Loops and Branches of Coexistence States in a Lotka-Volterra Competition Model

Y. Lou
Department of Mathematics
Ohio State University
Columbus, Ohio 43210, USA

S. Martínez
Departamento de Ingeniería Matemática
and Centro de Modelamiento Matemático
Universidad de Chile
Casilla 170 Correo 3, Santiago, Chile

P. Poláčik
School of Mathematics
University of Minnesota
Minneapolis, MN 55455, USA

January 10, 2006

Abstract. A two-species Lotka-Volterra competition-diffusion model with spatially inhomogeneous reaction terms is investigated. The two species are assumed to be identical except for their interspecific competition coefficients. Viewing their common diffusion rate μ as a parameter, we describe the bifurcation diagram of the steady states, including stability, in terms of two real functions of μ. We also show that the bifurcation diagram can be rather complicated. Namely, given any two positive integers l and b, the interspecific competition coefficients can be chosen such that there exist at least l bifurcating branches of positive stable steady states which connect two semi-trivial steady states of the same type (they vanish at the same component), and at least b other bifurcating branches of positive stable steady states that connect semi-trivial steady states of different types.

Key words: Reaction-diffusion, competing species, spatial heterogeneity, bifurcation, stability
AMS Classification: 35B40, 35K57, 92D10, 92D25

Contents

1 Introduction

For more than two decades, the effects of the spatial heterogeneity of environment on the invasion of new species and coexistence of multiple species have attracted the attention of both mathematicians and ecologists. Spatial heterogeneity of the environment not only seems to be crucial in creating large amount of patterns, it also brings about interesting mathematical questions. Reaction-diffusion equations have long been used as standard models to mathematically address questions related to spatial heterogeneity. Among these, two-species Lotka-Volterra competition-diffusion models with spatially heterogeneous interactions are probably most studied, see [2]-[12], [14], [18]-[23], [27, 28, 30, 31, 33] and references therein. In this paper we consider such equations with the goal of understanding the effect of a specific feature of the interaction, the difference in the interspecific competition rates, on the coexistence of the competing species.

To motivate our discussions, we start with the semilinear parabolic system

$$u_t = \mu\Delta u + u\,[a(x) - u - v] \qquad \text{in } \Omega \times (0,\infty), \tag{1.1a}$$

$$v_t = \mu\Delta v + v\,[a(x) - u - v] \qquad \text{in } \Omega \times (0,\infty), \tag{1.1b}$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \qquad \text{on } \partial\Omega \times (0,\infty). \tag{1.1c}$$

Here $u(x,t)$ and $v(x,t)$ represent the densities of two competing species at location x and time t, the habitat Ω is a bounded region in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$, and n is the outward unit normal vector on $\partial\Omega$. The zero-flux boundary condition (1.1c) means that no individuals cross the boundary of the habitat. The diffusion rate μ is a positive constant, and $a(x)$ denotes the intrinsic growth rate of species. Observe that in this system the two species are identical in all aspects. This means, in effect, that $u + v$ can be view as the density of one species, and, after adding up the two equations, the system reduces to a scalar logistic reaction-diffusion equation.

From another point of view, the special form of the system means that under natural assumptions, there is a stable curve of steady states which attracts all solutions with nonnegative nontrivial initial data. It is an interesting problem, both mathematically and biologically, to determine how this structure changes under small perturbations.

To make the discussion of the problem more specific, we make the following standing hypotheses on the function $a(x)$.

(A1) The function $a(x)$ is nonconstant, Hölder continuous in $\overline{\Omega}$, and $\int_\Omega a > 0$.

It is well-known that if (A1) holds, the scalar equation

$$\mu\Delta\theta + \theta[a(x) - \theta] = 0 \qquad \text{in } \Omega, \qquad \frac{\partial\theta}{\partial n}\Big|_{\partial\Omega} = 0 \tag{1.2}$$

has a unique positive solution $\theta \in C^2(\overline{\Omega})$ for every $\mu > 0$. Moreover, θ is linearly stable, in particular it is nondegenerate. Hence, by the implicit function theorem, θ depends analytically (as a $W^{2,p}(\Omega)$-valued function, for any $p > 1$) on $\mu \in (0,\infty)$ and $a(x) \in C(\overline{\Omega})$. The following asymptotic behaviors of θ are also well-known (see, e.g., [5, 20]), and will be needed later:

$$\lim_{\mu \to 0+} \theta = a_+, \tag{1.3a}$$

$$\lim_{\mu \to \infty} \theta = \frac{1}{|\Omega|} \int_\Omega a(x)\, dx \tag{1.3b}$$

in $L^\infty(\Omega)$, where $a_+(x) = \max\{a(x), 0\}$. Hence, we may define $\theta(0) = a_+$ and $\theta(\infty) = \int_\Omega a/|\Omega|$.

A steady state (u_e, v_e) with both components positive is referred as a *coexistence state*; (u_e, v_e) is called a *semi-trivial steady state* if one component is positive and the other one is zero.

By assumption (A1), we see that (1.1) has a family of coexistence states, given by $\{(s\theta, (1-s)\theta) : \ 0 < s < 1\}$. Moreover, for any nonnegative non-trivial initial data, the solution of (1.1) converges to $(s_0\theta, (1-s_0)\theta)$ for some $s_0 \in (0,1)$, where s_0 depends on the initial data. This is a consequence of the special structure of the problem mentioned above. The following question arises quite naturally.

Question. What happens when the two species are slightly different, that is, when system (1.1) is perturbed?

Biologically, the question is motivated by the following considerations. Consider a species with intrinsic growth rate $a(x)$, and suppose that random mutation produces a phenotype of species which is slightly different from the original species, for example it has different diffusion rates, or different intrinsic growth rates. It is fairly reasonable to expect that in the race for survival, these two species might have to compete for the same limited resources. The major concern is whether the mutant can invade when rare; if so, will the mutant force the extinction of the original species or coexist with it?

Mathematically, the question leads to the study of various perturbations of system (1.1) and various bifurcation diagrams. Several interesting and surprising phenomena have already been revealed using this approach. One of the first works in this direction appears in [9], where the authors study the parabolic system

$$u_t = \mu \Delta u + u[a(x) - u - v] \qquad \text{in } \Omega \times (0,\infty), \tag{1.4a}$$

$$v_t = (\mu + \tau)\Delta v + v[a(x) - u - v] \qquad \text{in } \Omega \times (0,\infty), \tag{1.4b}$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \qquad \text{on } \partial\Omega \times (0,\infty), \tag{1.4c}$$

where τ is a nonzero constant. Here, the original species and the mutant are identical except for their diffusion rates. Among other things, it is shown in [9] that if (A1) holds and $\tau > 0$, then $(u, v) \to (\theta, 0)$ as $t \to \infty$ for any nonnegative nontrivial initial data. Biologically, this implies that if the two species interact identically with the environment, then the slower diffuser always drive the faster diffuser to extinction, and there is no coexistence state in such scenario. Similar results hold true for the case of nonlocal dispersions, and we refer to [25] for the details. However, when the intrinsic growth rate is periodic in time, it is shown in [21] that the slower diffuser may not always be the winner.

In [24] another perturbation of (1.1) is considered. The system studied there has the form

$$u_t = \mu\Delta u + u[a(x) + \tau g(x) - u - v] \qquad \text{in } \Omega \times (0, \infty), \tag{1.5a}$$

$$v_t = \mu\Delta v + v[a(x) - u - v] \qquad \text{in } \Omega \times (0, \infty), \tag{1.5b}$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \qquad \text{on } \Omega \times (0, \infty). \tag{1.5c}$$

Here the two species are almost identical except for their intrinsic growth rates which differ by a function of $\tau g(x)$, where τ is a positive constant and $g(x)$ is a smooth function. In this situation, a new phenomenon is discovered. By (A1), for small τ, (1.5) has two semi-trivial states in the form of $(\tilde{u}, 0)$ and $(0, \theta)$ for every $\mu > 0$. For small τ, it is shown in [24] that for any fixed positive integer k, one can choose the function g such that $(\tilde{u}, 0)$ and $(0, \theta)$ exchange their stability at least k times as the diffusion rate μ varies over $(0, \infty)$. As a consequence, there are at least k branches of coexistence states of (1.5) which connect $(\tilde{u}, 0)$ and $(0, \theta)$. Biologically, this implies that with small variations of the phenotype, the stability of the two species varies with diffusion in a very complex manner, and it is unpredictable which species will survive. Even though the two species can coexist, they do so only for very narrow regions of μ: the projection of these branches of coexistence states onto μ-axis is of the length of $O(\tau)$.

One of the goals of this paper is to study another perturbation of (1.1). We consider the system

$$u_t = \mu\Delta u + u\,\{a(x) - u - [1 + \tau g(x)]v\} \qquad \text{in } \Omega \times (0, \infty), \tag{1.6a}$$

$$v_t = \mu\Delta v + v\,\{a(x) - v - [1 + \tau h(x)]u\} \qquad \text{in } \Omega \times (0, \infty), \tag{1.6b}$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \qquad \text{on } \Omega \times (0, \infty). \tag{1.6c}$$

Thus now the two species are almost identical except for their interspecific competition rates which are given by $1 + \tau g(x)$ and $1 + \tau h(x)$, respectively, where τ is a positive constant and $g(x)$, $h(x)$ are two smooth functions. As it turns out, within this model new structure of coexistence equilibria is observed. In fact, the bifurcation diagram (viewing μ as a parameter again) can differ considerably from the diagrams found in the previous models. On the other hand, it is interesting that, similarly as in [24], the bifurcation diagram can be described completely in terms of simple real functions of μ.

Let us refer to u, v as the densities of the original species and the mutant, respectively. Define

$$\Omega_+ = \{x \in \Omega : \ g(x) > 0 > h(x)\}, \qquad \Omega_- = \{x \in \Omega : \ g(x) < 0 < h(x)\}.$$

In Ω_+, the mutant has competitive advantage: if the diffusion is not present, then the mutant not only can invade, but also goes to fixation, that is, it forces the extinction of the original phenotype. The outcome is reversed in Ω_-, where the original species has competitive advantage: without diffusion, the mutant goes to extinction in Ω_-. Biologically, when diffusion is present, it would be very interesting to find out whether the mutant can coexist with the original species if Ω_+ is nonempty, and/or whether the mutant can invade even if Ω_- is nonempty. Clearly, such phenomena can occur only when spatial heterogeneity is involved since the answer is negative if both g and h are constant functions. The goal of this paper is to show that for suitably chosen smooth functions g and h with Ω_+ and/or Ω_- being nonempty, the two species can coexist for a wide range of diffusion rates.

Since g and h can be rather general, the dynamics of (1.6) and the structures of coexistence states can potentially be very complicated, and it seems impossible to find any simple criteria which could characterize them. However, quite amazingly, for small τ, the dynamics and coexistence states of (1.6) essentially depend on two scalar functions of $\mu \in (0, \infty)$ defined as follows

$$G(\mu) = \int_\Omega g(x)\theta^3(x,\mu)\,dx, \tag{1.7a}$$

$$H(\mu) = \int_\Omega h(x)\theta^3(x,\mu)\,dx. \tag{1.7b}$$

The following theorem shows how G and H determine the structure of coexistence states and their stability.

Theorem 1.1. *Assume that functions G and H have no common roots. Let μ_1 and μ_2 be two consecutive roots of the function GH and assume that they are both simple roots.*

(i) *If $GH < 0$ in (μ_1, μ_2), then for $\mu \in [\mu_1, \mu_2]$, system* (1.6) *has no coexistence states provided that τ is small and positive.*

(ii) *If $GH > 0$ in (μ_1, μ_2), then for each sufficiently small $\tau > 0$ there exist numbers $\underline{\mu} = \underline{\mu}(\tau) \approx \mu_1$, $\overline{\mu} = \overline{\mu}(\tau) \approx \mu_2$ and a smooth $C(\bar{\Omega}) \times C(\bar{\Omega})$-valued function $\mu \mapsto (u(\mu), v(\mu))$ on $[\underline{\mu}, \overline{\mu}]$ such that for each $\mu \in (\underline{\mu}, \overline{\mu})$ the pair $(u(\mu), v(\mu))$ is a unique coexistence state of* (1.6) *and $(u(\underline{\mu}), v(\underline{\mu}))$, $(u(\overline{\mu}), v(\overline{\mu}))$, are semitrivial states of* (1.6)*. Moreover, the coexistence state $(u(\mu), v(\mu))$ is stable if both $G(\mu)$ and $H(\mu)$ are negative in (μ_1, μ_2) and it is unstable if both $G(\mu)$ and $H(\mu)$ are positive in (μ_1, μ_2).*

In statement (ii) of the theorem, the following two possibilities can occur:

(a) $(u(\underline{\mu}), v(\underline{\mu}))$ and $(u(\overline{\mu}), v(\overline{\mu}))$ are semi-trivial states of the same type, that is, each of them equals $(\theta(\mu), 0)$ (at the corresponding value of μ) or each of them equals $(0, \theta(\mu))$,

(b) $(u(\underline{\mu}), v(\underline{\mu}))$ and $(u(\overline{\mu}), v(\overline{\mu}))$ are of different types: one of them equals $(\theta(\mu), 0)$ and the other one equals $(0, \theta(\mu))$.

Abusing the language slightly, in the case (a) we call the curve $\{(u(\mu), v(\mu)) : \mu \in (\underline{\mu}, \overline{\mu})\}$ a *branch* between $\underline{\mu}$ and $\overline{\mu}$; in the case (b) we call it a *loop*. If the coexistence states on the branch or loop are stable we call it a *stable branch* or a *stable loop*, respectively. See Figure 1.

The next result states that (1.6) can have an arbitrarily high number of stable loops and branches.

Theorem 1.2. *Suppose that* (A1) *holds, $a \in C^\gamma(\overline{\Omega})$ and $a_+^3 \notin C^{\gamma+1}(\overline{\Omega})$ for some $\gamma > 0$. Then, for any given positive integers l and b, there exist smooth functions g and h such that* (1.6) *has at least l stable loops and at least b stable branches for each sufficiently small $\tau > 0$.*

Theorem 1.2 reveals complex and intriguing effects of diffusion and spatial heterogeneity of the environment on the invasion of rare species and coexistence of interacting species. The existence of (stable) loops appears to be

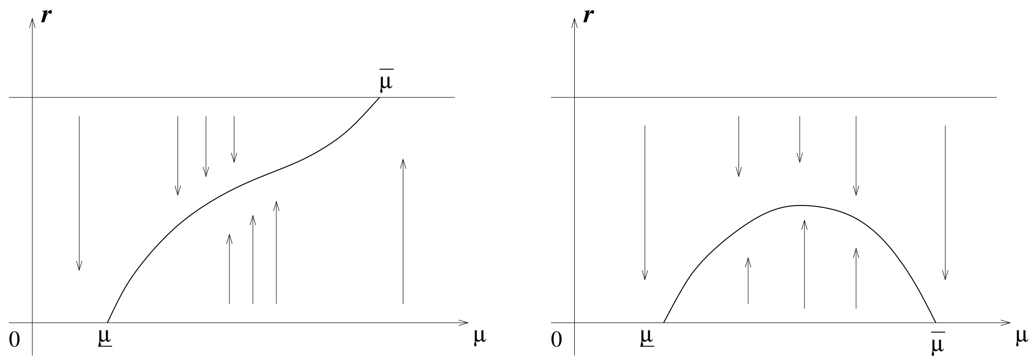

Figure 1:
A stable branch and a stable loop. The vertical axis is $r = \|u\|/(\|u\| + \|v\|)$; the semitrivial steady states correspond to $r = 0$ and $r = 1$.

a new phenomenon, it does not occur in the model studied in [24]. Also, in contrast to the results of [24], the range of coexistence in terms of μ, that is, the projection of a branch or loop of coexistence states onto the $\mu-$axis, is of order O(1) as $\tau \to 0$.

The reminder of paper is organized as follows. Section 2 contains preliminary material on local and global asymptotic stability of coexistence and semi-trivial states of (1.6). In Section 3 we discuss the local stability of semi-trivial states of (1.6). In theorems proved there, we do not restrict to the case of small τ. Section 4 is devoted to results on the existence and stability of coexistence states and the bifurcation of branches and loops. In particular, Theorem 1.1 is proved in Subsection 4.3 and Theorem 1.2 is proved Subsection 4.4.

2 Preliminaries

In this section we summarize some statements regarding the stability of steady states of (1.6) for later purposes. Since the materials here are similar to those in Section 2 of [24], our discussions will be brief and we refer to [24] for details.

By standard theory (see, e.g., [15, 29]), (1.6) is well posed on $\mathcal{X} := C(\overline{\Omega}) \times C(\overline{\Omega})$, in fact, it defines a smooth dynamical system on $\mathcal{X}$. The stability of steady states of (1.6) is understood with respect to the topology of $\mathcal{X}$. We say an equilibrium (u_e, v_e) is the *global attractor* if it is stable and for each nontrivial initial data $(u_0, v_0) \in \mathcal{X}$ with $u_0 \geq 0$, $v_0 \geq 0$, $(u(\cdot, t), v(\cdot, t))$ converges uniformly to (u_e, v_e) as $t \to \infty$, where $(u(\cdot, t), v(\cdot, t))$ is the solution of (1.6) with the initial data (u_0, v_0).

Due to the monotonicity of two species Lotka-Volterra competition systems, we have the following well known results (see [17, Chapt. 4]):

(a) If there is no coexistence state, then one of the semi-trivial equilibria is unstable and the other one is the global attractor.

(b) If there is a unique coexistence state and it is stable, then it is the global attractor (in particular, both semi-trivial equilibria are unstable)

(c) If all coexistence states are asymptotically stable, then there is at most one of them.

For the linearized stability of a steady state (u, v) of (1.6), it suffices to consider the eigenvalue problem

$$\mu\Delta\varphi + [a - 2u - (1 + \tau g)v]\varphi + (-u)(1 + \tau g)\psi = -\lambda\varphi \quad \text{in } \Omega, \tag{2.1a}$$

$$\mu\Delta\psi + (-v)(1 + \tau h)\varphi + [a - (1 + \tau h)u - 2v]\psi = -\lambda\psi \quad \text{in } \Omega, \tag{2.1b}$$

$$\frac{\partial\varphi}{\partial n} = \frac{\partial\psi}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{2.1c}$$

It is well known (see, e.g. [17]) that (2.1) has a principal eigenvalue λ_1 which is real, algebraically simple and all other eigenvalues have their real parts greater than λ_1. Moreover, there is an eigenfunction (φ, ψ) associated to λ_1 satisfying $\varphi > 0$, $\psi < 0$, and λ_1 is the only eigenvalue with such positivity property. The linearized stability of (u, v) is determined by the sign of the principal eigenvalue: (u, v) is stable if $\lambda_1 > 0$; it is unstable if $\lambda_1 < 0$.

When (u, v) is a semi-trivial state, e.g., $(u, v) = (\theta, 0)$, then (2.1) simplifies to a triangular system and the stability of $(\theta, 0)$ is determined by the principal eigenvalue of the scalar problem

$$\mu\Delta\psi + [a - (1 + \tau h)\theta]\psi = -\lambda\psi \qquad \text{in } \Omega, \qquad \frac{\partial\psi}{\partial n}\Big|_{\partial\Omega} = 0. \tag{2.2}$$

Similarly, if $(u, v) = (0, \theta)$, then the principal eigenvalue of (2.1) coincides with the principal eigenvalue of the scalar problem

$$\mu\Delta\varphi + [a - (1 + \tau g)\theta]\varphi = -\lambda\varphi \quad \text{in } \Omega, \qquad \frac{\partial\varphi}{\partial n}\Big|_{\partial\Omega} = 0. \tag{2.3}$$

We remark that since the principal eigenvalue is always simple, it inherits the smoothness properties of the data in the problem. Indeed, since $\theta(\cdot,\mu)$ is analytic in μ, by standard analytic perturbation theory (see [26]), the principal eigenvalue of (2.1) is an analytic function of $\tau > 0$ and $\mu > 0$.

3 Stability of semi-trivial steady states

The goal of this section is to study the linearized stability of the semi-trivial steady states $(\theta, 0)$ and $(0, \theta)$ of (1.6) for general $\tau > 0$, and the main results are Theorems 3.4-3.7. We shall focus on the stability of $(\theta, 0)$, the discussion for $(0, \theta)$ is similar. Here, of course, $\theta = \theta(\cdot, \mu)$ depends on μ, although we often omit the argument μ for brevity.

Let λ_1 be the principal eigenvalue of (2.2) and ψ_1 be the corresponding eigenfunction such that $\psi_1 > 0$ in $\overline{\Omega}$ and $\max_{\overline{\Omega}} \psi_1 = 1$. Hence we have

$$\mu\Delta\psi_1 + [a - (1+\tau h)\theta]\psi_1 = -\lambda_1\psi_1 \quad \text{in} \ \ \Omega, \qquad \frac{\partial \psi_1}{\partial n}\Big|_{\partial\Omega} = 0. \tag{3.1}$$

Define ψ^* by $\psi_1 = \theta\psi^*$. By (3.1) and (1.2), we see that ψ^* satisfies

$$\mu(\theta\Delta\psi^* + 2\nabla\theta\cdot\nabla\psi^*) - \tau h\theta^2\psi^* = -\lambda_1\theta\psi^* \quad \text{in} \ \ \Omega, \qquad \frac{\partial \psi^*}{\partial n}\Big|_{\partial\Omega} = 0. \tag{3.2}$$

Multiplying the first equation in (3.2) by θ, we can rewrite (3.2) as

$$\mu\nabla\cdot(\theta^2\nabla\psi^*) - \tau h\theta^3\psi^* = -\lambda_1\theta^2\psi^* \quad \text{in} \ \ \Omega, \qquad \frac{\partial \psi^*}{\partial n}\Big|_{\partial\Omega} = 0. \tag{3.3}$$

For every $\mu > 0$, define

$$C(\mu) := \inf_{\psi\in S_\mu} \frac{\int_\Omega \theta^2|\nabla\psi|^2\,dx}{-\int_\Omega h\theta^3\psi^2\,dx}, \tag{3.4}$$

where

$$S_\mu = \left\{\psi \in H^1(\Omega) : \ \int_\Omega h\theta^3\psi^2\,dx < 0\right\}. \tag{3.5}$$

We set $C(\mu) = +\infty$ if $S_\mu = \emptyset$, that is, if $h \geq 0$. Clearly, $C(\mu) \geq 0$. It is well known (see, e.g., [5]) that $C(\mu) > 0$ if and only if h changes sign and $\int_\Omega h(x)\theta^3(x,\mu)\,dx > 0$. By (3.3) and (3.4), the connection between λ_1 and $C(\mu)$ is given by the following lemma. Its proof is very similar to the proof of Lemma 3.1 in [24] and we refer the reader to that paper.

Lemma 3.1. *Given $\tau > 0$, $\lambda_1 > 0$ if $\tau < \mu C(\mu)$, $\lambda_1 = 0$ if $\tau = \mu C(\mu)$ and $\lambda_1 < 0$ if $\tau > \mu C(\mu)$.*

In particular, if $\int_\Omega h(x)\theta^3(x,\mu)\,dx \le 0$, then $C(\mu) = 0$ and $\lambda_1 < 0$ for any $\tau > 0$, i.e., $(\theta, 0)$ is always unstable; If $h \ge 0$, $(\theta, 0)$ is always stable.

In this section, we also assume that

(A2) $H(0) \neq 0 \neq H(\infty)$, the equation $H(\mu) = 0$ has only finitely many solutions $0 < \mu_1 < \mu_2 < ... < \mu_k < \infty$ in $(0,\infty)$ and they are all simple.

(A3) $\{x \in \Omega : h(x) < 0\} \cap \{x \in \Omega : a(x) > 0\} \neq \emptyset$.

Under assumption (A2), there are four cases for us to consider:

I. $H(0) > 0$, $H(\infty) > 0$;
II. $H(0) > 0 > H(\infty)$;
III. $H(0) < 0 < H(\infty)$;
IV. $H(0) < 0$, $H(\infty) < 0$.

We first establish the following result.

Lemma 3.2. *Suppose that* (A3) *holds. Then*

$$\lim_{\mu \to 0+} \mu C(\mu) = 0. \tag{3.6}$$

Proof. As $\mu \to 0+$, we have $\theta \to a_+$ in L^∞. By (A3), we can find ψ_0 such that $\psi_0 \in C^1(\bar{\Omega})$ has compact support in $\{h < 0\} \cap \{a > 0\}$ and $\int_\Omega h a_+^3 \psi_0^2\,dx < 0$. Hence, for μ small,

$$\int_\Omega h\theta^3\psi_0^2\,dx \le \frac{1}{2}\int_\Omega h a_+^3 \psi_0^2\,dx < 0. \tag{3.7}$$

By (1.2) and the maximum principle [32], we have $\|\theta\|_{L^\infty} \le \|a\|_{L^\infty}$. Choose $\psi = \psi_0$ in (3.4). By (3.7),

$$C(\mu) \le \frac{\int_\Omega \theta^2|\nabla\psi_0|^2\,dx}{-\int_\Omega h\theta^3\psi_0^2\,dx} \le \frac{2\|a\|_{L^\infty}^2 \int_\Omega |\nabla\psi_0|^2\,dx}{-\int_\Omega h a_+^3\psi_0^2\,dx} < +\infty \tag{3.8}$$

for small $\mu > 0$. Hence, $C(\mu)$ is uniformly bounded for small μ, which implies that (3.6) holds. $\square$

Lemma 3.3. *Suppose that h changes sign, $\int_\Omega h > 0$, and $\int_\Omega a > 0$. Then $\lim_{\mu\to\infty} C(\mu) = |\Omega| C_\infty / (\int_\Omega a\,dx) > 0$, where*

$$C_\infty = \inf_{\{\psi \in H^1(\Omega) : \int_\Omega h\psi^2 < 0\}} \frac{\int_\Omega |\nabla\psi|^2\,dx}{-\int_\Omega h\psi^2\,dx} > 0. \tag{3.9}$$

Proof. Since h changes sign and $\int_\Omega h > 0$, we have $C_\infty > 0$. The rest of Lemma 3.3 follows from (1.3b). $\square$

We say that the steady state $(\theta, 0)$ (or $(0, \theta)$) *changes stability* at μ_0 if for μ close to μ_0 the steady state is stable on one side of μ_0 and unstable on the other side of μ_0. A steady state changes stability k times if it changes stability at k different values of μ.

In Case I, the function H has an even number of roots, hence, $k = 2l$ for some $l \geq 1$. In this situation, we have the following stability result for $(\theta, 0)$.

Theorem 3.4. *Suppose that function H is as in Case* I*, and assumptions* (A1)-(A3) *hold. Then, for every fixed $\tau > 0$, $(\theta, 0)$ is unstable for small μ and stable for large μ. Moreover, there exist $\{\tau_i\}_{i=0}^{l}$ with $0 = \tau_0 < \tau_1 \leq ... \leq \tau_l$ such that for every $1 \leq i \leq l$ and every $\tau \in (\tau_{i-1}, \tau_i)$, $(\theta, 0)$ changes stability at least $2(l - i) + 3$ times.*

Proof. By Lemma 3.2, $\tau > \mu C(\mu)$ if $\mu \ll 1$. Hence, by Lemma 3.1, we see that $(\theta, 0)$ is unstable for small μ. By Lemma 3.3, $\lim_{\mu\to\infty} \mu C(\mu) = \infty$, which implies that $\tau < \mu C(\mu)$ for $\mu \gg 1$. Therefore, by Lemma 3.1, $(\theta, 0)$ is stable for large μ.

Set $\mu_0 = 0$. By Lemma 3.1 and assumption (A2), we see that $\mu C(\mu)$ is positive in $\cup_{i=1}^{l}(\mu_{2i-2}, \mu_{2i-1}) \cup (\mu_{2l}, \infty)$ and is zero elsewhere. For every $i = 1, ..., l$, define $M_i = \max_{\mu\in[\mu_{2i-2},\mu_{2i-1}]} \mu C(\mu)$. We reorder $\{M_i\}_{i=1}^{l}$ into an ordered set $\{\tau_i\}_{i=1}^{l}$ with $0 = \tau_0 < \tau_1 \leq ... \leq \tau_l$. For every $1 \leq i \leq l$ and every $\tau \in (\tau_{i-1}, \tau_i)$, $\mu C(\mu) = \tau$ has at least $2(l - i) + 3$ roots, one of which lies in the interval (μ_{2l}, ∞) since $C(\mu_{2l}) = 0$ and $\lim_{\mu\to\infty} \mu C(\mu) = \infty$. Furthermore, $\mu C(\mu) - \tau$ changes sign at least $2(l - i) + 3$ times: if not, the only possibility is that there exists an interval $[\underline{\mu}, \bar{\mu}]$ which is contained in $\cup_{i=1}^{l}(\mu_{2i-2}, \mu_{2i-1}) \cup (\mu_{2l}, \infty)$ such that $\mu C(\mu) \equiv \tau$ in $[\underline{\mu}, \bar{\mu}]$. By Lemma 3.1, we obtain $\lambda_1(\mu, \tau) \equiv 0$ for every $\mu \in [\underline{\mu}, \bar{\mu}]$. Since λ_1 is analytic in μ, $\lambda_1(\mu, \tau) \equiv 0$ for every $\mu > 0$, which contradicts $\lambda_1 < 0$ for small μ. Therefore, by Lemma 3.1, $(\theta, 0)$ changes stability at least $2(l - i) + 3$ times. This completes the proof of Theorem 3.4. $\square$

Similar results hold for Cases II-IV. Since the proofs are rather similar, we omit them and state only the conclusions accordingly. In Case II, k is odd. Hence, we may assume that $k = 2l - 1$ for some $l \geq 1$. We then have the following result.

Theorem 3.5. *Suppose that function H is as in Case* II *and assumptions* (A1)-(A3) *hold. Then for every fixed $\tau > 0$, $(\theta, 0)$ is unstable for both small μ and large μ. Moreover, there exist $\{\tau_i\}_{i=0}^{l}$ with $0 = \tau_0 < \tau_1 \leq ... \leq \tau_l$ such that for every $1 \leq i \leq l$ and every $\tau \in (\tau_{i-1}, \tau_i)$, $(\theta, 0)$ changes stability at least $2(l - i) + 2$ times.*

In Case III, k is odd: $k = 2l - 1$ for some $l \geq 1$. The following result holds true.

Theorem 3.6. *Suppose that function H is as in Case* III*, and assumptions* (A1)-(A3) *hold. Then for every $\tau > 0$, $(\theta, 0)$ is unstable for small μ and is stable for large μ. Moreover, if $l \geq 2$, there exist $\{\tau_i\}_{i=0}^{l-1}$ with $0 = \tau_0 < \tau_1 \leq ... \leq \tau_{l-1}$ such that for every $1 \leq i \leq l - 1$ and $\tau \in (\tau_{i-1}, \tau_i)$, $(\theta, 0)$ changes stability at least $2(l - i) + 1$ times.*

Finally, in Case IV, k is even, $k = 2l$ for some $l \geq 1$, and the following holds true.

Theorem 3.7. *Suppose that function H is as in Case* IV*, and assumptions* (A1)-(A3) *hold. Then for every $\tau > 0$, $(\theta, 0)$ is unstable for both small and large μ. Moreover, there exist $\{\tau_i\}_{i=0}^{l}$ with $0 = \tau_0 < \tau_1 \leq ... \leq \tau_l$ such that for every $1 \leq i \leq l$ and every $\tau \in (\tau_{i-1}, \tau_i)$, $(\theta, 0)$ changes stability at least $2(l - i) + 2$ times.*

Remark 3.8. If assumption (A2) does not hold, we can still show that $(\theta, 0)$ changes stability various times in some cases: (i) If $H(0) > 0 > H(\infty)$ and assumption (A3) holds, then there exists $\tau_1 > 0$ such that for every $\tau \in (0, \tau_1)$, $(\theta, 0)$ changes stability at least twice; (ii) If $H(0) < 0 < H(\infty)$, then for every $\tau > 0$, as μ varies, $(\theta, 0)$ changes stability at least once. The proofs of these results are similar to that of Theorem 3.4, and are omitted.

4 Coexistence states and their stability

In this section we will focus on the existence and stability of coexistence states when $\tau \ll 1$ and μ stays away from zero. In Subsection 4.1 we will parameterize the branches of coexistence states using a Lyapunov-Schmidt reduction for $\tau \ll 1$ and for μ between two consecutive roots of GH. Subsection 4.2 is devoted to the study of stability of coexistence states found in Subsection 4.1. Finally, we prove Theorems 1.1 and 1.2 in Subsections 4.3 and 4.4, respectively.

4.1 Lyapunov-Schmidt reduction

Consider the system

$$\mu\Delta u + u[a - u - (1+\tau g)v] = 0 \qquad \text{in } \Omega, \tag{4.1a}$$
$$\mu\Delta v + v[a - v - (1+\tau h)u] = 0 \qquad \text{in } \Omega, \tag{4.1b}$$
$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \qquad \text{on } \partial\Omega. \tag{4.1c}$$

Referring to solutions of (4.1), we mean, depending on the context, either a pair (u, v) satisfying the equations and the boundary condition (with μ fixed) or a triple (μ, u, v) satisfying (4.1). Also we only consider nontrivial solutions, regardless of whether this is mentioned explicitly or not.

In this subsection we are concerned with solutions near the surface

$$\Sigma = \{(\mu, s\theta(\mu), (1-s)\theta(\mu)) : \ \mu \in [\mu_1, \mu_2], \ s \in [0,1]\}, \tag{4.2}$$

where μ_1 and μ_2 are consecutive roots of GH. Note that for every $\mu > 0$,

$$\Sigma_\mu := \{(s\theta(\mu), (1-s)\theta(\mu)) : \ s \in [0,1]\} \tag{4.3}$$

is the set of nontrivial nonnegative solutions of (4.1) when $\tau = 0$.

Choose $p > N$, so that the Sobolev space $W^{2,p}(\Omega)$ is continuously imbedded in $C^1(\overline{\Omega})$. Set

$$X = \left\{(y,z) \in W^{2,p}(\Omega) \times W^{2,p}(\Omega) : \ \frac{\partial y}{\partial n} = \frac{\partial z}{\partial n} = 0 \ \text{ on } \partial\Omega\right\}, \tag{4.4a}$$
$$X_1 = \operatorname{span}\{(\theta, -\theta)\}, \tag{4.4b}$$
$$X_2 = \left\{(y,z) \in X : \ \int_\Omega (y-z)\theta\, dx = 0\right\}, \tag{4.4c}$$
$$Y = L^p(\Omega) \times L^p(\Omega). \tag{4.4d}$$

The rest of this subsection is devoted the proof of the following result.

Theorem 4.1. *Assume that functions G and H have no common roots, and let μ_1 and μ_2 be two consecutive roots of function GH.*

(i) *If $GH < 0$ in (μ_1, μ_2), then system (4.1) has no coexistence states near Σ provided that τ is small and positive.*

(ii) *If* $GH > 0$ *in* (μ_1, μ_2)*, then there exists a neighborhood* U *of* Σ *and* $\delta > 0$ *such that for* $\tau \in (0, \delta)$*, the set of solutions of* (4.1) *in* U *consists of the semitrivial solutions* $(\mu, \theta(\cdot, \mu), 0)$*,* $(\mu, 0, \theta(\cdot, \mu))$*, and the set* $\Gamma \cap U$*, where*

$$\Gamma = \{(\mu, u(\mu, \tau), v(\mu, \tau)) : \ \mu_1 - \delta \le \mu \le \mu_2 + \delta\}.$$

Here

$$u(\mu, \tau) = s^*(\mu, \tau)[\theta(\cdot, \mu) + \bar{y}(\mu, \tau)], \tag{4.5a}$$

$$v(\mu, \tau) = [1 - s^*(\mu, \tau)][\theta(\cdot, \mu) + \bar{z}(\mu, \tau)], \tag{4.5b}$$

for some smooth functions s^* *and* $(\bar{y}, \bar{z})$ *taking values in* $\mathbb{R}$ *and* X_2*, respectively, and satisfying*

$$s^*(\mu, 0) = s_0(\mu) := G(\mu)/[G(\mu)+H(\mu)], \quad \bar{y}(\mu, 0) = \bar{z}(\mu, 0) = 0. \tag{4.6}$$

Moreover, if μ_1 *and* μ_2 *are simple roots of* GH*, then there are smooth functions* $\underline{\mu}(\tau)$ *and* $\overline{\mu}(\tau)$ *on* $[0, \delta)$ *such that* $\underline{\mu}(0) = \mu_1$*,* $\overline{\mu}(0) = \mu_2$*, and for any* $\tau \in [0, \delta)$ *one has* $s^*(\mu, \tau)[1 - s^*(\mu, \tau)] = 0$ *with* $\mu \in (\mu_1 - \delta, \mu_2 + \delta)$ *if and only if* $\mu \in \{\underline{\mu}(\tau), \overline{\mu}(\tau)\}$*.*

Remark 4.2. Note that since $\theta(\mu) > 0$ in $\bar{\Omega}$, (4.5) and (4.6) imply that for τ sufficiently small we have $u(\mu, \tau) > 0$, $v(\mu, \tau) > 0$ if and only if $s^*(\mu, \tau) \in (0, 1)$. The last statement of the theorem implies that this is true if and only if $\mu \in (\underline{\mu}(\tau), \overline{\mu}(\tau))$.

Proof of Theorem 4.1. Clearly, each solution of (4.1) near Σ can be written as

$$(u, v) = (s\theta(\cdot, \mu), (1 - s)\theta(\cdot, \mu)) + (y, z), \tag{4.7}$$

where $s \in \mathbb{R}$, and $(y, z) \in X_2$ is in a neighborhood of $(0, 0)$. We thus seek the solutions in this form.

For some small constant $\delta_1 > 0$, define the map $F : X \times (\mu_1 - \delta_1, \mu_2 + \delta_1) \times (-\delta_1, \delta_1) \times (-\delta_1, 1 + \delta_1) \to Y$ by

$$F(y, z, \mu, \tau, s) = \begin{pmatrix} \mu\Delta y + (a - \theta)y - s\theta(y + z) + f_1(y, z, \mu, \tau, s) \\ \mu\Delta z + (a - \theta)z - (1 - s)\theta(y + z) + f_2(y, z, \mu, \tau, s) \end{pmatrix}, \tag{4.8}$$

where

$$f_1(y, z, \mu, \tau, s) = -y(y + z) - s\tau g\theta[(1 - s)\theta + z)] - \tau gy[(1 - s)\theta) + z],$$

$$f_2(y, z, \mu, \tau, s) = -z(y + z) - (1 - s)\tau h\theta(s\theta + z) - \tau hz(s\theta + y)$$

(and we suppress the argument μ of θ as usual). Clearly F is smooth and, by (1.2), (u, v) given by (4.7) satisfies (4.1) if and only if $F(y, z, \mu, \tau, s) = (0, 0)^T$. Note that we have the following identities

$$F(0, 0, 0, \mu, 0, s) = 0, \quad F(0, 0, \mu, \tau, 0) = F(0, 0, \mu, \tau, 1) = 0 \tag{4.9}$$

for all admissible values of μ, s and τ.

Define the linearized operator $L(\mu, s) : X \to Y$ by

$$L(\mu, s) = D_{(y,z)}F(0, 0, \mu, 0, s). \tag{4.10}$$

By a direct calculation, we see that $L = L(\mu, s)$ is given by

$$L \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi + (a - \theta)\varphi - s\theta(\varphi + \psi) \\ \mu\Delta\psi + (a - \theta)\psi - (1 - s)\theta(\varphi + \psi) \end{pmatrix}. \tag{4.11}$$

Since X is compactly imbedded in Y, L is a Fredholm operator of index zero. We claim that

$$\ker(L) = \operatorname{span}\{(\theta, -\theta)\} = X_1, \tag{4.12a}$$

$$R(L) = \left\{(y, z) \in Y : \ (1 - s) \int_\Omega \theta y \, dx - s \int_\Omega \theta z \, dx = 0\right\}, \tag{4.12b}$$

where $R(L)$ stands for the range of L. To show this, first observe that $(\theta, -\theta)$ is in $\ker(L)$. Using the fact that the principal eigenvalue of L, when viewed as operator on Y with domain X, is simple (cf. Section 2), one then verifies that the kernel is given by (4.12a).

Now define the operator $P = P(\mu, s)$ on Y by

$$P \begin{pmatrix} y \\ z \end{pmatrix} = \frac{1}{\int_\Omega \theta^2(x, \mu) \, dx} \left[\int_\Omega \theta \left[(1 - s)y - sz\right] \, dx\right] \begin{pmatrix} \theta \\ -\theta \end{pmatrix}. \tag{4.13}$$

Then $R(P) = X_1$ and one easily verifies that

$$P^2 = P, \quad PL = 0. \tag{4.14}$$

Hence P is the projection on the kernel of L which commutes with L. This in particular proves (4.12b).

Following the Lyapunov-Schmidt procedure, we consider the system

$$P(\mu, s)F(y, z, \mu, \tau, s) = 0, \tag{4.15a}$$
$$[I - P(\mu, s)]F(y, z, \mu, \tau, s) = 0, \tag{4.15b}$$

where $(y, z) \in X_2$. Since $L(\mu, s)$ is an isomorphism from X_2 to $R(L(\mu, s))$, we can apply the implicit function theorem to solve (4.15b) for (y, z). Combining this with a compactness argument, we conclude that there exist $\delta_2 > 0$, a neighborhood U_1 of $(0, 0)$ in X_2, and a smooth function

$$(y_1(\mu, \tau, s), z_1(\mu, \tau, s)) : (\mu_1 - \delta_2, \mu_2 + \delta_2) \times (-\delta_2, \delta_2) \times (-\delta_2, 1 + \delta_2) \to X_2$$

such that $y_1(\mu, 0, s) = z_1(\mu, 0, s) = 0$ and $(y, z, \mu, \tau, s) \in U_1 \times (\mu_1 - \delta_2, \mu_2 + \delta_2) \times (-\delta_2, \delta_2) \times (-\delta_2, 1 + \delta_2)$ satisfies $F(y, z, \mu, \tau, s) = 0$ if and only if $y = y_1(\mu, \tau, s)$, $z = z_1(\mu, \tau, s)$, and (μ, τ, s) solves

$$P(\mu, s)F(y_1(\mu, \tau, s), z_1(\mu, \tau, s), \mu, \tau, s) = 0. \tag{4.16}$$

Using in particular the immediate solutions given (4.9), we obtain

$$y_1(\mu, 0, s) = z_1(\mu, 0, s) = 0, \tag{4.17a}$$
$$y_1(\mu, \tau, 0) = z_1(\mu, \tau, 0) = 0, \tag{4.17b}$$
$$y_1(\mu, \tau, 1) = z_1(\mu, \tau, 1) = 0. \tag{4.17c}$$

By (4.13), there exists a smooth scalar function $\xi(\mu, \tau, s)$ such that

$$\xi(\mu, \tau, s) \begin{pmatrix} \theta(\cdot, \mu) \\ -\theta(\cdot, \mu) \end{pmatrix} = P(\mu, s)F(y_1(\mu, \tau, s), z_1(\mu, \tau, s), \mu, \tau, s). \tag{4.18}$$

Hence, it suffices to solve $\xi(\mu, \tau, s) = 0$. We first establish some properties of $\xi(\mu, \tau, s)$. By (4.9) and (4.17) we have

$$\xi(\mu, 0, s) \equiv 0, \tag{4.19}$$
$$\xi(\mu, \tau, 0) = \xi(\mu, \tau, 1) \equiv 0. \tag{4.20}$$

These relations imply that $\xi(\mu, \tau, s)$ can be expressed as

$$\xi(\mu, \tau, s) = \tau s(1 - s)\xi_1(\mu, \tau, s) \tag{4.21}$$

for some smooth function ξ_1. Thus, we need to solve $\xi_1(\mu, \tau, s) = 0$.

Differentiating both sides of (4.18) with respect to τ at $\tau = 0$ and recalling the fact that $y_1(\mu, 0, s) = z_1(\mu, 0, s) = 0$ we find

$$\xi_\tau(\mu, 0, s) \begin{pmatrix} \theta(\cdot, \mu) \\ -\theta(\cdot, \mu) \end{pmatrix} = P(\mu, s)L(\mu, s) \begin{pmatrix} y_{1,\tau}(\mu, 0, s) \\ z_{1,\tau}(\mu, 0, s) \end{pmatrix} \\ + P(\mu, s)F_\tau(0, 0, \mu, 0, s) = P(\mu, s)F_\tau(0, 0, \mu, 0, s), \quad (4.22)$$

where the second equality follows from (4.14). From (4.8) we obtain

$$F_\tau(0, 0, \mu, 0, s) = -s(1-s) \begin{pmatrix} g\theta^2(\cdot, \mu) \\ h\theta^2(\cdot, \mu) \end{pmatrix}. \quad (4.23)$$

Hence,

$$P(\mu, s)F_\tau(0, 0, \mu, 0, s) = s(1-s)\frac{sH(\mu) - (1-s)G(\mu)}{\int_\Omega \theta^2(\cdot, \mu)\, dx} \begin{pmatrix} \theta(\cdot, \mu) \\ -\theta(\cdot, \mu) \end{pmatrix}. \quad (4.24)$$

By (4.21), (4.22), and (4.24) we have

$$\xi_1(\mu, 0, s) = \frac{sH(\mu) - (1-s)G(\mu)}{\int_\Omega \theta^2(\cdot, \mu)\, dx}. \quad (4.25)$$

If $G(\tilde{\mu})H(\tilde{\mu}) < 0$, choosing δ_2 smaller if necessary, by (4.25) we see that the equation $\xi_1(\mu, \tau, s) = 0$ has no solution in the domain $(\tilde{\mu} - \delta_2, \tilde{\mu} + \delta_2) \times (-\delta_2, \delta_2) \times (-\delta_2, 1 + \delta_2)$. By a finite covering argument, the equation has no solution in $(\mu_1 - \delta_2, \mu_2 + \delta_2) \times (-\delta_2, \delta_2) \times (-\delta_2, 1 + \delta_2)$, if $\delta_2 > 0$ is small enough. It follows that (4.1) has no coexistence states near Σ. This proves part (i).

For the proof of (ii) assume that $GH > 0$ in (μ_1, μ_2). It is clear that $s_0(\mu) = G(\mu)/[G(\mu) + H(\mu)]$ is the unique zero of $\xi_1(\mu, 0, \cdot)$ and

$$\xi_{1,s}(\mu, 0, s) = \frac{G(\mu) + H(\mu)}{\int_\Omega \theta^2(\cdot, \mu)\, dx} \neq 0. \quad (4.26)$$

Therefore, by the implicit function theorem, for any $\tilde{\mu} \in [\mu_1, \mu_2]$ there exists $\delta_3 > 0$ such that all solutions of $\xi_1(\mu, \tau, s) = 0$ in the neighborhood $(\tilde{\mu} - \delta_3, \tilde{\mu} + \delta_3) \times (-\delta_3, \delta_3) \times (-\delta_3, 1 + \delta_3)$ are given by $s = s^*(\mu, \tau)$ for $\tau \in (-\delta_3, \delta_3)$ and $\mu \in (\tilde{\mu} - \delta_3, \tilde{\mu} + \delta_3)$, where $s^*(\mu, \tau)$ is a smooth function satisfying $s^*(\mu, 0) =$

$s_0(\mu)$. A finite covering argument in the μ interval shows that the above assertion still holds for $(\mu, \tau, s) \in (\mu_1 - \delta_3, \mu_2 + \delta_3) \times (-\delta_3, \delta_3) \times (-\delta_3, 1 + \delta_3)$ provided that δ_3 is chosen smaller if necessary. Hence the set of solutions of $\xi(\mu, \tau, s) = 0$ consists exactly of the surfaces $\tau = 0$, $s = 0$, $s = 1$, and $s = s^*(\mu, \tau)$.

Summarizing the above conclusions, we have found out that the solutions (μ, u, v) of (4.1) near Σ, aside from the semitrivial ones, are given by (4.7) with $y = y_1(\mu, \tau, s)$, $z = z_1(\mu, \tau, s)$ and $s = s^*(\mu, \tau)$. By (4.17b), (4.17c), we can write

$$(y_1(\mu, \tau, s), z_1(\mu, \tau, s)) = (s\tilde{y}_1(\mu, \tau, s), (1 - s)\tilde{z}_1(\mu, \tau, s))$$

for some smooth functions $\tilde{y}_1$, $\tilde{z}_1$. Thus the solutions can be represented as in (4.5) with

$$\bar{y}(\mu, \tau) = \tilde{y}_1(\mu, \tau, s^*(\mu, \tau)), \quad \bar{z}(\mu, \tau) = \tilde{z}_1(\mu, \tau, s^*(\mu, \tau)).$$

To prove the last statement of the theorem, we consider the case $G(\mu_1) = 0$, i.e., $s_0(\mu_1) = 0$; the case $H(\mu_1) = 0$, i.e. $1 - s_0(\mu_1) = 0$, is analogous. For small $\tau > 0$, we look for solutions of $s^*(\mu, \tau) = 0$ near μ_1. Since $s^*(\mu, 0) = G(\mu)/[G(\mu) + H(\mu)]$, we have $s^*(\mu_1, 0) = 0$ and $s^*_\mu(\mu_1, 0) = G'(\mu_1)/H(\mu_1) \neq 0$. By the implicit function theorem, there exist $\delta_4 > 0$ and a smooth function $\underline{\mu}$ on $[0, \delta_4)$ such that $\underline{\mu}(0) = \mu_1$ and $\mu = \underline{\mu}(\tau)$ is the unique solution of $s^*(\mu, \tau) = 0$ near μ_1. Similarly one proves the existence of a function $\overline{\mu}(\tau)$ which gives the unique solution of $s^*(\mu, \tau)(1 - s^*(\mu, \tau)) = 0$ near μ_2. Since $s^*(\mu, \tau) \approx s_0(\mu)$, it is clear that for small δ there are no other solutions of $s^*(\mu, \tau)(1 - s^*(\mu, \tau)) = 0$ in $(\mu_1 - \delta, \mu_2 + \delta)$ if $\tau \in (0, \delta)$. The proof is now complete. $\square$

4.2 Stability of coexistence states

In this subsection we study the stability of the branch of solutions of (4.1) found in Subsection 4.1. Throughout the subsection we assume that $\mu_1 < \mu_2$ are two consecutive roots of GH, they are both simple, and $GH > 0$ in (μ_1, μ_2). For $\tau \in (0, \delta)$, $\mu \in (\mu_1 - \delta, \mu + \delta)$, with $\delta > 0$ sufficiently small, we use the representation (4.5) for solutions of (4.1) contained in Γ. Also, as in Theorem 4.1, $\underline{\mu}(\tau)$ and $\overline{\mu}(\tau)$ are uniquely defined roots of $s^*(\mu, \tau)[1 - s^*(\mu, \tau)] = 0$ with $\underline{\mu}(0) = \mu_1$, $\overline{\mu}(0) = \mu_2$.

Let $(\mu, u, v) = (\mu, u(\mu, \tau), v(\mu, \tau))$ be a coexistence state contained in Γ. As discussed in Section 2, the stability of (u, v) is determined by the sign of λ_1, the principal eigenvalue of the problem

$$\mu\Delta\varphi + \varphi[a - 2u - (1+\tau g)v] + \psi(-u)(1+\tau g) = -\lambda_1\varphi \qquad \text{in } \Omega, \quad (4.27a)$$
$$\mu\Delta\psi + \varphi(-v)(1+\tau h) + \psi[a - 2v - (1+\tau h)u] = -\lambda_1\psi \qquad \text{in } \Omega, \quad (4.27b)$$
$$\frac{\partial\varphi}{\partial n} = \frac{\partial\psi}{\partial n} = 0 \qquad \text{on } \partial\Omega. \quad (4.27c)$$

For small τ, we can choose the principal eigenfunction (φ, ψ) as

$$\varphi(\mu, \tau) = \theta(\mu) + \tau\varphi_1(\mu, \tau), \quad (4.28a)$$
$$\psi(\mu, \tau) = -\theta(\mu) + \tau\psi_1(\mu, \tau), \quad (4.28b)$$

where φ_1 and ψ_1 are smooth functions of (μ, τ).

In the following lemma we establish a formula for λ_1, which will be needed later to determine its sign.

Lemma 4.3. *Under the above notation, for each small $\tau > 0$ the principal eigenvalue $\lambda_1 = \lambda_1(\mu, \tau)$ of (4.27) satisfies*

$$\frac{\lambda_1}{\tau}\int_\Omega(\varphi v - \psi u) = 2\int_\Omega guv\psi - 2\int_\Omega huv\varphi - \int_\Omega h\psi u^2 + \int_\Omega g\varphi v^2. \quad (4.29)$$

Proof. Multiplying (4.26a) by v and integrating by parts, by (4.1) we obtain

$$-\lambda_1\int_\Omega \varphi v = \tau\int_\Omega huv\varphi - \int_\Omega uv\varphi - \tau\int_\Omega g\varphi v^2 - \int_\Omega uv\psi - \tau\int_\Omega guv\psi. \quad (4.30)$$

Similarly by (4.1) and (4.26b) we have

$$-\lambda_1\int_\Omega \psi u = \tau\int_\Omega guv\psi - \int_\Omega uv\psi - \tau\int_\Omega h\psi u^2 - \int_\Omega uv\varphi - \tau\int_\Omega huv\varphi. \quad (4.31)$$

Subtracting (4.30) from (4.31) we obtain (4.29). $\square$

To determine the sign of λ_1 for small τ, we should consider three different situations: μ close to μ_1, μ close to μ_2, and μ bounded away from μ_1, μ_2. In the last case, the sign of λ_1 can be determined by the following result.

Lemma 4.4. *For any $\eta > 0$,*

$$\lim_{\tau\to 0+} \frac{\lambda_1(\mu,\tau)}{\tau} = -\frac{G(\mu)H(\mu)}{G(\mu)+H(\mu)} \frac{1}{\int_\Omega \theta^2(x,\mu)\,dx} \tag{4.32}$$

uniformly for $\mu \in [\mu_1+\eta, \mu_2-\eta]$.

Proof. By (4.5) and (4.28) we have $(u(\mu,\tau), v(\mu,\tau)) \to (s_0(\mu)\theta(\mu), [1-s_0(\mu)]\theta(\mu))$, and $(\varphi,\psi) \to (\theta(\mu), -\theta(\mu))$ as $\tau \to 0$. Hence, if $\tau \to 0$, we get

$$\int_\Omega (\varphi v - \psi u)\,dx \to \int_\Omega \theta^2\,dx \tag{4.33}$$

and

$$\begin{aligned} & 2\int_\Omega guv\psi\,dx - 2\int_\Omega huv\varphi\,dx - \int_\Omega h\psi u^2\,dx + \int_\Omega g\varphi v^2\,dx \\ & \to -2s_0(\mu)[1-s_0(\mu)]G(\mu) - 2s_0(\mu)[1-s_0(\mu)]H(\mu) \\ & \quad + s_0^2(\mu)H(\mu) + [1-s_0(\mu)]^2 G(\mu) \\ & = -\frac{G(\mu)H(\mu)}{G(\mu)+H(\mu)}, \end{aligned} \tag{4.34}$$

where the last equality follows from $s_0 = G/(G+H)$. Relation (4.32) follows from (4.29), (4.33), and (4.34). $\square$

For definiteness, we consider the case $G(\mu_1) = 0$ (the case $H(\mu_1) = 0$ can be treated similarly). We thus have $s^*(\underline{\mu},\tau) = 0$, where $\underline{\mu} = \underline{\mu}(\tau)$, and also

$$(u(\underline{\mu},\tau), v(\underline{\mu},\tau)) = (0, \theta(\underline{\mu})).$$

The sign of $\lambda_1(\mu,\tau)$ when μ is close to μ_1 is determined from the following lemma.

Lemma 4.5. *Suppose that $G(\mu_1) = 0$. Then the following holds.*

$$\lim_{(\mu,\tau)\to(\mu_1,0)} \frac{\lambda_1(\mu,\tau)}{\tau(\mu-\underline{\mu})} = -\frac{G'(\mu_1)}{\int_\Omega \theta^2(x,\mu_1)\,dx}. \tag{4.35}$$

Proof. We observe that at the bifurcation value $\overline{\mu}$ we have $\lambda_1(\underline{\mu},\tau) = 0$, and the corresponding $\varphi(\underline{\mu},\tau)$ satisfies

$$\underline{\mu}\Delta\varphi + \varphi\left[a - (1+\tau g)\theta(\underline{\mu})\right] = 0 \qquad \text{in } \Omega, \qquad \frac{\partial\varphi}{\partial n} = 0 \qquad \text{on } \partial\Omega. \tag{4.36}$$

Multiplying (4.36) by $v(\underline{\mu},\tau)$ $(=\theta(\underline{\mu}))$ and integrating by parts we obtain

$$\int_\Omega g\varphi(\underline{\mu},\tau)v^2(\underline{\mu},\tau)\,dx = 0. \tag{4.37}$$

Denote $I(\mu,\tau)$ the right-hand side of (4.29). Then $u(\underline{\mu},\tau)=0$ and (4.37) imply $I(\underline{\mu},\tau)=0$. Therefore, by the mean value theorem, we have

$$I(\mu,\tau)=(\mu-\underline{\mu})I_\mu(\mu^*,\tau) \tag{4.38}$$

for some $\mu^*=\mu^*(\mu,\tau)$ between μ and $\underline{\mu}(\tau)$.

The derivative of I with respect to μ can be written as

$$\begin{aligned} I_\mu(\mu,\tau) =& 2\int_\Omega g(u_\mu v\psi+uv_\mu\psi+uv\psi_\mu)-2\int_\Omega h(u_\mu v\varphi+uv_\mu\varphi+uv\varphi_\mu) \\ &-\int_\Omega h(\psi_\mu u^2+2\psi uu_\mu)+\int_\Omega g(\varphi_\mu v^2+2\varphi vv_\mu). \end{aligned} \tag{4.39}$$

By (4.5) and (4.28), if $\tau\to 0$ and $\mu\to\mu_1$, we have $u\to 0$, $v\to\theta(\mu_1)$, $\varphi\to\theta(\mu_1)$, $\psi\to-\theta(\mu_1)$, $u_\mu\to s_0'(\mu_1)\theta(\mu_1)$, $v_\mu\to -s_0'(\mu_1)\theta(\mu_1)+\theta_\mu(\mu_1)$, $\varphi_\mu\to\theta_\mu(\mu_1)$, and ψ_μ is uniformly bounded. Hence, by the assumption $G(\mu_1)=0$, we have

$$I_\mu(\mu_1,0)=-2s_0'(\mu_1)H(\mu_1)+G'(\mu_1). \tag{4.40}$$

Since $G(\mu_1)=0$, we get $s_0'(\mu_1)=G'(\mu_1)/H(\mu_1)$. Therefore,

$$I_\mu(\mu_1,0)=-G'(\mu_1). \tag{4.41}$$

Relation (4.35) follows from (4.41) and Lemma 4.3. $\square$

The case when μ is close to μ_2 can be treated similarly. We formulate the result, omitting the proof. Assume that $G(\mu_2)=0$ (the case $H(\mu_2)=0$ is analogous). We then have $s^*(\overline{\mu},\tau)=0$, where $\overline{\mu}=\overline{\mu}(\tau)$. The sign of $\lambda_1(\mu,\tau)$ is determined from the following.

Lemma 4.6. *Suppose that $G(\mu_2)=0$. Then the following holds.*

$$\lim_{(\mu,\tau)\to(\mu_2,0)}\frac{\lambda_1(\mu,\tau)}{\tau(\mu-\overline{\mu})}=-\frac{G'(\mu_2)}{\int_\Omega\theta^2(x,\mu_2)\,dx}. \tag{4.42}$$

Now we can establish the main result of this subsection, which is a consequence of Lemmas 4.4, 4.5 and 4.6.

Theorem 4.7. *Suppose that μ_1, μ_2 are two consecutive zeros of GH, they are both simple, and $GH > 0$ in (μ_1, μ_2). Then there exists $\tau_0 > 0$ such that for every $\tau \in (0, \tau_0)$ and every $\mu \in (\underline{\mu}(\tau), \overline{\mu}(\tau))$, we have*

(i) $\lambda_1(\mu, \tau) > 0$ *provided that $G < 0$ and $H < 0$ in (μ_1, μ_2);*

(ii) $\lambda_1(\mu, \tau) < 0$ *provided that $G > 0$ and $H > 0$ in (μ_1, μ_2).*

Proof. We only prove part (i), (ii) is analogous. We argue by contradiction. Suppose that there are sequences $\tau_i \to 0$ and $\mu_i \in (\underline{\mu}(\tau_i), \overline{\mu}(\tau_i))$ with $\lambda_1(\mu_i, \tau_i) \leq 0$ for all $i = 1, 2 \ldots$. Passing to a subsequence if necessary, we may assume that $\mu_i \to \mu^*$. Since $\underline{\mu}(\tau_i) \to \mu_1$ and $\underline{\mu}(\tau_i) \to \mu_2$, we have $\mu^* \in [\mu_1, \mu_2]$. There are two cases for us to consider:
Case I. $\mu^* \in (\mu_1, \mu_2)$. By Lemma 4.4 we have

$$\lim_{i\to\infty} \frac{\lambda_1(\mu_i, \tau_i)}{\tau_i} = -\frac{G(\mu^*)H(\mu^*)}{G(\mu^*) + H(\mu^*)} > 0.$$

Hence, $\lambda_1(\mu_i, \tau_i)$ is positive for large i, in contradiction to our assumption $\lambda_1(\mu_i, \tau_i) \leq 0$.
Case II. $\mu^* = \mu_1$ or $\mu^* = \mu_2$. For the case $\mu^* = \mu_1$, without loss of generality, we may assume that $G(\mu_1) = 0$. Since $G < 0$ in (μ_1, μ_2) and μ_1 is a simple root of G, $G'(\mu_1) < 0$. By Lemma 4.5, we have

$$\lim_{i\to\infty} \frac{\lambda_1(\mu_i, \tau_i)}{\tau_i(\mu_i - \underline{\mu}(\tau_i))} = -\frac{G'(\mu_1)}{\int_\Omega \theta^2(x, \mu_1)\, dx} > 0. \tag{4.43}$$

Since $\mu_i > \underline{\mu}(\tau_i)$, by (4.43) we have $\lambda_1(\mu_i, \tau_i) > 0$ for large i. Again, we have reached a contradiction. The case $\mu^* = \mu_2$ can be treated similarly. □

4.3 Proof of Theorem 1.1

Theorem 1.1 is a global statement; we first claim that if $\tau > 0$ is sufficiently small, then all nontrivial solutions (μ, u, v) of (4.1), with μ close to $[\mu_1, \mu_2]$ and $u \geq 0$, $v \geq 0$ are located near Σ.

Assume this is not true. Then there exist $\tilde{\mu} \in [\mu_1, \mu_2]$ and sequences $\tau_k \to 0$, $\mu_k \to \tilde{\mu}$, and $(u_k, v_k) \in X$ such that (u_k, v_k) is a nontrivial nonnegative solution of (4.1) with $\mu = \mu_k$, $\tau = \tau_k$ and

$$\mathrm{dist}_{\mathbb{R}\times X}((\mu_k, u_k, v_k), \Sigma) \geq \epsilon_0 \quad (k = 1, 2, \dots) \tag{4.44}$$

for some $\epsilon_0 > 0$. Using the maximum principle, one easily shows that (u_k, v_k) are uniformly bounded in the L^∞-norm. From standard elliptic estimates (specifically, the L^p-estimates and then the Schauder estimates), we conclude, passing to subsequences if necessary, that (u_k, v_k) converges in X to a solution $(\tilde{u}, \tilde{v})$ of (4.1) with $\mu = \tilde{\mu}$, $\tau = 0$. For $\tau = 0$, the solution $(\tilde{\mu}, \tilde{u}, \tilde{v})$ is either contained in Σ or it is trivial: $(\tilde{u}, \tilde{v}) = (0, 0)$. The former contradicts (4.44), we next rule out the latter. Assume it holds and consider the eigenvalue problem

$$\mu\Delta\varphi + [a - u - (1 + \tau g)v]\varphi = -\lambda\varphi \quad \text{in } \Omega, \qquad \frac{\partial\varphi}{\partial n}\Big|_{\partial\Omega} = 0. \tag{4.45}$$

If $\mu = \tilde{\mu}$, $u = v = 0$, and $\tau = 0$, then by hypothesis (A1) the principal eigenvalue is negative. The same is true, by the continuity of the principal eigenvalue, if $\mu = \mu_k \approx \tilde{\mu}$, $u = u_k \approx 0$, $v = v_k \approx 0$ and $\tau = \tau_k \approx 0$, in particular, this is true for large k. On the other hand, if $u_k \not\equiv 0$, then (4.1) implies that $\varphi = u_k \geq 0$ is the principal eigenfunction with eigenvalue $\lambda = 0$ for this problem, a contraction. Hence $u_k \equiv 0$, for all large k. Similarly one shows that $v_k \equiv 0$ for all large k, contradicting the assumption that (u_k, v_k) is nontrivial. The claim is now proved.

Once we know that all nontrivial nonnegative solutions (u, v) of (4.1) are located near Σ, we can use the results from Subsections 4.1, 4.2 to complete the proof of Theorem 1.1. Specifically, statement (i) follows directly from Theorem 4.1, and statement (ii) follows from Theorem 4.1, Remark 4.2, and Theorem 4.7.

4.4 Loops and branches of coexistence states

This subsection is devoted to the proof of Theorem 1.2. The following two lemmas characterize the existence of loops and branches (as defined before theorem 1.2) through functions H and G. They are immediate consequences of Theorems 4.1 and 4.7.

Lemma 4.8. *Suppose that μ_*, μ^* are two consecutive roots of H, they are both simple, with $H < 0$ in (μ_*, μ^*), and $G < 0$ in $[\mu_*, \mu^*]$. Then for small $\tau > 0$, there exist $\underline{\mu}$ and $\overline{\mu}$ such that $\underline{\mu}(\tau) \to \mu_*$ and $\overline{\mu}(\tau) \to \mu^*$ as $\tau \to 0$, and* (4.1) *has a stable loop from $\mu = \underline{\mu}$ to $\mu = \overline{\mu}$.*

Lemma 4.9. *Suppose that μ_*, μ^* are two consecutive roots of GH, they are both simple, and $H(\mu_*) < G(\mu_*) = 0 = H(\mu^*) < G(\mu^*)$ (or with G and H switched). Then for small $\tau > 0$, there exist $\underline{\mu}(\tau)$ and $\overline{\mu}(\tau)$ such that $\underline{\mu}(\tau) \to \mu_*$ and $\overline{\mu}(\tau) \to \mu^*$ as $\tau \to 0$, and* (4.1) *has a stable branch from $\underline{\mu}$ to $\overline{\mu}$.*

In view of previous lemmas, we need to show that it is possible to choose g and h such that GH have appropriate simple zeroes and sign for Theorem 1.2 to hold. We start by proving the following technical result.

Lemma 4.10. *Suppose that $a \in C^\gamma(\overline{\Omega})$ and $a_+^3 \notin C^{\gamma+1}(\overline{\Omega})$ for some $\gamma > 0$. Then for each positive integer k, the set*

$$U_k \equiv \left\{(\mu_1, ..., \mu_k) \in \mathbb{R}_+^k : \ a_+^3, \theta^3(\mu_1), ..., \theta^3(\mu_k), 1 \text{ are linearly independent}\right\} \tag{4.46}$$

is open and dense in $\mathbb{R}_+^k$.

Proof. Recall that the Gram's determinant of functions $\psi_1, \ldots, \psi_m \in L^2(\Omega)$ is the determinant of the matrix $\left(\int_\Omega \psi_i \psi_j \, dx\right)_{i,j=1}^m$, and that it is nonzero if and only if the functions are linearly independent.

For positive values of μ_i $(1 \le i \le k)$ and nonnegative μ, let $D(\mu_1, ..., \mu_k, \mu)$ denote the Gram's determinant of $1, \theta^3(\mu_1), ..., \theta^3(\mu_k), \theta^3(\mu)$, where we apply the convention $\theta(0) = a_+$. Note that $D(\mu_1, ..., \mu_k, \mu)$ is analytic in its arguments. We have $(\mu_1, ..., \mu_k) \in U_k$ if and only if $D(\mu_1, ..., \mu_k, 0) \neq 0$. The continuity of $D(\mu_1, ..., \mu_k, 0)$ as a function of $\mu_1, ..., \mu_k$ immediately implies that U_k is open in $\mathbb{R}_+^k$.

The proof of the density is by induction in k. We first show that $U_1 = \mathbb{R}_+^1$. If not, then $a_+^3, \theta^3(\mu_1), 1$ are linearly dependent for some $\mu_1 > 0$. By $a \in C^\gamma$ and elliptic regularity, $\theta(\mu_1) \in C^{\gamma+1}$. Since $a_+^3 \notin C^{\gamma+1}$, we see that the only possibility is that $\theta^3(\mu_1)$ and 1 are linearly dependent. However, this is a contradiction since $\theta(\mu_1)$ is not a constant function. Therefore, the density conclusion holds for $k = 1$.

Now suppose that U_k is dense in $\mathbb{R}_+^k$. We show that U_{k+1} is dense in $\mathbb{R}_+^{k+1}$. Fix an arbitrary $(\mu_1, ..., \mu_k, \mu_{k+1}) \in \mathbb{R}_+^{k+1}$. By the induction hypothesis, we can choose $(\tilde{\mu}_1, ..., \tilde{\mu}_k) \in U_k$ arbitrarily close to $(\mu_1, ..., \mu_k)$. Since

$(\tilde{\mu}_1, ..., \tilde{\mu}_k) \in U_k$, we have $D(\tilde{\mu}_1, ..., \tilde{\mu}_k, 0) \neq 0$. Therefore, there exists $\delta > 0$ small such that

$$D(\tilde{\mu}_1, ..., \tilde{\mu}_k, \mu) \neq 0 \tag{4.47}$$

for $\mu \in (0, \delta)$. Since $D(\tilde{\mu_1}, ..., \tilde{\mu_k}, \cdot)$ is analytic in $(0, \infty)$ and not identically zero, its roots are isolated. Therefore, we can find $\tilde{\mu}_{k+1}$ arbitrarily close to μ_{k+1} such that $D(\tilde{\mu}_1, ..., \tilde{\mu}_{k+1}) \neq 0$. Hence, $\theta^3(\tilde{\mu}_1), ..., \theta^3(\tilde{\mu}_{k+1}), 1$ are linearly independent. Since $\theta^3(\tilde{\mu}_1), ...\theta^3(\tilde{\mu}_{k+1})$ are in $C^{\gamma+1}$ and $a_+^3 \notin C^{\gamma+1}$, we see that $\theta^3(\tilde{\mu}_1), ..., \theta^3(\tilde{\mu}_{k+1}), 1, a_+^3$ are linearly independent as well, that is,

$$(\tilde{\mu}_1, ..., \tilde{\mu}_k, \tilde{\mu}_{k+1}) \in U_{k+1}.$$

Since $(\tilde{\mu}_1, ..., \tilde{\mu}_{k+1}) \in U_{k+1}$ can be chosen arbitrarily close to $(\mu_1, ..., \mu_{k+1})$, the density is proved. This finishes the proof of Lemma 4.10. □

Finally, we are ready to prove Theorem 1.2.

Proof of Theorem 1.2. Fix arbitrary positive integer b, l. By Lemma 4.10, we can find $(\mu_1, ..., \mu_{4b}) \in U_{4b}$. Since $a_+^3, \theta^3(\mu_1), ..., \theta^3(\mu_{4b}), 1$ are linearly independent, we can choose a function $g_1 \in C^0(\overline{\Omega})$ (e.g. choose g_1 as a linear combination of $a_+^3, \theta^3(\mu_1), ..., \theta^3(\mu_{4b})$, 1) such that

$$\begin{gathered} \int_\Omega g_1(x)\theta^3(x, \mu_0)\, dx < 0 < \int_\Omega g_1(x)\theta^3(x, \mu_{4b+1})\, dx, \\ \int_\Omega g_1(x)\theta^3(x, \mu_i)\, dx \cdot \int_\Omega g_1(x)\theta^3(x, \mu_{i+1})\, dx < 0 \quad (i = 0, 1, ..., 4b) \end{gathered} \tag{4.48}$$

with the understanding that

$$\mu_0 = 0, \;\; \mu_{4b+1} \gg 1, \;\; \theta(x, \mu_0) = a_+(x)$$

and $\theta(x, \mu_{4b+1})$ is sufficiently close to $\int a/|\Omega|$. For such a g_1, the corresponding function G (with $g = g_1$ in (1.7a)) is negative near $\mu = 0$, positive near $\mu = \infty$, and it has at least $4b+1$ zeros. The same is true for any g in a sufficiently small $C^0(\Omega)$-neighborhood $\mathcal{U}$ of g_1. Now, similarly as in [24, Proof of Proposition 1.3], applying the parametric transversality [1, 16] to the map

$$(\mu, g) \mapsto \Psi(\mu, g) := \int_\Omega g(x)\theta^3(x, \mu)\, dx$$

we can choose a function g in this neighborhood such that the corresponding function G has only simple roots (and at least $4b+1$ of them). Specifically, since $\Psi(\mu, \cdot)$ is linear and surjective, the transversality theorem implies that for any g in an open and dense subset of $\mathcal{U}$, the function $G = \Psi(\cdot, g)$ has zero as a regular value. Obviously, we can then choose a smooth g with this property.

Fix such a g and let $\mu_1 < ... < \mu_k$, for some $k \geq 4b+1$, be the roots, all of them simple, of the corresponding function G. Without loss of generality, we may assume that $G < 0$ in (μ_1, μ_2); otherwise, we replace g by $-g$.

Now for the given l, we use similar arguments as above to find a smooth function h such that H has zeroes $\mu_{i,m}$ satisfying $\mu_{1,1}, ..., \mu_{1,s} \in (\mu_1, \mu_2)$ for some $s \geq 2l+1$, and $\mu_{j,1} \in (\mu_j, \mu_{j+1})$ for $2 \leq j \leq k-1$. The function H can have other zeroes, but h can be chosen such that H and G have no common roots and H has only simple roots. Then, we have at least $[\frac{s-1}{2}] \geq l$ of intervals among $\{(\mu_{1,j}, \mu_{1,j+1})\}_{j=1}^{s-1}$ in which $H < 0$. By Lemma 4.8, (4.1) has at least l stable loops in (μ_1, μ_2).

We also note that in (μ_1, μ_2), there are at least $[\frac{s-1}{2}] \geq l$ intervals among $\{(\mu_{1,j}, \mu_{1,j+1}\}_{j=1}^{s-1}$ in which $H > 0$, so that the above conclusion remains valid if H is replaced by $-H$. This observation will be needed later since we may have to replace H by $-H$.

Next we seek the existence of b stable branches. Recall that $k \geq 4b+1$. There are at least $2b$ intervals among $\{(\mu_j, \mu_{j+1})\}_{j=1}^{k-1}$ in which $G < 0$. In the following we consider two possibilities for these intervals:
(a) In at least b intervals, out of the ones where $G < 0$, the number of zeroes of H is odd. For any such interval, there exist $\mu_* < \mu^*$ (one of them being an end point of the interval) such that $H(\mu_*) = 0 = G(\mu^*)$ and $H, G < 0$ in (μ_*, μ^*), or $G(\mu_*) = H(\mu^*) = 0$ and $H, G < 0$ in (μ_*, μ^*). By Lemma 4.9, there exists a stable branch between μ_* and μ^*. Hence, there will be at least b stable branches in total in this case.
(b) There are at least $[\frac{k-1}{2}] - (b-1) \geq b+1$ intervals, out of the ones where $G < 0$, in which the number of zeroes of H is even. Divide such intervals into two subgroups: (i) both $H(\mu_j)$ and $H(\mu_{j+1})$ are negative; (ii) both $H(\mu_j)$ and $H(\mu_{j+1})$ are positive. If the number of intervals in group (i) is at least $[\frac{b+1}{2}]$, then we have at least $2[\frac{b+1}{2}] \geq b$ stable branches. If not, the number of intervals in group (ii) is at least $[\frac{b+1}{2}]$. For this case, replace H by $-H$ and repeat the argument as in (i). By the observation made earlier, by replacing H by $-H$, the number of stable loops in (μ_1, μ_2) is at least l. This completes the proof of Theorem 1.2. $\square$

Acknowledgment. S.M. was was partially supported by Fondecyt Grant #

1050754, FONDAP de Matemáticas Aplicadas and Nucleus Millennium P04-069-F Information and Randomness; P. P. was supported by NSF grant DMS-0400702; The visits of S.M. to Ohio State University was partially supported by Fondecyt Grant # 1050754, MRI and MBI at Ohio State University. This work is supported in part by NSF grant upon Agreement No. 0112050.

References

[1] J. Abraham and R. Robbin, *Transversal Mappings and Flows,* Benjamin, New York, 1967.

[2] R. S. Cantrell and C. Cosner, *The effects of spatial heterogeneity in population dynamics*, J. Math. Biol. **29** (1991) 315-338.

[3] R. S. Cantrell and C. Cosner, *Should a park be an island?* SIAM J. Appl. Math. **53** (1993) 219-252.

[4] R. S. Cantrell and C. Cosner, *On the effects of spatial heterogeneity on the persistence of interacting species*, J. Math. Biol. **37** (1998) 103-145.

[5] R. S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Series in Mathematical and Computational Biology, John Wiley and Sons, Chichester, UK, 2003.

[6] R. S. Cantrell, C. Cosner, and V. Hutson, *Permanence in ecological systems with diffusion*, Proc. Roy. Soc. Edin. **123A** (1993a) 553-559.

[7] R. S. Cantrell, C. Cosner, and V. Hutson, *Ecological models, permanence and spatial heterogeneity*, Rocky Mount. J. Math. **26** (1996) 1-35.

[8] R.S. Cantrell, C. Cosner, and Y. Lou, *Multiple reversals of competitive dominance in ecological reserves via external habitat degradation*, J. Dyn. Diff. Eqs. **16** (2004) 973-1010.

[9] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski, *The evolution of slow dispersal rates: a reaction-diffusion model*, J. Math. Biol. **37** (1998) 61-83.

[10] Y. Du, *Effects of a degeneracy in the competition model, Part II. Perturbation and dynamical behavior*, J. Diff. Eqs. **181** (2002) 133-164.

[11] Y. Du, *Realization of prescribed patterns in the competition model*, J. Diff. Eqs. **193** (2003) 147-179.

[12] J.E. Furter and J. López-Gómez, *Diffusion-mediated permanence problem for a heterogeneous Lotka-Volterra competition model*, Proc. Roy. Soc. Edin. **127A** (1997) 281-336.

[13] D. Gilbarg and N. Trudinger, *Elliptic Partial Differential Equation of Second Order, 2nd Ed.*, Springer-Verlag, Berlin, 1983.

[14] A. Hastings, *Spatial heterogeneity and ecological models*, Ecology **71** (1990) 426-428.

[15] D. Henry, *Geometric Theory of Semilinear Parabolic Equations*, Springer, New York, 1981.

[16] D. Henry, *Perturbation of the Boundary for Boundary Value Problems of Partial Differential Operators*, Cambridge University Press, Cambridge, 2005.

[17] P. Hess, *Periodic Parabolic Boundary Value Problems and Positivity*, Longman Scientific & Technical, Harlow, UK, 1991.

[18] E.E. Holmes, M.A. Lewis, J.E. Banks, and R.R. Veit, *Partial differential equations in ecology: spatial interactions and population dynamics*, Ecology **75** (1994) 17-29.

[19] S. Hsu, H. Smith, and P. Waltman, *Competitive exclusion and coexistence for competitive systems on ordered Banach spaces*, Trans. Amer. Math. Soc. **348** (1996) 4083–4094.

[20] V. Hutson, J. López-Gómez, K. Mischaikow, and G. Vickers, *Limit behavior for a competing species problem with diffusion*, in *Dynamical Systems and Applications*, World Sci. Ser. Appl. Anal. 4, World Scientific, River Edge, NJ, 1995, 501–533.

[21] V. Hutson, K. Mischaikow, and P. Poláčik, *The evolution of dispersal rates in a heterogeneous time-periodic environment*, J. Math. Biol. **43** (2001) 501-533.

[22] V. Hutson, Y. Lou, and K. Mischaikow, *Spatial heterogeneity of resources versus Lotka-Volterra dynamics*, J. Diff. Eqs. **185** (2002) 97-136.

[23] V. Hutson, Y. Lou, and K. Mischaikow, *Convergence in competition models with small diffusion coefficients*, J. Diff. Eqs. **211** (2005) 135-161.

[24] V. Hutson, Y. Lou, K. Mischaikow, and P. Poláčik, *Competing species near the degenerate limit*, SIAM J. Math. Anal. **35** (2003) 453-491.

[25] V. Hutson, S. Martinez, K. Mischaikow, and G.T. Vickers, *The evolution of dispersal*, J. Math. Biol. **47** (2003) 483-517.

[26] T. Kato, *Perturbation Theory for Linear Operators*, Springer Verlag, New York, 1966.

[27] J. López-Gómez, *Coexistence and meta-coexistence for competing species*, Houston J. Math. (2003) 483-536.

[28] J. López-Gómez and M. Molina-Meyer, *Superlinear indefinite system beyond Lotka-Volterra models*, J. Diff. Eqs. (2005), in press.

[29] A. Lunardi, *Analytic Semigroups and Optimal Regularity in Parabolic Problems*, Birkhäuser, Berlin, 1995.

[30] S. Pacala and J. Roughgarden, *Spatial heterogeneity and interspecific competition*, Theor. Pop. Biol. **21** (1982) 92-113.

[31] A.B. Potapov and M.A. Lewis, *Climate and competition: the effect of moving range boundaries on habitat invasibility*, Bull. Math. Biol. (2004) 975-1008.

[32] M. H. Protter and H. F. Weinberger, *Maximum Principles in Differential Equations, 2nd Ed.*, Springer-Verlag, Berlin, 1984.

[33] N. Shigesada and K. Kawasaki, *Biological Invasions: Theory and Practice, Oxford Series in Ecology and Evolution*, Oxford University Press, Oxford, New York, Tokyo, 1997.