{(y,z)}F(0,0,\mu,0,s) = L_{\mu,s}$ and that $Ker\,(L_{\mu,s}) = X_1$ and that $X_1 \cap X_2 = \{(0,0)\}$. Thus, we can apply the implicit function theorem to solve (3.18) through the map $(\mu,\tau,s) \to (y(\mu,\tau,s),z(\mu,\tau,s))$ with $(y(\mu,0,s),z(\mu,0,s)) = (0,0)$. Moreover, there exists a neighborhood V of $(0,0)$ in X_2 and δ_1 such that $(y,z,\mu,\tau,s) \in V \times (\mu_1-\delta_1,\mu_2+\delta_1) \times (-\delta_1,\delta_1) \times (-\delta_1,1+\delta_1)$ satisfies $F(y,z,\mu,\tau,s) = 0$ if and only if $(y,z) = (y(\mu,\tau,s),z(\mu,\tau,s))$ and it solves (3.17). We observe that

$$\begin{aligned}
&y(\mu,\tau,\sigma_2(\mu,\tau)) = -\sigma_2(\mu,\tau),\\
&z(\mu,\tau,\sigma_1(\mu,\tau)) = \sigma_1(\mu,\tau) - 1.
\end{aligned} \tag{3.19}$$

We define $\xi(\mu,\tau,s)$ by the formula

$$P_sF(y(\mu,\tau,s),z(\mu,\tau,s),\mu,\tau,s) = \xi(\mu,\tau,s)(1,-1),$$

and using (3.16) we have that it admits the following decomposition

$$\xi(\mu,\tau,s) = (\sigma_1(\mu,\tau) - s)(s - \sigma_2(\mu,\tau))\tau\xi_1(\mu,\tau,s).$$

It is easy to check that

$$\xi(\mu,\tau,s) = \frac{1}{|\Omega|}\int_\Omega (y+z)(sz - (1-s)y),$$

therefore $\xi_\tau(\mu,0,s) = 0$. Then,

$$\xi(\mu,\tau,s) = (\sigma_1(\mu,\tau) - s)(s - \sigma_2(\mu,\tau))\tau^2\xi_2(\mu,\tau,s).$$

To find the nontrivial solutions of (3.18) we need to solve

$$\xi_2(\mu,\tau,s) = 0, \tag{3.20}$$

with $s \in (0,1)$, which will be done by using the implicit function theorem, expressing the solutions of (3.20) as $(\mu,\tau,s(\mu,\tau))$ with $(\mu,0,s(\mu,0))$ being solutions of $\xi_2(\mu,0,s)$. Differentiating the above equation we obtain that

$$\xi_{\tau\tau}(\mu,0,s) = 2s(1-s)\xi_2(\mu,0,s). \tag{3.21}$$

After a simple computation we have that

$$\xi_{\tau\tau}(\mu,0,s)=\frac{2}{|\Omega|}\int_\Omega (z_1+y_1)(sz_1-(1-s)y_1), \tag{3.22}$$

where $y_1=y_\tau(\mu,0,s)$, $z_1=z_\tau(\mu,0,s)$. If we differentiate equation (3.18) with respect to τ and evaluate it at $\tau=0$ we obtain that $(y_1,z_1)\in X_2$ satisfy

$$\begin{cases} \mu(1+\gamma)\Delta y_1+\mu\gamma s\Delta(y_1+z_1)-s(y_1+z_1)+\mu s\Delta\rho_1=0 \text{ in } \Omega,\\ \mu(1+\gamma)\Delta z_1+\mu\gamma(1-s)\Delta(y_1+z_1)-(1-s)(y_1+z_1)+\mu(1-s)\Delta\rho_2=0 \text{ in } \Omega,\\ \frac{\partial y_1}{\partial\nu}=\frac{\partial y_2}{\partial\nu}=0 \text{ on } \partial\Omega. \end{cases} \tag{3.23}$$

Adding the two equations of (3.23), we obtain that $w=y_1+z_1$ is the unique solution of

$$\mu(1+2\gamma)\Delta w-w+\mu s\Delta\rho_1+\mu(1-s)\Delta\rho_2=0 \text{ in } \Omega,\ \frac{\partial w}{\partial\nu}=0 \text{ on } \partial\Omega. \tag{3.24}$$

Define w_1, w_2 the unique solutions of

$$\mu(1+2\gamma)\Delta w_1-w_1+\mu(\Delta\rho_1-\Delta\rho_2)=0 \text{ in } \Omega,\ \frac{\partial w_1}{\partial\nu}=0 \text{ on } \partial\Omega, \tag{3.25}$$

$$\mu(1+2\gamma)\Delta w_2-w_2+\mu\Delta\rho_2=0 \text{ in } \Omega,\ \frac{\partial w_2}{\partial\nu}=0 \text{ on } \partial\Omega, \tag{3.26}$$

respectively. Adding the equations (3.25) and (3.26) we obtain that $w=sw_1+w_2$. Moreover, replacing y_1+z_1 by w in (3.23) we obtain that $y_1=su_1$, $z_1=(1-s)v_1$ where u_1,v_1 satisfy

$$\mu(1+\gamma)\Delta u_1+\mu\gamma\Delta w-w+\mu\Delta\rho_1=0 \text{ in } \Omega, \tag{3.27}$$

$$\mu(1+\gamma)\Delta v_1+\mu\gamma\Delta w-w+\mu\Delta\rho_2=0 \text{ in } \Omega, \tag{3.28}$$

$$\frac{\partial u_1}{\partial\nu}=\frac{\partial u_2}{\partial\nu}=0 \text{ on } \partial\Omega.$$

Subtracting (3.27), (3.28) we obtain that

$$u_1-v_1=\frac{1}{1+\gamma}(\rho_2-\rho_1+C), \tag{3.29}$$

where $C=\fint_\Omega(\rho_1-\rho_2)$. Since $y_1+z_1=w$ we have that

$$su_1+(1-s)v_1=w, \tag{3.30}$$

which together with (3.29) gives that

$$u_1 = sw_1+w_2+\frac{s-1}{1+\gamma}(\rho_1-\rho_2-C), \tag{3.31}$$

$$v_1 = sw_1+w_2+\frac{s}{1+\gamma}(\rho_1-\rho_2-C). \tag{3.32}$$

Replacing the expressions for u_1,v_1 in (3.21), (3.22), and using $\fint_\Omega w=0$ we obtain that

$$\xi_2(\mu,0,s)=\frac{1}{|\Omega|}\int_\Omega w(\rho_1-\rho_2)=\frac{1}{(1+\gamma)|\Omega|}\int_\Omega (sw_1+w_2)(\rho_1-\rho_2). \tag{3.33}$$

Thus, to have bifurcation s should satisfy

$$s\int_\Omega w_1(\rho_1-\rho_2)+\int_\Omega w_2(\rho_1-\rho_2)=0. \tag{3.34}$$

Since $w_1=\mu T_\mu^{-1}\Delta(\rho_1-\rho_2)$ and $w_2=\mu T_\mu^{-1}\Delta\rho_2$, thus if $\nabla(\rho_1-\rho_2)\not\equiv 0$ we have

$$\int_\Omega w_1(\rho_1-\rho_2)=\mu\int_\Omega (T_\mu^{-1}\Delta(\rho_1-\rho_2))(\rho_1-\rho_2)<0. \tag{3.35}$$

Therefore, by the implicit function theorem there exists $\delta>0$ such that we can find a solution $s(\mu,\tau)$ of (3.20) satisfying

$$s(\mu,0)=\frac{\int_\Omega w_2(\rho_2-\rho_1)}{\int_\Omega w_1(\rho_1-\rho_2)}. \tag{3.36}$$

Using the functions $G(\mu)$ and $H(\mu)$ we can rewrite the above condition as

$$s(\mu,0)=\frac{G(\mu)}{G(\mu)+H(\mu)}, \tag{3.37}$$

and we observe that in order to have $0<s(\mu,0)<1$ we must have that

$$G(\mu)>0,\ \ H(\mu)>0. \tag{3.38}$$

To conclude (3.11) and (3.12) we set

$$\bar{y}(\mu,\tau)=y(\mu,\tau,s(\mu,\tau)),\quad \bar{z}(\mu,\tau)=z(\mu,\tau,s(\mu,\tau)).$$

□

Remark 3.1. Using (3.19) it is easy to prove that when (3.12) holds in Theorem 3.1, then the solution $(u(\mu,\tau),v(\mu,\tau))$ can be expressed as

$$\begin{aligned} u(\mu,\tau)&=(s(\mu,\tau)-\sigma_2(\mu,\tau))(1+\tau\tilde{y}(\mu,\tau)),\\ v(\mu,\tau)&=(\sigma_1(\mu,\tau)-s(\mu,\tau))(1+\tau\tilde{z}(\mu,\tau)), \end{aligned} \tag{3.39}$$

where $(\tilde{y}(\mu,\tau),\tilde{z}(\mu,\tau))\in X_2$ are smooth functions.

As a consequence of this remark we can refine alternative (1) of Theorem 3.1.

Proposition 3.2. *Suppose that the hypothesis of Theorem* 3.1 (1) *hold and that* μ_1 *is a simple zero of* GH. *Then, there exists* $\tau_1>0$ *and a smooth function* $\underline{\mu}:[0,\tau_1]\to I\!R$ *such that* $\underline{\mu}(0)=\mu_1$ *and for* $\tau\in(0,\tau_1]$ *the steady states of* (1.3) *as given in* (3.11)-(3.12) *are positive whenever* $\underline{\mu}(\tau)<\mu<\mu_2-\delta$ *and semitrivial if* $\mu=\underline{\mu}(\tau)$, *where* δ *is taken as in Theorem* 3.1 (1).

Proof. We consider the case $G(\mu_1)=0$ and we prove the existence of the function $\underline{\mu}$. The case $H(\mu_1)=0$ is similar. Observe that by (3.39) the functions $u(\mu,\tau)$ and $v(\mu,\tau)$ are positive when $s(\mu,\tau)>\sigma_2(\mu,\tau)$ and $s(\mu,\tau)<\sigma_1(\mu,\tau)$. Since $s(\mu,0)=G(\mu)/(G(\mu)+H(\mu))$, we just have to prove our result when $\mu\sim\mu_1$. By assumption $\frac{\partial s}{\partial\mu}(\mu_1,0)=G'(\mu_1)/H(\mu_1)>0$, and since $\sigma_2(\mu,0)=0$ we have $\frac{\partial\sigma_2}{\partial\mu}(\mu_1,0)=0$, hence we can use the implicit function theorem to find $\tau_1>0$ and a function $\underline{\mu}:[0,\tau_1]\to I\!R$ satisfying $s(\underline{\mu}(\tau),\tau)-\sigma_2(\underline{\mu}(\tau),\tau)=0$. Since $\frac{\partial s}{\partial\mu}(\mu_1,0)>0$ we have that $s(\mu,\tau)-\sigma_2(\mu,\tau)>0$ for $\mu\sim\mu_1$ whenever $\mu>\underline{\mu}(\tau)$. □

Corollary 3.1. *Suppose that*

$$\int_\Omega |\nabla\rho_1|^2 > \int_\Omega \nabla\rho_1\cdot\nabla\rho_2 \text{ and } \int_\Omega |\nabla\rho_2|^2 > \int_\Omega \nabla\rho_1\cdot\nabla\rho_2. \tag{3.40}$$

Then, there exists $\mu_0 > 0$ *such that for every* $0<\mu<\mu_0$ *there is a* τ_4 *for which system* (1.3) *admits a unique positive solution provided that* $0<\tau<\tau_4$.

Proof. To apply the theorem above we just need to prove that for μ small enough we have that $G(\mu)>0$ and $H(\mu)>0$. By doing a standard blow-up argument, it is easy to show that if $f\in C(\overline{\Omega})$ then as $\mu\to 0$ we have $T_\mu^{-1}(f)\to f$ uniformly in Ω. Therefore as $\mu\to 0$,

$$H(\mu)\to\int_\Omega \Delta\rho_1(\rho_2-\rho_1),\quad G(\mu)\to\int_\Omega \Delta\rho_2(\rho_1-\rho_2),$$

and integrating by parts we obtain from (3.40) that $H(\mu)>0$ and $G(\mu)>0$ if μ is small enough. □

Corollary 3.2. *Suppose that for* $i=1,2$

$$\int_\Omega\int_\Omega(\rho_i(x)-\rho_i(y))^2dx\,dy > \int_\Omega\int_\Omega(\rho_1(x)-\rho_1(y))(\rho_2(x)-\rho_2(y))dx\,dy. \tag{3.41}$$

Then, there exists $\mu_1>0$ *such that for every* $\mu>\mu_1$ *there is a* τ_5 *for which system* (1.3) *admits a unique positive solution provided that* $0<\tau<\tau_5$.

Proof. As in the previous corollary, we just have to check that $G(\mu)>0$ and $H(\mu)>0$ for μ large enough. It is easy to check that as $\mu\to\infty$ we have that

$$\mu(1+2\gamma)T_\mu^{-1}(\Delta\rho_i)\to -\rho_i+\bar{\rho}_i \text{ for } i=1,2,$$

uniformly in Ω, where $\bar{\rho}_i=(1/|\Omega|)\int_\Omega\rho_i$. Thus, as $\mu\to\infty$

$$\mu(1+2\gamma)H(\mu)\to\int_\Omega(\rho_1-\bar{\rho}_1)(\rho_1-\rho_2) \text{ and } \mu(1+2\gamma)G(\mu)\to\int_\Omega(\rho_2-\bar{\rho}_2)(\rho_2-\rho_1).$$

After a simple expansion, it is easy to verify that the conditions (3.41) are equivalent to $H(\mu)>0$ and $G(\mu)>0$. □

Observe that the hypothesis in Corollaries 3.1, 3.2 hold if $\Omega=(0,1)$ and ρ_1 increasing and ρ_2 decreasing in $(0,1)$, or ρ_1 decreasing and ρ_2 increasing in $(0,1)$. Indeed, one can prove that in this case $G(\mu)>0$ and $H(\mu)>0$ for every $0<\mu<\infty$.

Corollary 3.3. *Suppose that* $\Omega=(0,1)$, $\rho_1'(x)\ge 0\ge\rho_2'(x)$ *or* $\rho_1'(x)\le 0\le\rho_2'(x)$ *for all* $x\in(0,1)$, *and* $\rho_1'\not\equiv 0$, $\rho_2'\not\equiv 0$. *Then for all* $0<\mu<\infty$, *there exists* τ_6 *such that* $G(\mu)>0$ *and* $H(\mu)>0$ *provided that* $0<\tau<\tau_6$.

Proof. We only consider the case ρ_1 increasing and ρ_2 decreasing in $(0,1)$. Note that because the operator T_μ^{-1} is self adjoint we have that

$$H(\mu)=\int_\Omega T_\mu^{-1}(\rho_2-\rho_1)\Delta\rho_1 \text{ and } G(\mu)=\int_\Omega T_\mu^{-1}(\rho_1-\rho_2)\Delta\rho_2.$$

Since $\rho_2-\rho_1$ is decreasing and nontrivial, the solution $f=T_\mu^{-1}(\rho_2-\rho_1)$ of

$$-\mu(1+2\gamma)f''+f=\rho_2-\rho_1 \text{ in } (0,1),\ f'(0)=f'(1)=0$$

is decreasing with $f' < 0$ in $(0,1)$. Therefore, using integration by parts

$$H(\mu) = \int_\Omega f \rho_1'' = -\int_\Omega f' \rho_1' > 0.$$

Similarly, we can show that $G(\mu) > 0$. □

Similar as previous corollary, we have the following

Corollary 3.4. *Suppose that $\Omega = (0,1)$, $\rho_1'(x) \ge \rho_2'(x) \ge 0$ or $\rho_1'(x) \le \rho_2'(x) \le 0$ for all $x \in (0,1)$. Then for all $\mu > 0$, there exists τ_7 such that for $0 < \tau < \tau_7$, $G(\mu)H(\mu) < 0$.*

The next result, which is an generalization of Proposition 2.2, states that a necessary condition to have nonconstant positive steady states for small τ is that both ρ_1 and ρ_2 must be nonconstant.

Proposition 3.3. *Suppose that $\rho_2 \ge 0$ is constant. Then for every $\mu > 0$, there exists τ_8 such that* (1.3) *does not admit any nonconstant positive solutions for any $0 < \tau < \tau_8$.*

Proof. We just need to consider the case $\rho_1 \ge 0$ nonconstant. We argue by contradiction. Suppose that we have a sequence (u_τ, v_τ) of nonconstant positive steady states, with $\tau \to 0$. Then, we can write $u_\tau = \overline{u}_\tau + y_\tau$, $v_\tau = \overline{v}_\tau + z_\tau$, with $\int_\Omega y_\tau = \int_\Omega z_\tau = 0$, $||y_\tau||_\infty + ||z_\tau||_\infty \ne 0$ and $(y_\tau, z_\tau) \to (0,0)$ in $C^{2,\gamma}(\overline{\Omega})$. In this situation we have that $H(\mu) > 0$ and $G(\mu) = 0$. Therefore, by (3.20) and (3.37) we obtain that $\overline{u}_\tau \to 0$ and $\overline{v}_\tau \to 1$ as $\tau \to 0$. Moreover, using that $\int_\Omega (1 - u_\tau - v_\tau) v_\tau = 0$ we can deduce that there exists a constant $C > 0$ such that

$$|1 - \overline{u}_\tau - \overline{v}_\tau| \le C \left(||y_\tau||_\infty^2 + ||z_\tau||_\infty^2 \right). \tag{3.42}$$

After doing some expansions, and using the inequality above we can prove that

$$\begin{aligned} &\mu(1+\gamma)\Delta y_\tau = -\mu\tau(\bar{u}_\tau + \bar{v}_\tau)\bar{u}_\tau \Delta\rho_1 + f_\tau \text{ in } \Omega, \\ &\mu(1+\gamma)\Delta z_\tau + \mu\gamma\Delta(y_\tau + z_\tau) - y_\tau - z_\tau = g_\tau \text{ in } \Omega, \end{aligned} \tag{3.43}$$

with $||f_\tau||_{2,p} + ||g_\tau||_{2,p} \le o(1)(||y_\tau||_{2,p} + ||z_\tau||_{2,p})$. By (3.43), and using the fact that $\int_\Omega y_\tau = \int_\Omega z_\tau = 0$, we conclude by elliptic regularity that

$$||y_\tau||_{2,p} + ||z_\tau||_{2,p} \le C\tau\bar{u}_\tau,$$

for some constant $C > 0$. Define $\tilde{y}_\tau = y_\tau/\tau\bar{u}_\tau$, $\tilde{z}_\tau = z_\tau/\tau\bar{u}_\tau$. Using the above estimate, considering possibly a subsequence, we have that $\tilde{y}_\tau \to \tilde{y}$, $\tilde{z}_\tau \to \tilde{z}$ as $\tau \to 0$. Doing some expansions we find that $\tilde{y}$ and $\tilde{z}$ are solutions of

$$\begin{aligned} &\mu(1+\gamma)\Delta\tilde{y} + \mu\Delta\rho_1 = 0 \text{ in } \Omega, \\ &\mu(1+\gamma)\Delta\tilde{z} + \mu\gamma\Delta(y+z) - \tilde{z} - \tilde{y} = 0 \text{ in } \Omega, \\ &\tfrac{\partial\tilde{y}}{\partial\nu} = \tfrac{\partial\tilde{z}}{\partial\nu} = 0 \text{ on } \partial\Omega, \ \textstyle\int_\Omega \tilde{y} = \int_\Omega \tilde{z} = 0. \end{aligned} \tag{3.44}$$

Hence, we have that $\tilde{y} = \frac{1}{1+\gamma}(-\rho_1 + \bar{\rho}_1)$, where $\bar{\rho}_1$ denotes the average in Ω of ρ_1. If we expand in Fourier series $\rho_1 = \sum_{i=0}^\infty \rho_1^k \varphi_k$, where (φ_k, λ_k), for $k \ge 0$, are the eigenfunctions and eigenvalues of

$$\Delta\varphi_k + \lambda_k\varphi_k = 0 \ \text{ in } \Omega, \ \frac{\partial\varphi_k}{\partial\nu} = 0 \text{ on } \ \partial\Omega, \tag{3.45}$$

we have that

$$\tilde{y} = -\frac{1}{1+\gamma}\sum_{i=1}^{\infty}\rho_1^k\varphi_k, \quad \tilde{z} = \frac{1}{(1+\gamma)}\sum_{i=1}^{\infty}\frac{(\mu\gamma\lambda_k+1)\rho_1^k}{\mu(1+2\gamma)\lambda_k+1}\varphi_k. \tag{3.46}$$

Now, if we integrate the first equation of (1.3) and we divide it by $\tau\bar{u}_\tau$ we obtain that

$$\int_\Omega \tilde{y}_\tau(\tilde{y}_\tau+\tilde{z}_\tau) = \frac{|\Omega|}{\tau^2\bar{u}_\tau}(1-\bar{u}_\tau-\bar{v}_\tau) \le C\bar{u}_\tau \ \to 0 \tag{3.47}$$

as $\tau \to 0$, where the last inequality holds in view of (3.42). On the other hand, by (3.46) we obtain that

$$\int_\Omega \tilde{y}(\tilde{y}+\tilde{z}) = -\frac{\mu}{1+\gamma}\sum_{i=1}^{\infty}\frac{\lambda_k(\rho_1^k)^2}{(1+2\gamma)\mu\lambda_k+1} < 0,$$

which contradicts (3.47). □

4. Stability of steady states

In this section we study the stability of steady states including both positive steady states constructed in Theorem 3.1 and two semi-trivial steady states of (1.1). The main results of this section are Propositions 4.1 and 4.2 and Theorem 4.1.

For each solution (u,v) of (1.3) we have the following eigenvalue problem

$$\begin{cases} \mu\Delta[(1+(\gamma+\tau\rho_1)(u+v))\varphi] + \mu\Delta[(\gamma+\tau\rho_1)(\varphi+\psi)u] + \alpha\varphi - (\varphi+\psi)u & = \lambda\varphi \\ \mu\Delta[(1+(\gamma+\tau\rho_2)(u+v))\psi] + \mu\Delta[(\gamma+\tau\rho_2)(\varphi+\psi)v] + \alpha\psi - (\varphi+\psi)v & = \lambda\psi \\ \frac{\partial\varphi}{\partial\nu} = \frac{\partial\psi}{\partial\nu} = 0 \end{cases} \tag{4.48}$$

where $\alpha = (1-u-v)$. Observe that (4.48) above corresponds to the linearization of (1.1) at the equilibrium (u,v). It follows from [38], that if all the eigenvalues of (4.48) have negative real parts, then the equilibrium (u,v) is asymptotically stable, while if (4.48) has eigenvalues with positive real parts, then a local unstable manifold arises.

After some computations it is easy to obtain the following relation:

$$\begin{aligned} \frac{\lambda}{\mu}\int_\Omega(\varphi v - \psi u) = \ & \tau\left\{\int_\Omega \Delta[\rho_1(u+v)\varphi]v + \int_\Omega \Delta[\rho_1(\varphi+\psi)u]v \right. \\ & - \int_\Omega \Delta[\rho_2(u+v)v]\varphi - \int_\Omega \Delta[\rho_2(u+v)\psi]u \\ & \left. - \int_\Omega \Delta[\rho_2(\varphi+\psi)v]u + \int_\Omega \Delta[\rho_1(u+v)u]\psi\right\} \\ & +\gamma\left\{\int_\Omega \Delta[(u+v)\varphi]v + \int_\Omega \Delta[(\varphi+\psi)u]v \right. \\ & - \int_\Omega \Delta[(u+v)\psi]u - \int_\Omega \Delta[(\varphi+\psi)v]u \\ & \left. + \int_\Omega \Delta[(u+v)u]\psi - \int_\Omega \Delta[(u+v)v]\varphi\right\}. \end{aligned} \tag{4.49}$$

We start by studying the stability properties of the semitrivial steady states.

4.1. Stability of the semitrivial steady states.

We consider the semitrivial steady state solution $(\theta_1(\mu,\tau),0)$ of (1.1), for $\tau > 0$ small. The stability properties of this steady state is given by the sign of the principal eigenvalue $\lambda_u(\mu,\tau)$ of

$$\begin{cases} \mu\Delta\left[(1+(\gamma+\tau\rho_2)\theta_1)\psi\right] + (1-\theta_1)\psi = \lambda_u(\mu,\tau)\psi \ \text{ in } \Omega, \\ \frac{\partial\psi}{\partial\nu} = 0 \ \text{ on } \partial\Omega. \end{cases} \tag{4.50}$$

In this situation formula (4.49) can be simplified as

$$\frac{\lambda_u(\mu,\tau)}{\mu}\int_\Omega \psi\theta_1=\int_\Omega \tau\left[\nabla\left(\rho_1\theta_1^2\right)\nabla\psi-\nabla\left(\rho_2\theta_1\psi\right)\nabla\theta_1\right]+\gamma\left[\nabla\theta_1^2\nabla\psi-\nabla(\theta_1\psi)\nabla\theta_1\right]. \tag{4.51}$$

We can expand the functions θ_1 and ψ as

$$\theta_1(\mu,\tau)=1+\tau\omega_1(\mu,\tau),\ \psi(\mu,\tau)=-1+\tau\psi_1(\mu,\tau), \tag{4.52}$$

where ω_1, ψ_1 are smooth functions. Thus, we obtain from (4.51) that

$$\frac{\lambda_u(\mu,\tau)}{\tau^2\mu}=\frac{M(\mu,\tau)}{\int_\Omega\psi\theta_1}, \tag{4.53}$$

where

$$\begin{aligned} M(\mu,\tau)= &\int_\Omega\left[\nabla\left(\rho_1(1+\tau\omega_1)^2\right)\nabla\psi_1+\nabla\left(\rho_2(1+\tau\omega_1)(1-\tau\psi_1)\right)\nabla\omega_1\right]\\ &+\gamma\int_\Omega\left[|\nabla\omega_1|^2+\nabla\omega_1\nabla\psi_1+\tau(\nabla\omega_1^2\nabla\psi_1-\nabla(\omega_1\psi_1)\nabla\omega_1)\right].\end{aligned}$$

In our first result we show that the stability of $(\theta_1(\mu,\tau),0)$ can be characterized in terms of the function $H(\mu)$ for τ small.

Lemma 4.1. *We have*

$$\lim_{\tau\to0}\frac{\lambda_u(\mu,\tau)}{\tau^2}=\frac{H(\mu)}{(1+\gamma)|\Omega|}.$$

Proof. Since τ is small and M is smooth, we can write the expansion $M(\mu,\tau)=M(\mu,0)+O(\tau)$, where

$$M(\mu,0)=\int_\Omega\gamma(|\nabla\omega_1(\mu,0)|^2+\nabla\psi_1(\mu,0)\nabla\omega_1(\mu,0))+\nabla\rho_1\nabla\psi_1(\mu,0)+\nabla\rho_2\nabla\omega_1(\mu,0).$$

It can be easily seen that $\omega_1(\mu,0),\psi_1(\mu,0)$ satisfy

$$\begin{cases}\mu(1+2\gamma)\Delta\omega_1-\omega_1=-\mu\Delta\rho_1 \ \text{ in } \Omega,\\ \mu(1+\gamma)\Delta\psi_1-\mu\gamma\Delta\omega_1+\omega_1=\mu\Delta\rho_2 \ \text{ in } \Omega,\\ \frac{\partial\omega_1}{\partial\nu}=\frac{\partial\psi_1}{\partial\nu}=0 \ \text{ on } \partial\Omega.\end{cases} \tag{4.54}$$

By some computations we obtain that

$$M(\mu,0)=-\frac{1}{\mu(1+\gamma)}\int_\Omega\omega_1(\mu,0)(\rho_2-\rho_1)dx=-\frac{H(\mu)}{1+\gamma},$$

since $\omega_1(\mu,0)=T_\mu^{-1}(\mu\Delta\rho_1)$. Using that $\int_\Omega\psi\theta_1dx\to-|\Omega|$ as $\tau\to0$ we conclude the desired result. □

The above result establishes the stability of the semi-trivial steady state $(\theta_1,0)$ at μ_1 for which $H(\mu)\neq0$. Suppose that $H(\mu^*)=0$ and $H'(\mu^*)\neq0$. In this situation, by Theorem 3.1 there exists a branch of nontrivial positive solutions bifurcating from $(\theta_1,0)$. More precisely, by Proposition 3.2 there exists a smooth function $\hat\mu(\tau)$, defined for small

$\tau \geq 0$ with $\hat{\mu}(0) = \mu^*$, such that $\lambda(\hat{\mu}(\tau), \tau) = 0$. In this situation we have that for $\mu \sim \mu^*$ and $\tau \sim 0$ the function $M(\mu, \tau)$ can be expanded as

$$\begin{aligned} M(\mu, \tau) &= M(\mu, \tau) - M(\hat{\mu}(\tau), \tau) \\ &= \tfrac{\partial M}{\partial \mu}(\mu_\tau, 0)(\mu - \hat{\mu}(\tau)) \\ &= -H'(\mu_\tau)(\mu - \hat{\mu}(\tau)), \end{aligned}$$

where μ_τ lies in the interval $[\mu, \hat{\mu}(\tau)]$ or $[\hat{\mu}(\tau), \mu]$. Therefore, the following result holds:

Lemma 4.2. *Suppose that $H(\mu^*) = 0$ and $H'(\mu^*) \neq 0$. Then*

$$\lim_{\tau \to 0} \frac{\lambda_u(\mu, \tau)}{\tau^2(\mu - \hat{\mu}(\tau))} = \frac{H'(\mu^*)}{(1+\gamma)|\Omega|}.$$

Thus, as a consequence of lemmas 4.1 and 4.2 we can prove the following result

Proposition 4.1. *For $0 < \mu^* < \infty$ the semi-trivial steady state $(\theta_1(\mu^*, \tau), 0)$ of (1.1) is asymptotically stable whenever $H(\mu^*) < 0$ and unstable when $H(\mu^*) > 0$ provided that $\tau > 0$ is small enough. Moreover if $H(\mu^*) = 0$ and $H'(\mu^*) \neq 0$ then there exists $\delta > 0$ such that for small τ we can find $\hat{\mu}(\tau)$, with $\hat{\mu}(0) = \mu^*$, such that for $\mu \in (\mu^* - \delta, \mu^* + \delta)$ the steady state $(\theta_1(\mu, \tau), 0)$ is unstable when $H'(\mu^*)(\mu - \hat{\mu}(\tau)) > 0$, and asymptotically stable when $H'(\mu^*)(\mu - \hat{\mu}(\tau)) < 0$.*

Similarly, we can prove the following result for $(0, \theta_2(\mu, \tau))$.

Proposition 4.2. *For $0 < \mu^* < \infty$ the semi-trivial steady state $(0, \theta_2(\mu, \tau))$ of (1.1) is asymptotically stable whenever $G(\mu^*) < 0$ and unstable when $G(\mu^*) > 0$ provided that $\tau > 0$ is small enough. Moreover if $G(\mu^*) = 0$ and $G'(\mu^*) \neq 0$ then there exists $\delta > 0$ such that for small τ we can find $\hat{\mu}(\tau)$, with $\hat{\mu}(0) = \mu^*$, such that for $\mu \in (\mu^* - \delta, \mu^* + \delta)$ the steady state $(0, \theta_2(\mu, \tau))$ is unstable when $G'(\mu^*)(\mu - \hat{\mu}(\tau)) > 0$, and asymptotically stable when $G'(\mu^*)(\mu - \hat{\mu}(\tau)) < 0$.*

4.2. **Stability of positive steady states.**

In this subsection we study the sign of the largest eigenvalue of (4.48) corresponding to solutions (u, v) close to $(s\theta, (1-s)\theta)$, for $s := s(\mu, 0) = G/(G+H)$, as given by Theorem 3.1 (1) and Proposition 3.2.

Choosing appropriately the eigenfunction (φ, ψ) associated to $\lambda(\mu, \tau)$, the *principal* eigenvalue of (4.48), they satisfy $\varphi \to 1$, $\psi \to -1$. Indeed, we have the following expansions

$$\begin{aligned} u &= s + \tau U_1(\mu, \tau) \\ v &= (1-s) + \tau V_1(\mu, \tau) \\ \varphi &= 1 + \tau \varphi_1(\mu, \tau) \\ \psi &= -1 + \tau \psi_1(\mu, \tau) \end{aligned} \tag{4.55}$$

where $\tau U_1(\mu, \tau) = \bar{y}(\mu, \tau)$, $\tau V_1(\mu, \tau) = \bar{z}(\mu, \tau)$ with $\bar{y}, \bar{z}$ as in (3.11)-(3.12) and the smooth functions $\varphi_1(\mu, \tau), \psi_1(\mu, \tau) \in \operatorname{span}\{((1-s), -s)\}^\perp$. By (3.23) we have that $(U_1(\mu, 0), V_1(\mu, 0))$ are solutions of

$$\begin{aligned} &\mu(1+\gamma)\Delta U_1 + \mu\gamma s \Delta(U_1 + V_1) - s(U_1 + V_1) + \mu s \Delta \rho_1 = 0 \ \text{ in } \Omega, \\ &\mu(1+\gamma)\Delta V_1 + \mu\gamma(1-s)\Delta(U_1 + V_1) - (1-s)(U_1 + V_1) + \mu(1-s)\Delta \rho_2 = 0 \ \text{ in } \Omega, \\ &\frac{\partial U_1}{\partial \nu} = \frac{\partial V_1}{\partial \nu} = 0 \ \text{ on } \partial\Omega, \end{aligned} \tag{4.56}$$

and after a simple expansion we have that $(\varphi_1(\mu,0),\psi_1(\mu,0))$ satisfy

$$\begin{aligned}&\mu(1+\gamma)\Delta\varphi_1+\mu\gamma s\Delta(\varphi_1+\psi_1)-s(\varphi_1+\psi_1)\\ &\qquad+\mu\gamma\Delta(U_1+V_1)-(U_1+V_1)+\mu\Delta\rho_1=0 \qquad \text{in } \Omega,\\ &\mu(1+\gamma)\Delta\psi_1+\mu\gamma(1-s)\Delta(\varphi_1+\psi_1)-(1-s)(\varphi_1+\psi_1)\\ &\qquad-\mu\gamma\Delta(U_1+V_1)+(U_1+V_1)-\mu\Delta\rho_2=0 \qquad \text{in } \Omega,\\ &\frac{\partial\varphi_1}{\partial\nu}=\frac{\partial\psi_1}{\partial\nu}=0 \ \text{ on } \partial\Omega.\end{aligned} \tag{4.57}$$

¿From now on we denote $U_1=U_1(\mu,0)$, $V_1=V_1(\mu,0)$, $\varphi_1=\varphi_1(\mu,0)$ and $\psi_1=\psi_1(\mu,0)$. Using (4.49) and

$$\int_\Omega \Delta U_1=\int_\Omega \Delta V_1=\int_\Omega \Delta\varphi_1=\int_\Omega \Delta\psi_1=0,$$

we obtain the following formula for λ/τ^2 in terms of (U_1,V_1), (φ_1,ψ_1),

$$\frac{\lambda|\Omega|}{\mu\tau^2}=I_1(\mu)+I_2(\mu)+I_3(\mu)+I_4(\mu)+\tau J(\mu,\tau), \tag{4.58}$$

where $J(\mu,\tau)$ is a smooth function and

$$\begin{aligned}I_1(\mu)&=\textstyle\int_\Omega[\Delta\rho_1+\gamma\Delta\varphi_1+\gamma\Delta(U_1+V_1)+s\gamma\Delta(\varphi_1+\psi_1)]V_1,\\ I_2(\mu)&=\textstyle\int_\Omega[\Delta\rho_2-\gamma\Delta\psi_1+\gamma\Delta(U_1+V_1)-(1-s)\gamma\Delta(\varphi_1+\psi_1)]U_1,\\ I_3(\mu)&=\textstyle\int_\Omega[-(1-s)\Delta\rho_2-\gamma\Delta V_1-(1-s)\gamma\Delta(U_1+V_1)]\varphi_1\\ I_4(\mu)&=\textstyle\int_\Omega[s\Delta\rho_1+\gamma\Delta U_1+\gamma s\Delta(U_1+V_1)]\psi_1.\end{aligned}$$

Multiplying the first equation of (4.57) by V_1 and the second by U_1 and integrating both by parts we obtain that

$$\begin{aligned}I_1(\mu)&=\tfrac{1}{\mu}\textstyle\int_\Omega[\mu\nabla\varphi_1\nabla V_1+s(\varphi_1+\psi_1)V_1+(U_1+V_1)V_1],\\ I_2(\mu)&=\tfrac{1}{\mu}\textstyle\int_\Omega[-\mu\nabla\psi_1\nabla U_1-(1-s)(\varphi_1+\psi_1)U_1+(U_1+V_1)U_1].\end{aligned} \tag{4.59}$$

Similarly, if we multiply the second equation of (4.56) by φ_1 and the first by ψ_1 and we integrate both by parts we get

$$\begin{aligned}I_3(\mu)&=\tfrac{1}{\mu}\textstyle\int_\Omega[-\mu\nabla V_1\nabla\varphi_1-(1-s)(U_1+V_1)\varphi_1],\\ I_4(\mu)&=\tfrac{1}{\mu}\textstyle\int_\Omega[\mu\nabla U_1\nabla\psi_1+s(U_1+V_1)\psi_1],\end{aligned} \tag{4.60}$$

therefore, replacing (4.59) and (4.60) in (4.58) we obtain the following expression

$$\frac{\lambda|\Omega|}{\tau^2}=\int_\Omega[(\varphi_1+\psi_1)(sV_1-(1-s)U_1)+(U_1+V_1)(s\psi_1-(1-s)\varphi_1+U_1+V_1)]+O(\tau), \tag{4.61}$$

where $s=s(\mu,\tau)$.

Proposition 4.3. *We have*

$$\frac{\lambda(\tau)|\Omega|}{\tau^2}=-\frac{1}{1+\gamma}\left[\frac{GH}{G+H}+O(\tau)\right]. \tag{4.62}$$

Proof. Using (4.56) and (4.57) we can easily check that $s\psi_1-(1-s)\varphi_1+U_1+U_2$ satisfies

$$\mu(1+\gamma)\Delta(s\psi_1-(1-s)\varphi_1+U_1+U_2)+\mu(1-2s)\Delta(\rho_2-\rho_1)=0 \quad \text{in } \Omega,$$

from where we conclude that

$$s\psi_1-(1-s)\varphi_1+U_1+V_1=\frac{(1-2s)(\rho_1-\rho_2)}{1+\gamma}+C_1, \tag{4.63}$$

where C_1 is a constant. By (4.56) we can deduce that $sV_1-(1-s)U_1$ satisfies

$$\mu(1+\gamma)\Delta(sV_1-(1-s)U_1)+\mu s(1-s)\Delta(\rho_2-\rho_1)=0,$$

thus

$$sV_1-(1-s)U_1=\frac{s(1-s)(\rho_1-\rho_2)}{1+\gamma}+C_2, \tag{4.64}$$

with C_2 a constant. Hence by (4.61) we have that

$$\frac{\lambda|\Omega|}{\tau^2}=\frac{1}{1+\gamma}\int_\Omega[(\varphi_1+\psi_1)s(1-s)(\rho_1-\rho_2)+(U_1+V_1)(1-2s)(\rho_1-\rho_2)]+O(\tau). \tag{4.65}$$

Now, adding both equations of (4.57) we can see that $\varphi_1+\psi_1$ satisfy (3.25) then $\varphi_1+\psi_1=w_1$ with $w_1=T_\mu^{-1}(\mu\Delta\rho_1-\mu\Delta\rho_2)$ as defined in (3.25). Analogously, by (4.56) we have that U_1+V_1 satisfies (3.24), thus $U_1+V_1=sw_1+w_2$ where $w_2=T_\mu^{-1}(\mu\Delta\rho_2)$. Thus, (4.65) can be rewritten as

$$\frac{\lambda|\Omega|}{\tau^2}=\frac{1}{1+\gamma}[-H(\mu)s(2-3s)+G(\mu)(1-4s+3s^2)]+O(\tau),$$

where we have used the definition of $G(\mu)$ and $H(\mu)$ as stated in (1.5). Finally, using that $s(\mu,0)=G(\mu)/(G(\mu)+H(\mu))$ we obtain from the expression above that

$$\frac{\lambda|\Omega|}{\tau^2}=-\frac{1}{1+\gamma}\left(\frac{G(\mu)H(\mu)}{H(\mu)+G(\mu)}\right)+O(\tau),$$

which proves the desired result. □

Observe that the proposition above gives the stability of the unique positive steady state of (1.1), provided by Theorem 3.1, whenever $H(\mu)>0$ and $G(\mu)>0$. When μ^* is a simple zero of H (or G) and $G(\mu^*)>0$ (and $H(\mu^*)>0$) we have, by Theorem 3.1 and Proposition 3.2, that a bifurcating branch of positive steady states arises. Since at μ^* we have that $[-G/(G+H)]'(\mu^*)<0$, we can proceed as in the proof of Lemma 4.2 to conclude that the bifurcating positive solutions are also asymptotically stable. Then, we can state the following result.

Theorem 4.1. *For every fixed $\mu>0$, there exists a $\tau_0>0$ such that if $0<\tau<\tau_0$, the unique positive steady state, if it exists, is asymptotically stable.*

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