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EFFECTS OF SMALL SPATIAL VARIATION OF THE REPRODUCTION RATE IN A TWO SPECIES COMPETITION MODEL

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Abstract. Of concern is the effect of a small spatially inhomogeneous perturbation of the reproduction rate of the first species in a two-species Lotka-Volterra competition-diffusion problem with spatially homogeneous reaction terms. Apart from this perturbation and the diffusion rates, the two species are assumed to be identical. Our main result shows that the first species can always invade, whereas the second species can only invade under certain conditions which yield uniform persistence of both species. The proof relies on comparison techniques and properties of the principal eigenvalue of reaction-diffusion equations.

1. Introduction

This paper addresses the invasion and co-existence in two species competition models with dispersal. The overarching biological question can be described in terms of a species competing with a mutant exhibiting one slightly different feature. This question has drawn much attention over the years. One of the first major contributions goes back to [1] and [6] where the authors address the difference in the dispersal rate under the assumption that the reproduction rate is spatially dependent. Specifically, it is shown in [1] and [6] that for $\kappa_1 < \kappa_2$, all solutions of

$$
\begin{gathered}
u_t = \kappa_1 \Delta u + u(a_0(x) - u - v), \quad x \in \Omega \\
v_t = \kappa_2 \Delta v + v(a_0(x) - u - v), \quad x \in \Omega \\
\frac{\partial u}{\partial \nu}(t, \cdot) = \frac{\partial v}{\partial \nu}(t, \cdot) = 0 \quad \text{on } \partial\Omega
\end{gathered}
\tag{1.1}
$$

which satisfy positive initial conditions, converge to the semi-trivial equilibria $(u^*, 0)$ (provided that $\int_\Omega a_0(x)dx > 0$ and $a_0(\cdot) \not\equiv$constant). Biologically, the "slower diffuser" persists and can invade (invasion means starting from small initial condition and survive). Similar results have been established for two species competition models with nonlocal diffusion (cf. [10]), but the situation is more complicated

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in time-dependent settings, cf. [9]. In a very recent work [11], the authors considered the invasion and co-existence for two species competition models in which two competing species have the same population dynamics, but different dispersal strategies: the movement of one species is purely by random walk while the other species adopts a non-local dispersal strategy. The above mentioned results for (1.1) have been partially extended to such competition models, and additional interesting results are obtained in [11].

A difference in the reproduction rate has been investigated in [8]. Consider

$$\begin{gathered} u_t = \kappa\Delta u + u(a_0(x) + \epsilon a(x) - u - v), \quad x \in \Omega \\ v_t = \kappa\Delta v + v(a_0(x) - u - v), \quad x \in \Omega \\ \frac{\partial u}{\partial \nu}(t,\cdot) = \frac{\partial v}{\partial \nu}(t,\cdot) = 0 \quad \text{on } \partial\Omega \end{gathered} \tag{1.2}$$

The authors assume that a_0 is a nonconstant smooth function on Ω with $\int_\Omega a_0 > 0$ and that a changes sign. Among other results, they establish for a large class of functions a and ϵ small that the stability of the two species varies in a complicated fashion as κ increases. Basically, the biological consequence is that it is unpredictable which species survives.

We are interested in the borderline case where $a_0 \in (0,\infty)$ is a constant, and $\int_\Omega a(x)\,dx = 0$. Moreover, we can allow the diffusion rates to be different which leads to

$$\begin{gathered} u_t = \kappa_1\Delta u + u(a_0 + \epsilon a(x) - u - v), \quad x \in \Omega \\ v_t = \kappa_2\Delta v + v(a_0 - u - v), \quad x \in \Omega \\ \frac{\partial u}{\partial \nu}(t,\cdot) = \frac{\partial v}{\partial \nu}(t,\cdot) = 0 \quad \text{on } \partial\Omega. \end{gathered} \tag{1.3}$$

Note that (1.3) possesses a continuum of stable equilibria for $\epsilon = 0$ regardless of the diffusion coefficients (cf. [2]) which suggest that the restriction to equal diffusions coefficient in (1.2) can be avoided here.

The biological interpretation in case $\kappa_1 = \kappa_2$ is that the original species v has not adapted to the environment, whereas the mutant u shows slight adaptation ($\epsilon \ll 1$), which proves to be an advantage in certain regions of the habitat, but a disadvantage in others.

As it is known, a small spatially variation favors the persistence in a single species population model with Neumann boundary condition. More precisely, all solutions of

$$\begin{gathered} u_t = \kappa\Delta u - u^2, \quad x \in \Omega \\ \frac{\partial u}{\partial \nu}(t,\cdot) = 0, \quad x \in \partial\Omega \end{gathered}$$

with positive initial conditions converge to 0 as $t \to \infty$ (hence the population cannot persist), while for any $a(x) \not\equiv 0$ with $\int_\Omega a(x)dx = 0$, all solutions of

$$\begin{gathered} u_t = \kappa\Delta u + u(a(x) - u), \quad x \in \Omega \\ \frac{\partial u}{\partial \nu}(t,\cdot) = 0, \quad x \in \partial\Omega \end{gathered}$$

with positive initial conditions converge to its unique positive equilibrium as $t \to \infty$ (hence the population persists). This follows directly from the fact that the principal eigenvalue $\lambda(b)$ of

$$\begin{gathered} \kappa\Delta u + b(x)u = \lambda u, \quad x \in \Omega, \\ \frac{\partial u}{\partial \nu}|_{\partial\Omega} \equiv 0 \end{gathered} \tag{1.4}$$

is greater than the principal eigenvalue $\lambda(\bar{b})(=\bar{b})$ of

$$\begin{gathered} \kappa\Delta u + \bar{b}u = \lambda u, \quad x \in \Omega, \\ \frac{\partial u}{\partial \nu}|_{\partial\Omega} \equiv 0 \end{gathered} \tag{1.5}$$

for all $b \in C^1(\bar{\Omega})$, $b \not\equiv \bar{b} := \frac{1}{\mathrm{vol}(\Omega)} \int_\Omega b(x)dx$.

It is natural to ask whether a small spatial variation in the reproduction rate of the species u in (1.3) gives u a better chance than v to survive no matter whether $\kappa_1 = \kappa_2$ or not, and whether such a small spatial variation still allows both species to co-exist. We find that the answer to the first question is yes and the answer to the second question depends on the size of κ_1, κ_2, a_0, and the frequency of the variation of a, that is, the mutant u always survives and can invade, whereas the species v can only co-exist and invade under certain circumstances. A typical biological situation for the latter would be a habitat which does not exhibit high frequency variation of the environment.

As for mutations primarily affecting competitiveness, a comprehensive study has been described in [12].

To state our main result, we introduce the following standing hypotheses:

- (H1) $N \in \mathbb{N}$, $\Omega \subset \mathbb{R}^N$ bounded domain with smooth boundary,
- (H2) $\epsilon \geq 0$, $a_0, \kappa_1, \kappa_2 > 0$, and $a \not\equiv 0$ belongs to $C^1(\bar{\Omega})$ with $\int_\Omega a(x)dx = 0$ and $\|a\|_\infty = 1$.

Under hypotheses (H1) and (H2), (1.3) has two semi-trivial equilibrium solutions $(u_\epsilon^*(\cdot), 0)$ and $(0, v^*(\cdot))$ with $u_\epsilon^*(x) > 0$ and $v^*(x) = a_0$ for $x \in \bar{\Omega}$.

Firstly, the fact that $\lambda(b) > \lambda(\bar{b})$ for $b \in C^1(\bar{\Omega})$ with $b \not\equiv \bar{b}$ (notations as in (1.4) and (1.5)) implies:

- For any $\epsilon > 0$, $(0, v^*)$ is unstable and hence the species u can invade when rare (see Theorem 2.1 (1)).

The above result shows that any spatially inhomogeneous perturbation in the reproduction rate of the species u will enable u to survive.

Let $\|\cdot\|_{k,p}$ be the norm on $W^{k,p}(\Omega)$. We write $\|\cdot\|_2$ for $\|\cdot\|_{0,2}$ and $\|\cdot\|_\infty$ for the norm on $L^\infty(\Omega)$. Denote by $\big(\mu_j\big)_{j\in\mathbb{Z}_+}$ the decreasing sequence of eigenvalues of $w \mapsto \Delta w$, $w \in W^{2,2}(\Omega)$, $\frac{\partial w}{\partial \nu}|_{\partial\Omega} \equiv 0$ counted by multiplicity, and by $\big(\varphi_j\big)_{j\in\mathbb{Z}_+}$ an orthogonal sequence of eigenfunction associated with $\big(\mu_j\big)_{j\in\mathbb{Z}_+}$. Note that $\mu_1 < \mu_0 = 0$, and we assume $\varphi_0 = \frac{1}{\mathrm{vol}(\Omega)}$ and $\|\varphi_j\|_{0,2} = 1$ for $j \in \mathbb{N}$. Let $a = \sum_{j=1}^\infty a_j\varphi_j$ be the eigenfunction expansion of a and

$$\lambda_2 = \frac{1}{\mathrm{vol}(\Omega)} \sum_{j=1}^\infty \frac{a_0^2 a_j^2}{\kappa_2|\mu_j|(a_0 + \kappa_1|\mu_j|)^2} \Big[1 - \frac{\kappa_1\kappa_2\mu_j^2}{a_0^2}\Big]. \tag{1.6}$$

Observe that

$$|\lambda_2| \leq \frac{1}{\min\{\kappa_1, \kappa_2\}|\mu_1|}. \tag{1.7}$$

We show that there are $\eta(\kappa_1, \kappa_2, a_0), \zeta(\kappa_1, \kappa_2, a_0) > 0$ such that for $0 < \epsilon < \min\{\eta(\kappa_1, \kappa_2, a_0) \cdot |\lambda_2|, \zeta(\kappa_1, \kappa_2, a_0)\}$,

- If $\lambda_2 < 0$, then $(u^*_\epsilon, 0)$ is asymptotically stable and hence the species v cannot invade when rare. In particular, if $|\mu_{j_0}| < \frac{a_0}{\sqrt{\kappa_1\kappa_2}} < |\mu_{j_0+1}|$ for some $j_0 \geq 0$ and $a_j = 0$ for $j \leq j_0$, then $(u^*_\epsilon, 0)$ is asymptotically stable (see Theorem 2.1 (2)).
- If $\lambda_2 > 0$, then $(u^*_\epsilon, 0)$ is unstable and hence (1.3) is strongly uniformly persistent. In particular, if $|\mu_{j_0}| < \frac{a_0}{\sqrt{\kappa_1\kappa_2}} < |\mu_{j_0+1}|$ for some $j_0 \geq 1$ and $a_j = 0$ for $j \geq j_0 + 1$, then $(u^*_\epsilon, 0)$ is unstable (see Theorem 2.1 (3)).

The above results reveal interesting effects of κ_1, κ_2, and a_0 on the dynamics of (1.3). They imply that if the square root of the product of the diffusion rates κ_1 and κ_2 is larger than $\frac{a_0}{|\mu_1|}$, then any spatially inhomogeneous perturbation in the reproduction rate of the species u drives the species v to extinction provided that v is small initially. They also show that the frequency of the variation of the environment plays a crucial role for the stability of $(u^*_\epsilon, 0)$. Roughly, consider the following two extreme cases: if a changes rapidly in the sense that the modes with low frequency are not present in its expansion, the species u drives v to extinction provided that v is small initially. If a changes slowly in the sense that the modes with high frequency are not present in its expansion, both u and v can coexist.

It should be pointed out that global asymptotic stability of $(u^*_\epsilon, 0)$ has been established in [4] for $\kappa_1 = \kappa_2 = \kappa$ and given $\epsilon > 0$, provided that κ is sufficiently large.

We will prove the above mentioned results in Section 2. Our proof relies on comparison arguments and properties of the principal eigenvalue, which allows us to determine the sign of the principal eigenvalue $\lambda^u(\epsilon)$ of the linearization of (1.3) at the semi-trivial equilibrium $(u^*_\epsilon, 0)$. The constant λ_2 is the first nonzero coefficient in the power series expansion of $\lambda^u(\epsilon)$ with respect to ϵ.

As the above results reveal, if one fixes a and a small ϵ and varies a_0 or κ_1 or κ_2, the stability of the semi-trivial solution $(u^*_\epsilon, 0)$ may change. To shed some light on the stability change of $(u^*_\epsilon, 0)$ and the global dynamics of (1.3), we present some numerical simulations in Section 3. They corroborate the theoretical findings obtained in this paper and indicate the relative dominance of the mutant even if both co-exist. Moreover, they suggest that the interior equilibrium, when it exists, is unique and globally stable.

General results on the existence and uniqueness of co-existence states can be found in [3].

It should be pointed out that similar results hold, e.g., for periodic boundary conditions assuming that the domain is a hypercube $\prod_{n=1}^N (a_j, b_j)$, $a_j < b_j$. However, for Dirichlet boundary conditions, the situation is different since the principal eigenvalue $\lambda(b)$ of (1.4) with $Bu = u$ may not be greater than the principal eigenvalue of (1.5) with $Bu = u$. We provide such an example in Section 4.

2. Uniform persistence induced by spatial variation

Throughout we assume that hypotheses (H1) and (H2) are satisfied and that $p > N$. It is well-known ([5], [13], [14]) that (1.3) generates a solution semi-flow on some fractional power space $X \hookrightarrow C^1(\bar\Omega)^2$ which leaves the positive cone invariant.

As for notation, we understand $\big(\mu_j\big)_{j\in\mathbb{Z}_+}$, $\big(\varphi_j\big)_{j\in\mathbb{Z}_+}$, and λ_2 as described in the introduction. Moreover, we write, $Bw = 0$ for $\frac{\partial w}{\partial \nu} = 0$ on $\partial\Omega$ in case that $w \in W^{2,2}(\Omega)$.

Let $(u^*_\epsilon, 0)$ and $(0, v^*)$ be the two semi-trivial stationary solutions of (1.3). Then $v^* = a_0$ and u^*_ϵ is the solution of

$$\begin{gathered} \kappa_1\Delta u + u(a_0 + \epsilon a(x) - u) = 0, \quad x \in \Omega, \\ Bu = 0, \end{gathered} \tag{2.1}$$

The eigenvalue problem of the linearization of the steady state version of (1.3) at $(u^*_\epsilon, 0)$ is given by

$$\begin{gathered} \kappa_1\Delta u + (a_0 + \epsilon a(x) - 2u^*_\epsilon(x))u - u^*_\epsilon(x)v = \lambda u, \quad x \in \Omega, \\ \kappa_2\Delta v + (a_0 - u^*_\epsilon(x))v = \lambda v, \quad x \in \Omega, \\ Bu = Bv = 0, \end{gathered} \tag{2.2}$$

and at $(0, v^*)$ by

$$\begin{gathered} \kappa_1\Delta u + \epsilon a(x)u = \lambda u, \quad x \in \Omega, \\ \kappa_2\Delta v - a_0u - a_0v = \lambda v, \quad x \in \Omega, \\ Bu = Bv = 0. \end{gathered} \tag{2.3}$$

Hence the stability of $(u^*_\epsilon, 0)$ is determined by the principal eigenvalue $\lambda^u(\epsilon)$ of the eigenvalue problem

$$\begin{gathered} \kappa_2\Delta v + (a_0 - u^*_\epsilon(x))v = \lambda v, \quad x \in \Omega, \\ Bv = 0, \end{gathered} \tag{2.4}$$

whereas the stability of $(0, v^*)$ is determined by the principal eigenvalue $\lambda^v(\epsilon)$ of the eigenvalue problem

$$\begin{gathered} \kappa_1\Delta u + \epsilon a(x)u = \lambda u, \quad x \in \Omega, \\ Bu = 0. \end{gathered} \tag{2.5}$$

Theorem 2.1. *Assume that* (H1, (H2) *are satisfied and* λ_2 *is given by* (1.6). *Then*

(1) $(0, v^*)$ *is unstable for* $\epsilon > 0$.

Moreover, there exist $\eta(\kappa_1, \kappa_2, a_0), \zeta(\kappa_1, \kappa_2, a_0) > 0$ *such that for any* $0 < \epsilon < \min\{\eta(\kappa_1, \kappa_2, a_0) \cdot |\lambda_2|, \zeta(\kappa_1, \kappa_2, a_0)\}$

(2) $(u^*_\epsilon, 0)$ *is asymptotically stable in case that* $\lambda_2 < 0$ *and*

(3) $(u^*_\epsilon, 0)$ *is unstable provided that* $\lambda_2 > 0$.

Corollary 2.2. *Let additionally* $\{\mu_j, j \geq 0\}$ *be understood as described in the introduction,* $J_1 := \{j \in \mathbb{N} : |\mu_j| < a_0/\sqrt{\kappa_1\kappa_2}\}$, *and* $J_2 := \{j \in \mathbb{N} : |\mu_j| > a_0/\sqrt{\kappa_1\kappa_2}\}$, *and assume* $0 < \epsilon < \min\{\eta(\kappa_1, \kappa_2, a_0) \cdot |\lambda_2|, \zeta(\kappa_1, \kappa_2, a_0)\}$.

(1) *If* $a_j = 0$ *for* $j \in J_1$ *and there is* $j_2 \in J_2$ *such that* $a_{j_2} \neq 0$, *then* $(u^*_\epsilon, 0)$ *is asymptotically stable.*

(2) *If* $a_j = 0$ *for* $j \in J_2$ *and there is* $j_1 \in J_1$ *such that* $a_{j_1} \neq 0$, *then* $(u^*_\epsilon, 0)$ *is unstable.*

Remark 2.3. The biological meaning is that the mutant u can invade under all circumstances and will always survive, whereas the species v needs a favorable environment, e.g., as described in the second alternative of the Corollary. The condition $a_j = 0$ for all $j \in J_2$ excludes coexistence in case of “high frequency” adaptation of the mutant in a highly heterogeneous habitat. Also, slower dispersal rates favors persistence as the roles of κ_1, κ_2 in the definition of J_2 reveals.

In order to prove Theorem 2.1, we first prove some lemmas and make a few observations.

Lemma 2.4. *Let $a^*(\cdot) \in C^1(\bar\Omega)$ and $u^*(\cdot)$ be the solution of*

$$\begin{gathered} \kappa_1 \Delta u^* + a_0(a^*(x) - u^*) = 0, \quad x \in \Omega \\ Bu^* = 0, \quad x \in \partial\Omega. \end{gathered} \tag{2.6}$$

Then $\|u^*\|_\infty \le \|a^*\|_\infty$.

Proof. Observe that $u = u^*$ is the unique solution of

$$\begin{gathered} -\kappa_1 \Delta u = a_0(a^*(x) - u), \quad x \in \Omega \\ Bu = 0, \quad x \in \partial\Omega. \end{gathered} \tag{2.7}$$

Note that $u = \|a^*\|_\infty$ is a super-solution of (2.7) and $u = -\|a^*\|_\infty$ is a sub-solution of (2.7). By comparison principle for elliptic equations, we have

$$-\|a^*\|_\infty \le u^*(x) \le \|a^*\|_\infty \quad \text{for } x \in \Omega$$

and hence

$$\|u^*\|_\infty \le \|a^*\|_\infty.$$

$\square$

Let u_1^* be the solution of

$$\begin{gathered} \kappa_1 \Delta u_1^* + a_0[a(x) - u_1^*] = 0, \quad x \in \Omega, \\ Bu_1^* = 0. \end{gathered} \tag{2.8}$$

By Lemma 2.4,

$$\|u_1^*\|_\infty \le \|a\|_\infty = 1. \tag{2.9}$$

The following calculations are meant in the L^2 sense. Write the expansions of a and u_1^* in terms of the orthogonal basis $\{\varphi_j\}$ as

$$a = \sum_{j=1}^\infty a_j \varphi_j, \quad u_1^* = \sum_{j=0}^\infty u_{1,j}^* \varphi_j, \tag{2.10}$$

(2.8) and (2.10) yield

$$\kappa_1 \sum_{j=0}^\infty \mu_j u_{1,j}^* \varphi_j + a_0[-u_{1,0}^* + \sum_{j=1}^\infty (a_j - u_{1,j}^*)\varphi_j] = 0 \tag{2.11}$$

for $j \in \mathbb{N} \cup \{0\}$. Using the orthogonality of $\{\varphi_j\}$, we have

$$u_{1,j}^* = \begin{cases} 0 & j = 0, \\ \frac{a_0 a_j}{a_0 + \kappa_1 |\mu_j|} & j \in \mathbb{N}. \end{cases} \tag{2.12}$$

Let u_2^* be the solution of

$$\begin{gathered} \kappa_1 \Delta u_2^* - a_0 u_2^* + u_1^*[a(x) - u_1^*] = 0, \quad x \in \Omega, \\ Bu_2^* = 0. \end{gathered} \tag{2.13}$$

By Lemma 2.4 and (2.9), we have

$$\|u_2^*\|_\infty \le \frac{2}{a_0}. \tag{2.14}$$

Let

$$u_2^* = \sum_{j=0}^{\infty} u_{2,j}^* \varphi_j \tag{2.15}$$

be the expansion of u_2^* in terms of $\{\varphi_j\}$. (2.10), (2.12), (2.13) and (2.15) yield

$$\kappa_1 \sum_{j=0}^{\infty} \mu_j u_{2,j}^* \varphi_j - a_0 \sum_{j=0}^{\infty} u_{2,j}^* \varphi_j + \sum_{j=1}^{\infty} u_{1,j}^* \varphi_j \sum_{j=1}^{\infty} (a_j - u_{1,j}^*)\varphi_j = 0. \tag{2.16}$$

Using the orthogonality of $\{\varphi_j\}$, we get

$$-a_0 u_{2,0}^* + \sum_{j=1}^{\infty} u_{1,j}^*(a_j - u_{1,j}^*) = 0,$$

hence

$$u_{2,0}^* = \sum_{j=1}^{\infty} \frac{a_j}{a_0 + \kappa_1|\mu_j|}\Big(a_j - \frac{a_0 a_j}{a_0 + \kappa_1|\mu_j|}\Big) = \sum_{j=1}^{\infty} \frac{\kappa_1|\mu_j| a_j^2}{(a_0 + \kappa_1|\mu_j|)^2}. \tag{2.17}$$

Lemma 2.5. *Let $u_1^*(x)$ and $u_2^*(x)$ be the solutions of* (2.8) *and* (2.13)*, respectively, and $M = \big(1 + \|2u_1^* u_2^* - a u_2^*\|_\infty\big)/a_0$. Then there exists an $\hat\epsilon(a_0) > 0$ such that*

$$|u_\epsilon^*(x) - \big(a_0 + \epsilon u_1^*(x) + \epsilon^2 u_2^*(x)\big)| \le \epsilon^3 M$$

for $x \in \Omega$, $0 < \epsilon < \hat\epsilon$.

Proof. Let

$$u_\epsilon^+ := a_0 + \epsilon u_1^* + \epsilon^2 u_2^* + \epsilon^3 M, u_\epsilon^- := a_0 + \epsilon u_1^* + \epsilon^2 u_2^* - \epsilon^3 M.$$

A direct calculation yields

$$\begin{aligned}
&\kappa_1 \Delta u_\epsilon^+ + u_\epsilon^+(a_0 + \epsilon a(x) - u_\epsilon^+)\\
&= \epsilon\kappa_1\Delta u_1^* + \epsilon^2\kappa_1\Delta u_2^* + (a_0 + \epsilon u_1^* + \epsilon^2 u_2^* + \epsilon^3 M)(\epsilon a - \epsilon u_1^* - \epsilon^2 u_2^* - \epsilon^3 M)\\
&= \epsilon a_0(u_1^* - a) + \epsilon^2 a_0 u_2^* + \epsilon^2 u_1^*(u_1^* - a)\\
&\quad + (a_0 + \epsilon u_1^* + \epsilon^2 u_2^* + \epsilon^3 M)(\epsilon a - \epsilon u_1^* - \epsilon^2 u_2^* - \epsilon^3 M)\\
&= -\epsilon^3[a_0 M + 2u_1^* u_2^* - a u_2^*] - \epsilon^4[u_2^* u_2^* + 2u_1^* M - aM] - 2\epsilon^5 u_2^* M - \epsilon^6 M^2\\
&=: R(\epsilon).
\end{aligned}$$

By $M = \big(1 + \|2u_1^* u_2^* - a u_2^*\|_\infty\big)/a_0$ and (2.9), (2.14), there exists an $\hat\epsilon = \hat\epsilon(a_0) > 0$ with $R(\epsilon) < 0$ for all $0 < \epsilon < \hat\epsilon$, hence u_ϵ^+ is a super-solution of

$$\begin{gathered}
-\kappa_1 \Delta u = u(a_0 + \epsilon a(x) - u), \quad x \in \Omega,\\
Bu = 0,
\end{gathered} \tag{2.18}$$

for $0 < \epsilon < \hat\epsilon$. Similarly, we have

$$\begin{aligned}
&\kappa_1 \Delta u_\epsilon^- + u_\epsilon^-(a_0 + \epsilon a(x) - u_\epsilon^-)\\
&= \epsilon\kappa_1\Delta u_1^* + \epsilon^2\kappa_1\Delta u_2^* + (a_0 + \epsilon u_1^* + \epsilon^2 u_2^* - \epsilon^3 M)(\epsilon a - \epsilon u_1^* - \epsilon^2 u_2^* + \epsilon^3 M)\\
&= \epsilon a_0(u_1^* - a) + \epsilon^2 a_0 u_2^* + \epsilon^2 u_1^*(u_1^* - a)\\
&\quad + (a_0 + \epsilon u_1^* + \epsilon^2 u_2^* - \epsilon^3 M)(\epsilon a - \epsilon u_1^* - \epsilon^2 u_2^* + \epsilon^3 M)\\
&= \epsilon^3[a_0 M - 2u_1^* u_2^* + a u_2^*] + \epsilon^4[-u_2^* u_2^* + 2u_1^* M + aM] + 2\epsilon^5 u_2^* M - \epsilon^6 M^2\\
&> 0
\end{aligned}$$

for $0 < \epsilon < \hat{\epsilon}$ by passing to a smaller $\hat{\epsilon}$, if necessary. Thus, u^- is a sub-solution of (2.18) for $0 < \epsilon < \hat{\epsilon}$. By possibly reducing the size of $\hat{\epsilon}$ once more, we can also ensure $u_\epsilon^- > 0$ for $0 < \epsilon < \hat{\epsilon}$, hence the fact that u_ϵ^* is the only positive solution of (2.18) yields

$$u_\epsilon^-(x) \le u_\epsilon^*(x) \le u_\epsilon^+(x)$$

for $0 < \epsilon < \hat{\epsilon}$. The lemma then follows. □

We remark that the size of $\hat{\epsilon}(a_0)$ depends on that of a_0.

Lemma 2.6. *Let $b^* \in C^1(\bar{\Omega})$ with $\int_\Omega b^*(x)dx = 0$ and v^* be the solution of*

$$\begin{gathered} \kappa_2 \Delta v^* + b^*(x) = 0, \quad x \in \Omega \\ Bv^* = 0, \quad x \in \partial\Omega \end{gathered} \tag{2.19}$$

with $\int_\Omega v^*(x)dx = 0$. Then there is C_0 independent of κ_2 and b^* such that

$$\|v^*\|_\infty \le C_0 \frac{\|b^*\|_\infty}{\kappa_2}.$$

Proof. Let $p \in [2, \infty)$, $D_p := \{w \in W^{2,p}(\Omega) : Bw = 0\}$, and $A_p : D_p \to L^p(\Omega)$ be defined by $A_p w := -\Delta w$. $(D_p, \|\cdot\|_{2,p})$ is a Banach space and A_p is a Fredholm operator of index 0 with kernel span$\{1\}$ and (closed) range $R_p := \{z \in L^p(\Omega) : \int_\Omega z = 0\}$ in $L^p(\Omega)$. The statements about kernel and range follow from the fact that A_2 is self-adjoint, $D_p \subset D_2$, and $A_p = A_2|_{D_p}$. Fix $p > N$, and set $\hat{D}_p := \{w \in D_p : \int_\Omega w = 0\}$. Then $A_p|_{\hat{D}_p}$ is a bounded bijective mapping from $\hat{D}_p$ onto R_p, hence $K_p := \big(A_p|_{\hat{D}_p}\big)^{-1}$ is bounded by the open mapping theorem. Since $\hat{D}_p \hookrightarrow L^\infty(\Omega)$ for $p > N$, there exists a $\sigma(p) > 0$ with $\|w\|_\infty \le \sigma(p)\|w\|_{2,p}$ for $w \in \hat{D}_p$ and $p > N$. Fixing a $p > N$, we get $\|v^*\|_\infty \le \frac{\sigma(p)}{\kappa_2}\|K_p\| \operatorname{vol}(\Omega)^{\frac{1}{p}} \|b^*\|_\infty$. The lemma follows with $C_0 = \sigma(p)\|K_p\| \operatorname{vol}(\Omega)^{\frac{1}{p}}$. □

Let v_1 be the solution of

$$\begin{gathered} \kappa_2 \Delta v_1 - u_1^* = 0, \quad x \in \Omega \\ Bv_1 = 0 \end{gathered} \tag{2.20}$$

satisfying $\int_\Omega v_1 = 0$ (such a solution exists in view of $\int_\Omega u_1^* = 0$ and is unique because of $\int_\Omega v_1 = 0$), and let $v_1 = \sum_{j=1}^\infty v_{1,j}\varphi_j$ be its expansion. Then (2.20) becomes

$$\kappa_2 \sum_{j=1}^\infty \mu_j v_{1,j}\varphi_j - \sum_{j=1}^\infty u_{1,j}^*\varphi_j = 0, \quad \forall\, j \in \mathbb{N}, \tag{2.21}$$

hence

$$v_{1,j} = \frac{u_{1,j}^*}{\kappa_2 \mu_j} = \frac{a_0 a_j}{\kappa_2 \mu_j (a_0 + \kappa_1 |\mu_j|)}, \quad j \in \mathbb{N}. \tag{2.22}$$

By Lemma 2.6 and (2.9), there is $C_1 > 0$ such that

$$\|v_1\|_\infty \le \frac{C_1}{\kappa_2}. \tag{2.23}$$

Let v_2 be a solution of

$$\begin{gathered} \kappa_2 \Delta v_2 - u_1^* v_1 - u_2^* = \lambda_2, \quad \text{in } \Omega \\ Bv_2 = 0 \end{gathered} \tag{2.24}$$

with $\int_\Omega v_2 = 0$ and

$$\lambda_2 = \frac{1}{\mathrm{vol}(\Omega)} \sum_{j=1}^{\infty} \frac{a_0^2 a_j^2}{\kappa_2 |\mu_j| (a_0 + \kappa_1 |\mu_j|)^2} \Big[1 - \frac{\kappa_1 \kappa_2 \mu_j^2}{a_0^2} \Big]$$

as defined in the introduction (such solution exists and is unique by the choice of λ_2). By Lemma 2.6 and (1.7), (2.9), (2.14), and (2.23), there is $C_2 > 0$ such that

$$\|v_2\|_\infty \le C_2 \frac{a_0 + \min\{\kappa_1, \kappa_2\}}{a_0 \cdot \kappa_2 \cdot \min\{\kappa_1, \kappa_2\}}. \tag{2.25}$$

Lemma 2.7. *There exist $\tilde{M}(\kappa_1, \kappa_2, a_0), \tilde{\epsilon}(\kappa_1, \kappa_2, a_0) > 0$ such that*

$$\epsilon^2 \lambda_2 - \epsilon^3 \tilde{M} \le \lambda^u(\epsilon) \le \epsilon^2 \lambda_2 + \epsilon^3 \tilde{M}$$

for $0 < \epsilon < \tilde{\epsilon}$.

Proof. First of all, consider

$$\begin{gathered} v_t = \kappa_2 \Delta v + (a_0 - u_\epsilon^*) v, \quad \text{in} \Omega \\ Bv(t, \cdot) = 0, \quad t > 0. \end{gathered} \tag{2.26}$$

For given v_0, let $v(t, \cdot; v_0)$ be the solution of (2.26). Then the principal eigenvalue theory yields

$$\lim_{t \to \infty} \frac{\ln \|v(t, \cdot; v_0)\|}{t} = \lambda^u(\epsilon)$$

for all v_0 with $v_0(x) > 0$ for $x \in \Omega$. Note that by Lemma 2.5, there exist an $M(a_0) > 0$, an $\hat{\epsilon}(a_0) > 0$, and a function $\psi(x, \epsilon)$ with $|\psi(x, \epsilon)| \le M$ such that

$$u_\epsilon^*(x) = a_0 + \epsilon u_1^*(x) + \epsilon^2 u_2^*(x) + \epsilon^3 \psi(x, \epsilon)$$

for $0 < \epsilon < \hat{\epsilon}$.

For given $\tilde{M} > 0$, let

$$\begin{aligned} v_\epsilon^+ &= (1 + \epsilon v_1 + \epsilon^2 v_2) e^{(\epsilon^2 \lambda_2 + \epsilon^3 \tilde{M}) t}, \\ v_\epsilon^- &= (1 + \epsilon v_1 + \epsilon^2 v_2) e^{(\epsilon^2 \lambda_2 - \epsilon^3 \tilde{M}) t}, \end{aligned}$$

where v_1 and v_2 are the solutions of (2.20) and (2.24) with $\int_\Omega v_1(x) dx = 0$ and $\int_\Omega v_2(x) dx = 0$, respectively. We then have

$$e^{-(\epsilon^2 \lambda_2 + \epsilon^3 \tilde{M}) t} (v_\epsilon^+)_t = (\epsilon^2 \lambda_2 + \epsilon^3 \tilde{M})(1 + \epsilon v_1 + \epsilon^2 v_2)$$

and

$$\begin{aligned} & e^{-(\epsilon^2 \lambda_2 + \epsilon^3 \tilde{M}) t} \Big(\kappa_2 \Delta v_\epsilon^+ + (a_0 - u_\epsilon^*) v_\epsilon^+ \Big) \\ &= \epsilon \kappa_2 \Delta v_1 + \epsilon^2 \kappa_2 \Delta v_2 - (\epsilon u_1^* + \epsilon^2 u_2^* + \epsilon^3 \psi)(1 + \epsilon v_1 + \epsilon^2 v_2) \\ &= \epsilon^2 \lambda_2 - \epsilon^3 [\psi + u_1^* v_2 + u_2^* v_1] - \epsilon^4 [\psi v_1 + u_2^* v_2] - \epsilon^5 \psi v_2. \end{aligned}$$

It then follows from (2.9), (2.14), (2.23), and (2.25) that there exist $\tilde{M}(\kappa_1, \kappa_2, a_0) > 0$ and $0 < \tilde{\epsilon}(\kappa_1, \kappa_2, a_0) < \hat{\epsilon}$ such that

$$(v_\epsilon^+)_t \ge \kappa_2 \Delta v_\epsilon^+ + (a_0 - u_\epsilon^*) v_\epsilon^+$$

for $0 < \epsilon < \tilde{\epsilon}$.

Similarly, we can prove by adjusting $\tilde{M}$ and $\tilde{\epsilon}$ if necessary that

$$(v_\epsilon^-)_t \le \kappa_2 \Delta v_\epsilon^- + (a_0 - u_\epsilon^*) v_\epsilon^-$$

for $0 < \epsilon < \tilde{\epsilon}$.

Let $v_0^\epsilon = 1 + \epsilon v_1 + \epsilon^2 v_2$. Then by comparison principle for parabolic equations, we have

$$v_\epsilon^- \le v(t, \cdot; v_0^\epsilon) \le v_\epsilon^+$$

for $0 < \epsilon < \tilde{\epsilon}$, which implies

$$\epsilon^2 \lambda_2 - \epsilon^3 \tilde{M} \le \lambda^u(\epsilon) = \lim_{t \to \infty} \frac{\ln \|v(t, \cdot; v_0^\epsilon)\|}{t} \le \epsilon^2 \lambda_2 + \epsilon^3 \tilde{M}$$

for $0 < \epsilon < \tilde{\epsilon}$ and proves the lemma. □

Proof of Theorem 2.1. (1) Assume that $\phi(x)$ is a positive principal eigenfunction of (2.5). Then we have

$$\frac{\kappa_1 \Delta \phi}{\phi} + \epsilon a(x) = \lambda^v(\epsilon).$$

Integrating the above equality over Ω, we have

$$\kappa_1 \int_\Omega \frac{(\phi_x(x))^2}{(\phi(x))^2} dx = \lambda^v(\epsilon).$$

By the assumption that $a(x) \not\equiv 0$ and $\int_\Omega a(x)dx = 0$, $\phi(x) \not\equiv$ constant. Hence for any $\epsilon > 0$, $\lambda^v(\epsilon) > 0$ and then $(0, v^*)$ is unstable.

(2) and (3) are direct consequences of Lemma 2.7. In fact, choose $\tilde{M}(\kappa_1, \kappa_2, a_0)$ and $\tilde{\epsilon}(\kappa_1, \kappa_2, a_0)$ as in Lemma 2.7. Let $\eta(\kappa_1, \kappa_2, a_0) = \frac{1}{\tilde{M}(\kappa_1, \kappa_2, a_0)}$ and $\zeta(\kappa_1, \kappa_2, a_0) = \tilde{\epsilon}(\kappa_1, \kappa_2, a_0)$. Then, if $0 < \epsilon < \min\{\eta(\kappa_1, \kappa_2, a_0) \cdot |\lambda_2|, \zeta(\kappa_1, \kappa_2, a_0)\}$ and $\lambda_2 < 0$, Lemma 2.7 yields $\lambda^u(\epsilon) \le \epsilon^2 \lambda_2 + \epsilon^3 \tilde{M} < 0$, which implies (2). On the other hand, if $0 < \epsilon < \min\{\eta(\kappa_1, \kappa_2, a_0) \cdot |\lambda_2|, \zeta(\kappa_1, \kappa_2, a_0)\}$ and $\lambda_2 > 0$, one obtains $\lambda^u(\epsilon) \ge \epsilon^2 \lambda_2 - \epsilon^3 \tilde{M} > 0$, which shows (3). □

3. Numerical simulations

All numerical simulations are performed for $\Omega = (0, 1)$, $\kappa_1 = \kappa_2 = \kappa$, and $a(x) = 0.01 \cos(\pi x)$ (hence $\epsilon = 0.01$) for different values of a_0 and κ using Matlab PDE solver. The number of grid points on Ω is $N = 100$. All equilibria are obtained by requiring that the difference in the l^2-norm between two successive iterations is less than 10^{-12}. The equilibrium of the system is denoted by $(\hat{u}, \hat{v})$. The simulation results are consistent with Theorem 2 as shown in the following figures. Moreover, they suggest that the interior equilibrium, when it exists, has a basin of attraction which has both semi-trivial equilibria as boundary points.

3.1. Stability of $(u_\epsilon^*, 0)$ when a_0 changes.

Fix $\kappa = 1$. Let $a(x) = 0.01 \cos(\pi x)$. Then one has $\lambda_2 < 0$ if $a_0 < \pi^2$ and $\lambda_2 > 0$ if $a_0 > \pi^2$. Simulations for several values of a_0 between 3 and 15 are performed. It is seen that $(u_\epsilon^*, 0)$ is stable when $a_0 \le 9.8$ and unstable when $a_0 \ge 9.9$. The simulations with $a_0 = 3$, 9.8, 9.9, and 15 are presented in the following (see Figures 1-4). They are done for two different initial values for each value of a_0: one is close to the semi-trivial equilibrium $(u_\epsilon^*, 0)$ and the other one is close to the semi-trivial equilibrium $(0, a_0)$. More specifically, the first initial value is $(u_\epsilon^* + 0.01, 0.01)$ and the second initial value is $(0.01, a_0 + 0.01)$.

The 4 graphs in Figure 1 show the results for $a_0 = 3 < \pi^2$ (thus, $\lambda_2 < 0$) with initial values $(u_0, v_0) = (u_\epsilon^* + 0.01, 0.01)$ and $(u_0, v_0) = (0.01, 3 + 0.01)$. The equilibrium $(\hat{u}, \hat{v})$ in both cases is $(u_\epsilon^*, 0)$. This suggests that $(u_\epsilon^*, 0)$ is asymptotically stable.

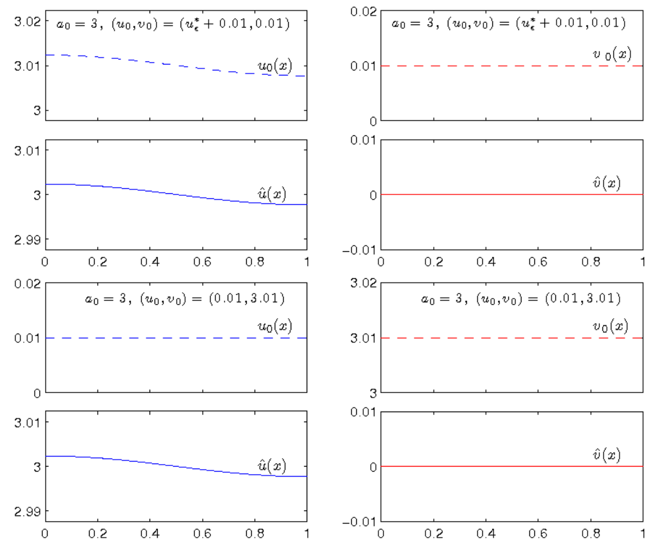

FIGURE 1.

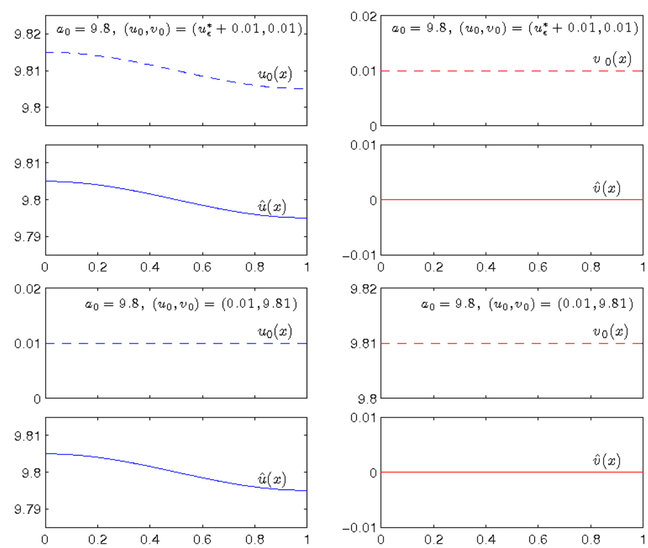

FIGURE 2.

The 4 graphs in Figure 2 show the results for $a_0 = 9.8 < \pi^2$ (thus, $\lambda_2 < 0$) with the initial values $(u_0, v_0) = (u_\epsilon^* + 0.01, 0.01)$ and $(u_0, v_0) = (0.01, 9.8 + 0.01)$. The equilibrium $(\hat{u}, \hat{v})$ in both cases is $(u_\epsilon^*, 0)$. This suggests that $(u_\epsilon^*, 0)$ is asymptotically stable.

The 4 graphs in Figure 3 show the results for $a_0 = 9.9 > \pi^2$ (thus, $\lambda_2 > 0$) with the initial values $(u_0, v_0) = (u_\epsilon^* + 0.01, 0.01)$ and $(u_0, v_0) = (0.01, 9.9 + 0.01)$.

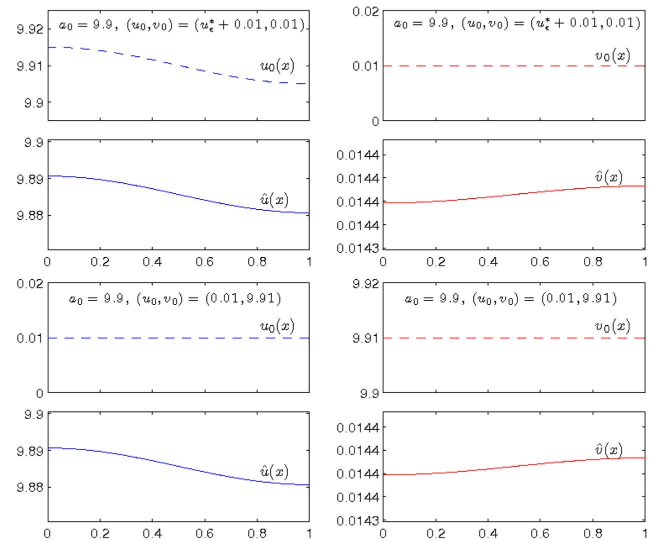

FIGURE 3.

The equilibrium $(\hat{u}, \hat{v})$ in both cases is an interior point of the positive cone. This suggests that $(u^*_\epsilon, 0)$ is unstable.

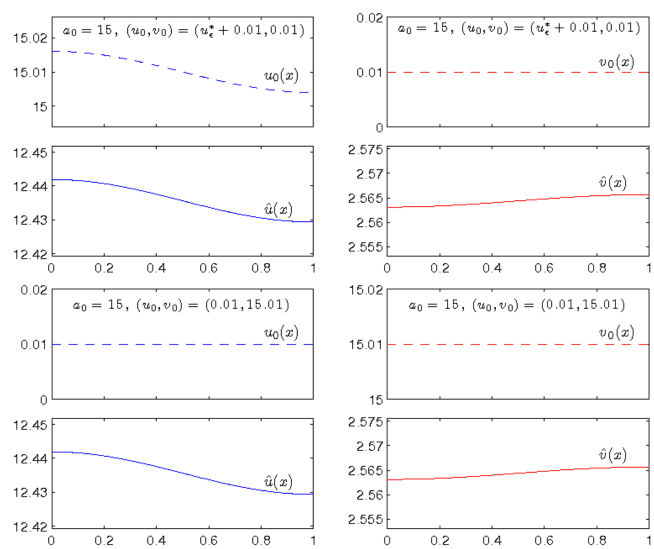

FIGURE 4.

The 4 graphs in Figure 4 show the results for $a_0 = 15 > \pi^2$ (thus, $\lambda_2 > 0$) with the initial values $(u_0, v_0) = (u^*_\epsilon + 0.01, 0.01)$ and $(u_0, v_0) = (0.01, 15 + 0.01)$. The equilibrium $(\hat{u}, \hat{v})$ in both cases is an interior point of the positive cone. This suggests that $(u^*_\epsilon, 0)$ is unstable.

3.2. **Stability of $(u^*_\epsilon, 0)$ when κ changes.** Fix $a_0 = 3$. Let $a(x) = 0.01\cos(\pi x)$. Then one has $\lambda_2 < 0$ if $\kappa > 3/\pi^2$ and $\lambda_2 > 0$ if $\kappa < 3/\pi^2$. Simulations for several values of κ between 0.01 and 1 are performed. It is seen that $(u^*_\epsilon, 0)$ is unstable when $\kappa \le 0.3$ and stable when $\kappa \ge 0.31$. The simulations with $\kappa = 0.01$, 0.3, 0.31, and 1 are presented in the following (see Figures 5-8). Again the simulations are done for two different initial values for each value of κ: one is $(u^*_\epsilon + 0.01, 0.01)$, which is close to the semi-trivial equilibrium $(u^*_\epsilon, 0)$ and the other is $(0.01, 3.01)$, which one is close to the semi-trivial equilibrium $(0, 3)$.

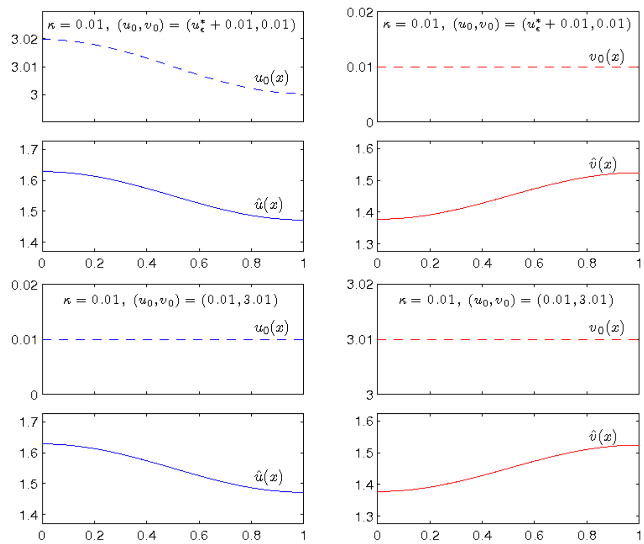

Figure 5.

The 4 graphs in Figure 5 show the results for $\kappa = 0.01 < 3/\pi^2$ (thus, $\lambda_2 > 0$) with initial values $(u_0, v_0) = (u^*_\epsilon + 0.01, 0.01)$ and $(u_0, v_0) = (0.01, 3.01)$. The equilibrium $(\hat{u}, \hat{v})$ in both cases is an interior point of the positive cone. This suggests that $(u^*_\epsilon, 0)$ is unstable.

The 4 graphs in Figure 6 show the results for $\kappa = 0.3 < 3/\pi^2$ (thus, $\lambda_2 > 0$) with initial values $(u_0, v_0) = (u^*_\epsilon + 0.01, 0.01)$ and $(u_0, v_0) = (0.01, 3.01)$. The equilibrium $(\hat{u}, \hat{v})$ in both cases is an interior point of the positive cone. This suggests that $(u^*_\epsilon, 0)$ is unstable.

The 4 graphs in Figure 7 show the results for $\kappa = 0.31 > 3/\pi^2$ (thus, $\lambda_2 < 0$) with initial values $(u_0, v_0) = (u^*_\epsilon + 0.01, 0.01)$ and $(u_0, v_0) = (0.01, 3.01)$. The equilibrium $(\hat{u}, \hat{v})$ in both cases is $(u^*_\epsilon, 0)$. This suggests that $(u^*_\epsilon, 0)$ is asymptotically stable.

The 4 graphs in Figure 8 show the results for $\kappa = 1 > 3/\pi^2$ (thus, $\lambda_2 < 0$) with initial values $(u_0, v_0) = (u^*_\epsilon + 0.01, 0.01)$ and $(u_0, v_0) = (0.01, 3.01)$. The equilibrium $(\hat{u}, \hat{v})$ in both cases is $(u^*_\epsilon, 0)$. This suggests that $(u^*_\epsilon, 0)$ is asymptotically stable.

4. The principal eigenvalue for Dirichlet boundary conditions

In this section, we provide an example which shows that the principal eigenvalue $\lambda(b)$ of (1.4) with $Bu = u$ can be smaller than the principal eigenvalue of (1.5) with $Bu = u$.

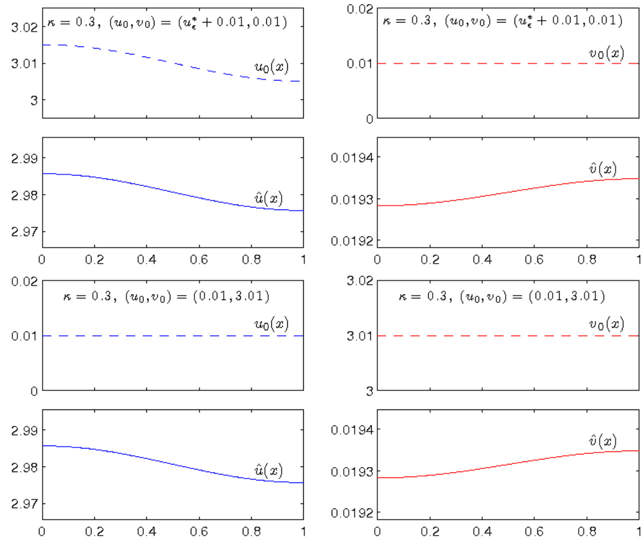

FIGURE 6.

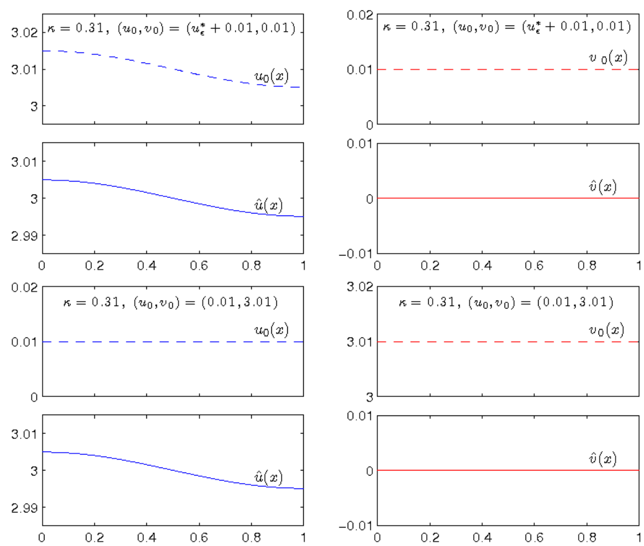

FIGURE 7.

Set $\phi_j(x) := \sqrt{2/\pi}\sin(jx)$ for $j \in \mathbb{N}$, $x \in [0,\pi]$ and $\psi_j(x) := \sqrt{2/\pi}\cos(jx)$ for $j \in \mathbb{Z}_+$, $x \in [0,\pi]$. Then (ϕ_j) is an orthonormal basis of eigenfunctions for

$$\begin{gathered} u'' = \mu u \quad 0 < x < \pi, \\ u(0) = 0 = u(\pi). \end{gathered} \tag{4.1}$$

with $(-j^2)_{j\in\mathbb{N}}$ the corresponding sequence of eigenvalues.

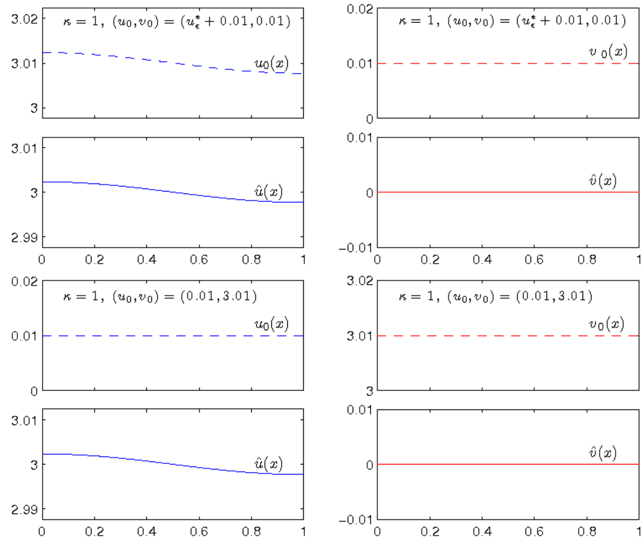

FIGURE 8.

The goal is to show that the principal eigenvalue $\lambda(\psi_2)$ of

$$\begin{gathered} u'' + \psi_2 u = \lambda u \quad 0 < x < \pi, \\ u(0) = 0 = u(\pi), \end{gathered} \tag{4.2}$$

is smaller than -1. Note that $\bar{\psi}_2 = \int_0^\pi \psi_2 = 0$ and the principal eigenvalue $\lambda(\bar{\psi}_2)$ of

$$\begin{gathered} u'' + \bar{\psi}_2 u = \lambda u \quad 0 < x < \pi, \\ u(0) = 0 = u(\pi), \end{gathered} \tag{4.3}$$

is -1. Hence $\lambda(\psi_2) < \lambda(\bar{\psi}_2)$.

Denote by u a principal eigenfunction of (4.2) with $\|u\|_{0,2} = 1$, then $\lambda(\psi_2) = \int_0^\pi \big[-(u')^2 + \psi_2 u^2\big]$. Let $\sum_{j=1}^\infty \alpha_j \phi_j$ be the eigenfunction expansion of u, then $\sum_{j=1}^\infty \alpha_j^2 = 1$. The trigonometric identity $\phi_j \phi_k = \frac{1}{2}\big[\psi_{j-k} - \psi_{j+k}\big]$ for $k \le j$ and the Cauchy product formula yield

$$u^2 = \sum_{j=1}^\infty \sum_{k=0}^{j-1} \alpha_j \alpha_{j-k} \phi_j \phi_{j-k} = \frac{1}{2} \sum_{j=1}^\infty \sum_{k=0}^{j-1} \alpha_j \alpha_{j-k} \big[\psi_k - \psi_{2j-k}\big],$$

hence

$$\begin{aligned} \int_0^\pi \psi_2 u^2 &= \frac{1}{2} \sum_{j=1}^\infty \sum_{k=0}^{j-1} \alpha_j \alpha_{j-k} \int_0^\pi \big[\psi_k - \psi_{2j-k}\big] \psi_2 \\ &= \frac{1}{2} \sum_{j=3}^\infty \alpha_j \alpha_{j-2} - \frac{1}{2} \alpha_1^2 \\ &\le \frac{1}{2} \sum_{j=1}^\infty \alpha_j^2 - \frac{1}{2} \alpha_1^2 = \frac{1}{2} \sum_{j=2}^\infty \alpha_j^2 \end{aligned}$$

Therefore,

$$\int_0^\pi \left[-(u')^2 + \psi_2 u^2\right] \le -\sum_{j=1}^\infty j^2\alpha_j^2 + \frac{1}{2}\sum_{j=2}^\infty \alpha_j^2 \le -\alpha_1^2 - \frac{7}{2}\sum_{j=2}^\infty \alpha_j^2 \tag{4.4}$$

But, $-\alpha_1^2 - \frac{7}{2}\sum_{j=2}^\infty \alpha_j^2 < -1$ unless $|\alpha_1| = 1$ and hence $\alpha_j = 0$ for $j \in \mathbb{N} \setminus \{1\}$. The second alternative is not satisfied, since ϕ_1 is not an eigenfunction of (4.2). Consequently, the principal eigenvalue satisfies $\lambda(\psi_2) < -1$.

We remark that the principal eigenvalue $\lambda(-\psi_2)$ of

$$\begin{gathered} u'' - \psi_2 u = \lambda u \quad 0 < x < \pi, \\ u(0) = 0 = u(\pi), \end{gathered} \tag{4.5}$$

is greater than -1, since $\int_0^\pi \psi_2\phi_1^2 < 0$. Hence $\lambda(-\psi_2) > \lambda(-\bar{\psi}_2) = -1$.

Therefore, in general, neither $\lambda(\bar{b}) \le \lambda$ nor $\lambda(\bar{b}) \ge \lambda$ is true in the case of Dirichlet boundary conditions, and we cannot expect any result similar to Theorem 2.1.

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