

# Symbiosis in competitive environments.

Julián López-Gómez  
Departamento de Matemática Aplicada  
Universidad Complutense de Madrid  
28040-Madrid, Spain  
e-mail: Lopez\_Gomez@mat.ucm.es

Marcela Molina-Meyer  
Departamento de Matemáticas  
Universidad Carlos III de Madrid  
28911-Leganés, Madrid, Spain  
e-mail: mmolinam@math.uc3m.es

This paper is dedicated to the memory of J. Esquinas and J. M. Fraile ,  
exceptional mathematicians and extraordinary friends.

### Abstract

The mathematical analysis of this paper shows how the effects of strategic local symbiosis provide us with an exceptional mechanism to increase productivity in extremely competitive environments. The most striking feature fallen down from our analysis relays in the fact that the productivity can blow-up in the areas of common interest of the species, though some of them might get extinct elsewhere as a result of the aggressions received from the competitors. As a by-product, it should be clear why minor symbiosis effects in population dynamics, or competitive markets, help to avoid massive extinction of populations, or industrial and financial companies. In a further stage of our analysis we have numerically detected that, in the presence of local symbiosis, high level aggressions might provoke dramatic increments of the complexity of the system; a mechanism that might held to explain the extraordinary bio-diversity of Earth's biosphere, as well as the complexity of global economy.

MATH. SUBJ. CLASS: 35J70, 65N35, 91A10, 91B02, 92B05

## 1 Introduction

In this paper we analyze the dynamics of the solutions of the parabolic problem

$$\begin{cases} \frac{\partial u}{\partial t} - \Delta u = \lambda u - u^2 - b(x)uv & (x, t) \in \Omega \times (0, \infty), \\ \frac{\partial v}{\partial t} - \Delta v = \mu v - v^2 - c(x)uv & \\ u = v = 0, & \text{on } \partial\Omega \times (0, \infty), \\ u(\cdot, 0) = u_0 \geq 0, \quad v(\cdot, 0) = v_0 \geq 0, & \end{cases} \quad (1.1)$$

where  $\Omega$  is a bounded domain of  $\mathbb{R}^N$ ,  $N \geq 1$ , of class  $C^{2+\nu}$  for some  $\nu \in (0, 1)$ ,  $\Delta$  stands for the Laplacian of  $\mathbb{R}^N$ ,  $b, c \in C^\nu(\bar{\Omega})$  are two functions such that, for some  $(x_+, x_-), (y_+, y_-) \in \Omega^2$ ,

$$b(x_-) < 0 < b(x_+) \quad \text{and} \quad c(y_-) < 0 < c(y_+),$$

i.e.,  $b$  and  $c$  change sign in  $\Omega$ , and  $u_0, v_0 \in W_0^{2,p}(\Omega)$ , for some  $p > N/2$ . Throughout this work, the constants  $\lambda, \mu \in \mathbb{R}$  will be regarded as real parameters.

Throughout this work, (1.1) is interpreted as a model for the evolution of two biological species with densities  $u(x, t)$  and  $v(x, t)$  in the habitat  $\Omega$ . Then,  $\lambda$  and  $\mu$  are the intrinsic growth rates of the species  $u$  and  $v$ , respectively. Such model is far from falling into the classical family of Lotka-Volterra models with diffusion, since the interaction patterns between the species  $u$  and  $v$ ,  $b(x)$  and  $c(x)$ , do not have constant sign in  $\Omega$ . Actually, if for any  $V \in C^\nu(\bar{\Omega})$  we denote

$$V^+ := \max\{V, 0\}, \quad V^- := -\min\{V, 0\},$$

$$\Omega_+^V := \text{Int supp } V^+, \quad \Omega_-^V := \text{Int supp } V^-,$$

and

$$\Omega_0^V := \text{Int}\{x \in \Omega : V(x) = 0\} = \Omega \setminus (\bar{\Omega}_-^V \cup \bar{\Omega}_+^V),$$

then,  $V = V^+ - V^-$ , and the species  $u$  and  $v$  interact in  $\Omega$  according to the following patterns:

1.  $u$  and  $v$  compete in  $\Omega_+^b \cap \Omega_+^c$  (the region where  $b > 0$  and  $c > 0$ ).
2.  $u$  and  $b$  cooperate in  $\Omega_-^b \cap \Omega_-^c$  (the region where  $b < 0$  and  $c < 0$ ).
3.  $u$  preys on  $v$  in  $\Omega_-^b \cap \Omega_+^c$ , while  $v$  preys on  $u$  in  $\Omega_+^b \cap \Omega_-^c$  (the regions where  $bc < 0$ ).
4.  $u$  is free from the action of  $v$  within  $\Omega_0^b$ , and  $v$  is free from the action of  $u$  within  $\Omega_0^c$  (the interior of the regions where  $bc = 0$ ).

Consequently, (1.1) allows all different types of interactions between  $u$  and  $v$  within  $\Omega$ . Although the analysis of these general problems was originally addressed in concluding [16, Section 7.3], this seems to be the first work focusing on them.

It should be noted that, thanks to the general assumptions on  $b$  and  $c$ , we have

$$\Omega_+^b \neq \emptyset, \quad \Omega_-^b \neq \emptyset, \quad \Omega_+^c \neq \emptyset, \quad \Omega_-^c \neq \emptyset. \quad (1.2)$$

Assumption (1.2) enables us considering (1.1) as a prototype model to analyze either the beneficial effects of symbiosis in competitive environments (e.g., to increase productivity and, at the

end of the day, diversity), or the *fitness effects* of competition in symbiotic environments (e.g., to design selection mechanisms); through an adequate choice of the interaction patterns  $b(x)$  and  $c(x)$ .

Under our general assumptions, for each  $p > N/2$  and  $u_0, v_0 \in W_0^{2,p}(\Omega)$ , there exists a —maximal— *existence time*

$$T = T(u_0, v_0, \lambda, \mu, b, c) \in (0, \infty]$$

such that (1.1) possesses a unique *local solution*

$$(u, v) := (u(x, t; u_0, v_0, \lambda, \mu, b, c), v(x, t; u_0, v_0, \lambda, \mu, b, c)), \quad (x, t) \in \Omega \times [0, T),$$

satisfying

$$u, v \in \mathcal{C}(\bar{\Omega} \times [0, T)) \cap \mathcal{C}^{2+\nu, 1+\frac{\nu}{2}}(\bar{\Omega} \times (0, T))$$

(c.f., e.g., D. Daners and P. Koch-Medina [5]). Moreover,

$$\lim_{t \uparrow T} (\|u(\cdot, t)\|_{\mathcal{C}(\bar{\Omega})} + \|v(\cdot, t)\|_{\mathcal{C}(\bar{\Omega})}) = \infty \quad \text{if } T < \infty,$$

and, thanks to the parabolic maximum principle, for any  $t \in (0, T)$ ,  $u(\cdot, t) \gg 0$  if  $u_0 > 0$ , while  $u = 0$  if  $u_0 = 0$ . Throughout this paper, a function  $h \in \mathcal{C}^1(\bar{\Omega})$  is said to satisfy  $h \gg 0$  if it lies in the interior of the cone of positive functions of the ordered Banach space  $\mathcal{C}^1(\bar{\Omega})$ . By symmetry, the component  $v$  satisfies the same property. In general  $T < \infty$ , as a result of the fact that  $b$  and  $c$  change of sign.

In the absence of the other, each of the species grows according to the logistic law

$$\begin{cases} \frac{\partial w}{\partial t} - \Delta w = \gamma w - w^2 & \text{in } \Omega \times (0, \infty), \\ w = 0 & \text{on } \partial\Omega \times (0, \infty), \\ w(\cdot, 0) = w_0 \geq 0, \end{cases} \quad (1.3)$$

and, hence, the corresponding limiting population distributions as  $t \uparrow \infty$  are determined by the non-negative steady states of (1.1) with a vanishing component. Also, note that the steady states of (1.1) are the non-negative solutions of the elliptic boundary value problem

$$\begin{cases} -\Delta u = \lambda u - u^2 - b(x)uv & \text{in } \Omega, \\ -\Delta v = \mu v - v^2 - c(x)uv & \text{in } \Omega, \\ u = v = 0 & \text{on } \partial\Omega. \end{cases} \quad (1.4)$$

In order to ascertain the dynamics of (1.1), one should first analyze the existence, multiplicity and stability properties of all non-negative solutions of (1.4). Consequently, at this early stage we will dedicate most of our effort to treat (1.4). Although under special circumstances the limiting profiles of the solutions of (1.1) can be given by the *metasolutions* of (1.4) (e.g., [14] and the references there in), in this work we shall restrict ourselves to the analysis of the classical solutions of (1.4).

Besides  $(0, 0)$ , problem (1.4) exhibits three types of non-negative solutions. Those of the form  $(u, 0)$ , or  $(0, v)$ , universally referred to as *semi-trivial* positive solutions, and the so called

### Symbiosis in competitive environments

*coexistence states*, which are the solutions of the form  $(u, v)$  with both components positive. In any circumstance, as a consequence from the strong maximum principle,  $u \gg 0$  if  $u > 0$ , and  $v \gg 0$  if  $v > 0$ .

Subsequently, for each smooth subdomain  $D \subset \Omega$  and  $V \in L^\infty(D)$ , we shall denote by  $\sigma[-\Delta + V; D]$  the *lowest eigenvalue* of the linear boundary value problem

$$\begin{cases} (-\Delta + V)w = \tau w & \text{in } D, \\ w|_{\partial D} = 0, \end{cases} \quad (1.5)$$

referred to as the *principal eigenvalue* of (1.5); it is algebraically simple, and its associated eigenfunction can be chosen to be *strongly positive* in  $D$ —the *principal eigenfunction*—. Actually,  $\sigma[-\Delta + V; D]$  is the unique eigenvalue for which (1.5) admits a positive eigenfunction.

It is folklore that (1.4) possesses a semi-trivial positive solution of the form  $(u, 0)$  if, and only if,  $\lambda > \sigma[-\Delta; \Omega]$ . Moreover, if we denote by  $\theta_\gamma$  the unique positive solution of

$$\begin{cases} -\Delta w = \gamma w - w^2 & \text{in } \Omega, \\ w|_{\partial\Omega} = 0, \end{cases} \quad (1.6)$$

then,  $(\theta_\lambda, 0)$  is the unique semi-trivial positive solution of the form  $(u, 0)$ . Similarly, (1.4) possesses a semi-trivial positive solution of the form  $(0, v)$  if, and only if,  $\mu > \sigma[-\Delta; \Omega]$ , and, in such case,  $(0, \theta_\mu)$  is the unique semi-trivial positive solution with the  $v$  component positive. Condition  $\lambda > \sigma[-\Delta; \Omega]$  measures the facilities (among them, the size and natural resources) that the habitat  $\Omega$  should offer to the species  $u$  to maintain it in the absence of  $v$ . Actually, in the absence of  $v$ ,  $u$  is driven to extinction if  $\lambda \leq \sigma[-\Delta; \Omega]$ . We have just introduced all necessary concepts and notations to describe the main results of this paper.

After doing the mathematical analysis of this work and carrying over a number of numerical experiments our main conclusion establishes that the competitive exclusion principle fails in the presence of local symbiosis, in the sense that, e.g., if the intrinsic birth rate of  $u$ ,  $\lambda$ , is sufficiently large, then  $u$  cannot be driven to extinction by  $v$ —even in the dramatic limiting case when the intrinsic growth rate of  $v$ , measured by  $\mu$ , take arbitrarily large values—. Of course, within the region where  $u$  suffers aggressions from  $v$ ,  $u$  will be driven to extinction if  $\mu \uparrow \infty$ , segregating itself and drastically increasing productivity within the areas where it preys on  $v$ , or cooperate with it. Thus, strategic local symbiosis seems to be an exceptional mechanism to increase productivity in extremely competitive environments, a simple idea that might have a number of important implications in applied and social sciences, as well as in engineering. The most striking feature fallen down from our mathematical analysis relays in the fact that the productivity can blow-up in the areas of common interest of the species, though some of them might get extinct elsewhere as a result of the aggressions received from the competitors. As a result of our theory, it should be clear why minor symbiosis effects in population dynamics, or competitive markets, help to avoid massive extinction of populations, or industrial and financial companies. In a further stage of our analysis we have numerically detected that, in the presence of local symbiosis, high level aggressions might provoke dramatic increments of the complexity of the system (diversity). The best example of this extremely striking phenomenology in real world occurred at the time when all alive organisms on our lonely planet consisted of exactly one cell. Strong competition mechanisms encouraged to that—independent?— primitive cells to work

together, in order to be more competitive, and, as a matter of fact, that extraordinary combination of symbiosis–competition mechanisms not only re-grouped that individual cells by pairs, triplets, and more complex structures... —no body knows—, but simultaneously generated the extraordinary diversity that we enjoy today in all aspects of life.

Focusing attention into the precise contents of this paper, more than in the eventual scientific significance of the ideas beyond its mathematical analysis, Section 2 analyzes the curves of change of stability of the semi-trivial positive solutions  $(\theta_\lambda, 0)$  and  $(0, \theta_\mu)$ . Such analysis is imperative in order to ascertain the shape of the so called *coexistence wedge* in population dynamics; the wedge where both semi-trivial states are linearly unstable. Section 3 analyzes the existence of coexistence states for (1.4) in the *low symbiosis* case. The main result establishes that the problem possesses a coexistence state if the symbiosis is sufficiently low and the semi-trivial positive solutions are linearly unstable. As a consequence from the main result, the species can coexist in the large, independently of the level of their mutual aggressions in the competition areas. Section 4 analyzes the point-wise behavior of the population distributions as one of their intrinsic growth rates, e.g.  $\mu$ , approximates infinity. The main result establishes that if the level of the aggressions received by  $v$  from  $u$ , controlled by  $c^+$ , is reasonably low, then the density of the population  $v$  approximates infinity everywhere in  $\Omega$  as  $\mu \uparrow \infty$ , while  $u$  completely segregates into the region where the population  $v$  is most favorable for  $u$ ,  $\Omega_0^b \cup \Omega_-^b$ , actually blowing-up within  $\Omega_-^b$ . Our numerical experiments strongly suggest that an adequate increment of  $c^+$  might result into very complex bifurcation diagrams of coexistence states of (1.4), whose level of complexity grows according to the amplitude of  $c^+$ . In particular, our main singular perturbation result might be false for sufficiently large  $c^+$ . As we plan to carry out a complete mathematical analysis of this problem elsewhere, we will not give more punctual details here. Finally, in Section 5 we shall discuss some further advances that one should give in order to fully describe the dynamics of the solutions of (1.1) within our general setting. One of the main points of this discussion being the fact that the limiting profile of the solutions of (1.1) might not be necessarily given by a classical steady-state, but, in many circumstances, by a meta-steady-state of (1.1) (cf. [14], and the references therein, for the precise concepts and underlying ideas).

## 2 Linear stability of semi-trivial positive solutions.

Subsequently, we denote

$$\sigma := \sigma[-\Delta; \Omega],$$

and  $\varphi \gg 0$  stands for the principal eigenfunction associated to  $\sigma$ , normalized so that

$$\int_{\Omega} \varphi^3 = 1.$$

Also, for any function  $a \in C(\bar{\Omega})$  we shall denote

$$a_L := \min_{\Omega} a, \quad a_M := \max_{\Omega} a.$$

The following result characterizes the linear stability of the semi-trivial positive solutions.

**Proposition 2.1** *Suppose  $\lambda > \sigma$ . Then,*

### Symbiosis in competitive environments

- $(\theta_\lambda, 0)$  is linearly asymptotically stable if, and only if,  $\mu < \sigma[-\Delta + c(x)\theta_\lambda; \Omega]$ .
- $(\theta_\lambda, 0)$  is linearly neutrally stable if, and only if,  $\mu = \sigma[-\Delta + c(x)\theta_\lambda; \Omega]$ .
- $(\theta_\lambda, 0)$  is linearly unstable if, and only if,  $\mu > \sigma[-\Delta + c(x)\theta_\lambda; \Omega]$ .

By symmetry, if  $\mu > \sigma$ , then

- $(0, \theta_\mu)$  is linearly asymptotically stable if, and only if,  $\lambda < \sigma[-\Delta + b(x)\theta_\mu; \Omega]$ .
- $(0, \theta_\mu)$  is linearly neutrally stable if, and only if,  $\lambda = \sigma[-\Delta + b(x)\theta_\mu; \Omega]$ .
- $(0, \theta_\mu)$  is linearly unstable if, and only if,  $\lambda > \sigma[-\Delta + b(x)\theta_\mu; \Omega]$ .

Moreover, by the linearized stability principle,  $(\theta_\lambda, 0)$  (resp.  $(0, \theta_\mu)$ ) is exponentially asymptotically stable if it is linearly asymptotically stable, and it is unstable if it is linearly unstable.

**Proof:** The linear stability of  $(\theta_\lambda, 0)$  is given by the sign of the real parts of the eigenvalues of the linearization of (1.4) at  $(\theta_\lambda, 0)$ . In other words, by the signs of the real parts of the  $\tau$ 's for which the following linear problem admits a classical solution  $(u, v) \neq (0, 0)$

$$\begin{cases} -\Delta u = (\lambda - 2\theta_\lambda)u - b(x)\theta_\lambda v + \tau u & \text{in } \Omega, \\ -\Delta v = (\mu - c\theta_\lambda)v + \tau v & \\ u = v = 0, & \text{on } \partial\Omega. \end{cases} \quad (2.1)$$

In case  $v = 0$ , (2.1) reduces to

$$\begin{cases} -\Delta u = (\lambda - 2\theta_\lambda)u + \tau u & \text{in } \Omega, \\ u|_{\partial\Omega} = 0. \end{cases} \quad (2.2)$$

By the definition of  $\theta_\lambda$  and the monotonicity properties of the principal eigenvalue, we find that

$$\sigma[-\Delta - \lambda + 2\theta_\lambda; \Omega] > \sigma[-\Delta - \lambda + \theta_\lambda; \Omega] = 0$$

and, hence, any eigenvalue  $\tau$  of (2.1) with an associated eigenfunction of the form  $(u, 0)$ ,  $u \neq 0$ , must be positive.

Now, suppose  $\tau$  is an eigenvalue with an associated eigenfunction  $(u, v)$  such that  $v \neq 0$ . Then,  $\tau$  must be an eigenvalue of  $-\Delta + c(x)\theta_\lambda - \mu$  in  $\Omega$  under homogeneous Dirichlet boundary conditions and, therefore, the linear stability of  $(\theta_\lambda, 0)$  is easily determined from the sign of

$$\sigma[-\Delta + c(x)\theta_\lambda - \mu; \Omega]$$

as stated by the theorem. The remaining assertions are easy consequences from the linearized stability principle.  $\square$

Thanks to Proposition 2.1, the curves

$$\mu = \sigma[-\Delta + c(x)\theta_\lambda; \Omega] \quad \text{and} \quad \lambda = \sigma[-\Delta + b(x)\theta_\mu; \Omega] \quad (2.3)$$

will be referred to as the *curves of change of stability* of the semi-trivial positive solutions  $(\theta_\lambda, 0)$  and  $(0, \theta_\mu)$ , respectively. Their knowledge is imperative in order to ascertain the dynamics of the positive solutions of (1.1). The following result provides us with some of their most important properties.

**Proposition 2.2** Suppose  $a \in C^\nu(\bar{\Omega})$  and set

$$f(\gamma) := \sigma[-\Delta + a(x)\theta_\gamma; \Omega], \quad \gamma > \sigma.$$

Then,  $f$  is real analytic in  $(\sigma, \infty)$ , and it has the asymptotic expansion

$$f(\gamma) = \sigma + (\gamma - \sigma) \int_{\Omega} a \varphi^3 + O(|\gamma - \sigma|^2) \quad \text{as } \gamma \downarrow \sigma. \quad (2.4)$$

Moreover,

$$\lim_{\gamma \uparrow \infty} \frac{f(\gamma)}{\gamma} = a_L. \quad (2.5)$$

In particular, if we define  $f(\sigma) := \sigma$ , then  $f \in C([\sigma, \infty))$ . Furthermore,

$$f(\gamma) \leq \sigma[-\Delta; \Omega_0^a \cup \Omega_-^a], \quad \gamma \geq \sigma, \quad (2.6)$$

and, actually, if  $a_L = 0$ , i.e.  $\Omega_-^a = \emptyset$ , and  $\Omega_0^a$  is a nice smooth open set, then

$$\lim_{\gamma \uparrow \infty} f(\gamma) = \sigma[-\Delta; \Omega_0^a]. \quad (2.7)$$

**Proof:** The fact that the map  $(\sigma, \infty) \rightarrow C^\nu(\bar{\Omega})$ ,  $\gamma \mapsto \theta_\gamma$ , is real analytic follows easily from the implicit function theorem, since  $\theta_\gamma$  is the unique positive solution of (1.6) and it is non-degenerate. By the continuity and simplicity properties of the principal eigenvalue it readily follows that  $f$  is real analytic in  $(\sigma, \infty)$ . Moreover, since

$$\lim_{\gamma \downarrow \sigma} \theta_\gamma = 0 \quad \text{in } C^\nu(\bar{\Omega}),$$

we have  $\lim_{\gamma \downarrow \sigma} f(\sigma) = \sigma$ , and, hence,  $f \in C([\sigma, \infty))$  if we define  $f(\sigma) := \sigma$ . The asymptotic expansion (2.4) follows easily from the main theorem of M. G. Crandall and P. H. Rabinowitz [4] by adapting the argument of the proof of [12, Lemma 3.6] (cf. [6, Lemma 4.3] as well).

Now, for each  $\gamma > \sigma$ , we have that

$$\frac{f(\gamma)}{\gamma} = \sigma[-\frac{1}{\gamma}\Delta + a(x)\vartheta_\gamma; \Omega],$$

where  $\vartheta_\gamma := \frac{\theta_\gamma}{\gamma}$ . A direct calculation shows that  $\vartheta_\gamma$  is the unique positive solution of the singular perturbation problem

$$\begin{cases} -\frac{1}{\gamma}\Delta w = w - w^2 & \text{in } \Omega, \\ w|_{\partial\Omega} = 0, \end{cases}$$

and, hence, thanks to, e.g., [8, Theorem 3.4],

$$\lim_{\gamma \uparrow \infty} \vartheta_\gamma = 1$$

uniformly in compact subsets of  $\Omega$ . Therefore, adapting the proof of [8, Lemma 3.1], one easily gets (2.5). The estimate (2.6) follows from the monotonicity of the principal eigenvalue with respect to the domain and the potential, since  $a \leq 0$  in  $\Omega_0^a \cup \Omega_-^a$ . Indeed, for each  $\gamma \geq \sigma$ ,

$$f(\gamma) = \sigma[-\Delta + a\theta_\gamma; \Omega] \leq \sigma[-\Delta + a\theta_\gamma; \Omega_0^a \cup \Omega_-^a] \leq \sigma[-\Delta; \Omega_0^a \cup \Omega_-^a].$$

### Symbiosis in competitive environments

The fact that (2.7) is satisfied if  $a_L = 0$  follows easily from [12, Theorem 3.4]. This concludes the proof.  $\square$

In applying Proposition 2.2 to ascertain the behavior of the curves of change of stability of the semi-trivial positive solutions of (1.4), one must impose that  $a$  changes of sign, since  $b$  and  $c$  do it. In such case  $a_L < 0$  and the sign of the slope

$$\lim_{\gamma \downarrow \sigma} f'(\sigma) = \int_{\Omega} a\varphi^3$$

at  $\gamma = \sigma$  depends upon the relative size of  $a_+$  and  $a_-$  against  $\varphi^3$ . Actually, there exists  $\varepsilon > 0$  such that  $f(\gamma)$  is increasing in  $[\sigma, \sigma + \varepsilon]$  if  $\int_{\Omega} a\varphi^3 > 0$ , while it is decreasing if  $\int_{\Omega} a\varphi^3 < 0$ . Thus, the local behaviour of  $f(\gamma)$  at  $\gamma = \sigma$  depends, among other things, upon the sign of  $\int_{\Omega} a\varphi^3$ . Thanks to (2.5), the map  $\gamma \mapsto f(\gamma)$  is asymptotic to the straight line  $\gamma \mapsto a_L\gamma$  at  $\gamma = \infty$ .

Note that, thanks to Proposition 2.1 and the estimate (2.6), within the quadrant

$$\lambda > \sigma[-\Delta; \Omega_0^b \cup \Omega_-^b], \quad \mu > \sigma[-\Delta; \Omega_0^c \cup \Omega_-^c], \quad (2.8)$$

each of the semi-trivial positive solutions,  $(\theta_\lambda, 0)$  and  $(0, \theta_\mu)$ , is linearly unstable.

Subsequently, we consider the following one-dimensional prototype model

$$\begin{cases} -u'' = \lambda u - u^2 - b(x)uv \\ -v'' = \mu v - v^2 - b(x)uv \\ u(0) = u(1) = v(0) = v(1) = 0, \end{cases} \quad \text{in } (0, 1), \quad (2.9)$$

where, for some constants  $b^+, b^- > 0$ ,

$$b(x) := \begin{cases} b^+ \sin\left(\frac{\pi x}{0.4}\right) & \text{if } 0.0 \leq x \leq 0.4, \\ -b^- \sin\left[\frac{\pi}{0.2}(x - 0.4)\right] & \text{if } 0.4 \leq x \leq 0.6, \\ b^+ \sin\left[\frac{\pi}{0.4}(x - 0.6)\right] & \text{if } 0.6 \leq x \leq 1.0. \end{cases} \quad (2.10)$$

Figure 2.1 shows a plot of the curves of change of stability of the semi-trivial positive solutions of (2.9) for the special choice

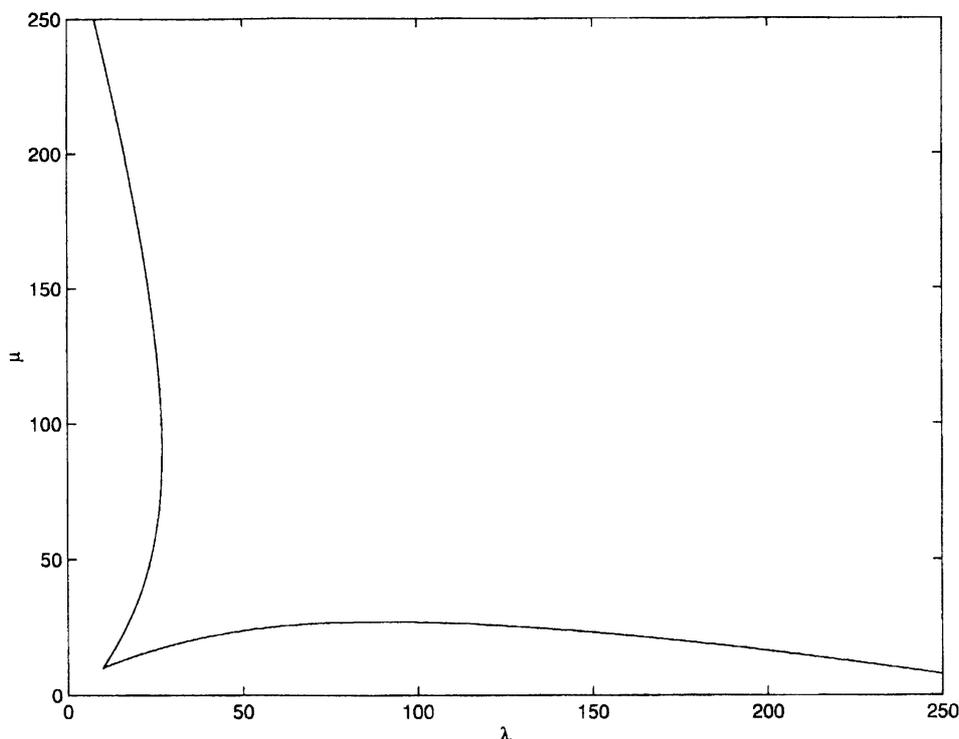
$$b^+ = 2, \quad b^- = 0.4. \quad (2.11)$$

To compute these curves we have coupled a path-following solver, to compute  $\theta_\lambda$  and  $\theta_\mu$ , with centered finite differences and the power inverse method, to compute the associated principal eigenvalues (cf. [3] for further technical details).

Thanks to Proposition 2.1, the region confined in between the curves of change of stability, equals the set of values of  $(\lambda, \mu)$  for which both semi-trivial positive solutions are linearly unstable. Moreover, thanks to Proposition 2.2,

$$\lim_{\lambda \uparrow \infty} \frac{\sigma\left[-\frac{d^2}{dx^2} + b(x)\theta_\lambda; (0, 1)\right]}{\lambda} = \lim_{\mu \uparrow \infty} \frac{\sigma\left[-\frac{d^2}{dx^2} + b(x)\theta_\mu; (0, 1)\right]}{\mu} = b_L = -0.4,$$

which provides us with the slopes at infinity of the two curves of change of stability, because of the symmetry of the problem ( $b = c$ ).



**Figure 2.1.** Curves of change of stability of semi-trivial states in case (2.11).

It should be noted that, for the choice (2.10), one has that

$$\Omega_0^b = \emptyset, \quad \Omega_-^b = (0.4, 0.6), \quad \Omega_+^b = (0.0, 0.4) \cup (0.6, 1.0),$$

and, hence, (2.8) becomes into

$$\lambda > 25\pi^2, \quad \mu > 25\pi^2.$$

Thus, within this quadrant both semi-trivial positive solutions are linearly unstable.

Figure 2.2 shows the corresponding curves of change of stability for the special choice

$$b^+ = 2, \quad b^- = 1.2. \quad (2.12)$$

Now, thanks to Proposition 2.2, we have that

$$\lim_{\lambda \uparrow \infty} \frac{\sigma[-\frac{d^2}{dx^2} + b(x)\theta_\lambda; (0, 1)]}{\lambda} = \lim_{\mu \uparrow \infty} \frac{\sigma[-\frac{d^2}{dx^2} + b(x)\theta_\mu; (0, 1)]}{\mu} = b_L = -1.2,$$

which provides us with the slopes at infinity of the two curves of change of stability, in fully agreement with our numerical computations.

As in the previous case, the curves of change of stability divide to the square plotted in Figure 2.2 into two regions. The upper area is the geometrical locus of the set of values of  $(\lambda, \mu)$  where both semi-trivial positive solutions are linearly unstable.

Rather naturally, as bigger is  $b^-$  as wider will be the region where both semi-trivial positive solutions are unstable, because any increment of  $b^-$  entails a reinforcement of the symbiosis between the species within  $(0.4, 0.6)$ . This explain why the region confined in between the curves of change of stability of the semi-trivial positive solutions is larger in Figure 2.2 than in Figure 2.1.

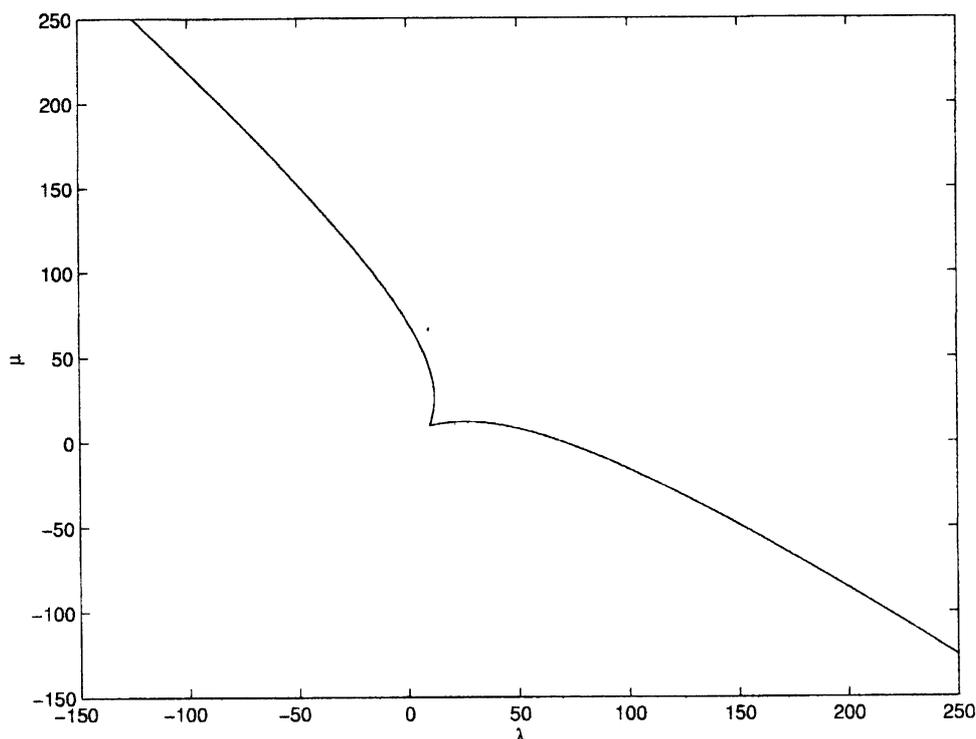


Figure 2.2. Curves of change of stability of semi-trivial states in case (2.12).

### 3 The existence of coexistence states

Adopting the point of view of global bifurcation theory, and due to [16, Theorem 7.2.2], if we fix  $\lambda > \sigma$  and regard to  $\mu$  as the main bifurcation parameter, then from the point

$$(\mu_0, u_0, v_0) = (\sigma[-\Delta + c\theta_\lambda; \Omega], \theta_\lambda, 0) \in X := \mathbb{R} \times \mathcal{C}_0^{2+\nu}(\bar{\Omega}) \times \mathcal{C}_0^{2+\nu}(\bar{\Omega})$$

it emanates an unbounded component  $\mathfrak{C}_{(\mu, \theta_\lambda, 0)}$  of the set of coexistence states of (1.4) in  $X$ . By symmetry, if we fix  $\mu > \sigma$  and regard to  $\lambda$  as the main bifurcation parameter, from the point

$$(\lambda_0, u_0, v_0) = (\sigma[-\Delta + b\theta_\mu; \Omega], 0, \theta_\mu) \in X$$

it emanates an unbounded component  $\mathfrak{C}_{(\lambda, 0, \theta_\mu)}$  of the set of coexistence states of (1.4). The main result of this section provides us with the  $\lambda$  and  $\mu$  projections of these components of coexistence states for *low intensity symbiosis*. In the case of *high intensity symbiosis* the limiting profiles of the positive solutions of (1.1) might consist of *meta-coexistence states*, instead of coexistence states (cf. [14] for further details in the case of pure competition). This might help to realize why the fact that (1.4) does not admit a *classical coexistence state* does not necessarily entail any further complexity in the dynamics of (1.1), as the limiting behavior of the solutions of (1.1) can be governed by meta-coexistence states which might be reached either at finite time, if there is blow-up, or after an eternity, if not.

Subsequently,  $\mathcal{P}_\gamma$  will stand for the  $\gamma$ -projection operator

$$\mathcal{P}_\gamma(\gamma, u, v) = \gamma.$$

**Theorem 3.1** *Suppose*

$$b_M^- = \|b^-\|_\infty < 1 \quad \text{and} \quad c_M^- = \|c^-\|_\infty < 1. \quad (3.1)$$

*Then, the following estimates are necessary for the existence of a coexistence state*

$$\lambda > (1 - b_M^- c_M^-) \sigma - b_M^- \mu, \quad \mu > (1 - b_M^- c_M^-) \sigma - c_M^- \lambda, \quad (3.2)$$

*and the next properties are satisfied:*

(a) *For each  $\lambda > \sigma$ , there exists  $\mu_0(\lambda) \in \mathbb{R}$  such that*

$$(1 - b_M^- c_M^-) \sigma - c_M^- \lambda < \mu_0(\lambda) \leq \sigma[-\Delta + c\theta_\lambda; \Omega] \quad (3.3)$$

*and*

$$\mathcal{P}_\mu \mathfrak{E}_{(\mu, \theta_\lambda, 0)} \in \{ [\mu_0(\lambda), \infty), (\sigma[-\Delta + c\theta_\lambda; \Omega], \infty) \}. \quad (3.4)$$

(b) *For each  $\mu > \sigma$ , there exists  $\lambda_0(\mu) \in \mathbb{R}$  such that*

$$(1 - b_M^- c_M^-) \sigma - b_M^- \mu < \lambda_0(\mu) \leq \sigma[-\Delta + b\theta_\mu; \Omega] \quad (3.5)$$

*and*

$$\mathcal{P}_\lambda \mathfrak{E}_{(\lambda, 0, \theta_\mu)} \in \{ [\lambda_0(\mu), \infty), (\sigma[-\Delta + b\theta_\mu; \Omega], \infty) \}. \quad (3.6)$$

*Therefore, if  $(\theta_\lambda, 0)$  and  $(0, \theta_\mu)$  are linearly unstable (simultaneously), i.e.  $(\lambda, \mu)$  satisfies*

$$\lambda > \sigma[-\Delta + b\theta_\mu; \Omega], \quad \mu > \sigma[-\Delta + c\theta_\lambda; \Omega], \quad (3.7)$$

*then, (1.4) possesses a coexistence state. In particular, (1.4) admits a coexistence state for each  $(\lambda, \mu)$  in the quadrant (2.8) and, consequently, the principle of competitive exclusion fails to be true for (1.1).*

**Proof:** Suppose (1.4) admits a coexistence state and let  $(u_0, v_0)$  be one of them. Then, since  $b = b^+ - b^-$  and  $c = c^+ - c^-$ ,

$$\begin{cases} -\Delta u_0 = \lambda u_0 - u_0^2 - b(x)u_0 v_0 \leq \lambda u_0 - u_0^2 + b^- u_0 v_0 \leq \lambda u_0 - u_0^2 + b_M^- u_0 v_0 & \text{in } \Omega, \\ -\Delta v_0 = \mu v_0 - v_0^2 - c(x)u_0 v_0 \leq \mu v_0 - v_0^2 + c^- u_0 v_0 \leq \mu v_0 - v_0^2 + c_M^- u_0 v_0 & \text{in } \Omega, \\ u_0 = v_0 = 0, & \text{on } \partial\Omega. \end{cases}$$

and, hence,  $(u_0, v_0)$  provides us with a positive subsolution of the auxiliary symbiotic system

$$\begin{cases} -\Delta u = \lambda u - u^2 + b_M^- uv & \text{in } \Omega, \\ -\Delta v = \mu v - v^2 + c_M^- uv & \text{in } \Omega, \\ u = v = 0, & \text{on } \partial\Omega. \end{cases} \quad (3.8)$$

Moreover, due to (3.1), for any constant

$$N \geq \max \left\{ \frac{\lambda}{1 - b_M^-}, \frac{\mu}{1 - c_M^-} \right\},$$

*Symbiosis in competitive environments*

the pair  $(N, N)$  provides us with a supersolution of (3.8). By enlarging  $N$ , if necessary, we have that  $(N, N) \geq (u_0, v_0)$ . Thus, thanks to [6, Theorem 8.7], (3.8) has a coexistence state  $(\hat{u}_0, \hat{v}_0)$  satisfying

$$u_0 \leq \hat{u}_0 \leq N, \quad v_0 \leq \hat{v}_0 \leq N, \quad (3.9)$$

and, hence, due to [6, Lemma 6.1], (3.2) must be satisfied and, actually,

$$\hat{u}_0 \leq \frac{\lambda + \mu b_M^-}{1 - b_M^- c_M^-}, \quad \hat{v}_0 \leq \frac{\mu + \lambda c_M^-}{1 - b_M^- c_M^-}. \quad (3.10)$$

In particular, (3.9) and (3.10) provide us with the following  $L^\infty(\Omega)$  a priori bounds

$$u_0 \leq \frac{\lambda + \mu b_M^-}{1 - b_M^- c_M^-}, \quad v_0 \leq \frac{\mu + \lambda c_M^-}{1 - b_M^- c_M^-}, \quad (3.11)$$

for any coexistence state  $(u_0, v_0)$  of (1.4). It should be noted that, thanks to (3.2),  $\lambda + \mu b_M^- > 0$  and  $\mu + \lambda c_M^- > 0$ . Therefore, the coexistence states of (1.4) possess uniform  $L^\infty$  a priori bounds in any compact subset of the parameter space  $(\lambda, \mu) \in \mathbb{R}^2$ .

Now, the remaining assertions of the theorem follow readily from the fact that  $\mathcal{C}_{(\mu, \theta, \lambda, 0)}$  and  $\mathcal{C}_{(\lambda, 0, \theta, \mu)}$  are unbounded connected subsets of  $X$ , by means of some rather standard arguments of global bifurcation theory whose details are omitted here.

The principle of competitive exclusion fails in the sense that if we fix, e.g.,  $\lambda > \sigma[-\Delta; \Omega_0^b \cup \Omega_0^c]$ , then  $u$  is not always driven to extinction by  $v$  if  $\mu \uparrow \infty$ , since (1.4) possesses a coexistence state for each  $\mu > \sigma[-\Delta; \Omega_0^c \cup \Omega_0^e]$ ; this in strong contrast with the situation described by the model when  $b_L > 0$  and  $c_L > 0$ , where  $u$  is always driven to extinction by  $v$  if  $\mu \uparrow \infty$ .  $\square$

The region (3.2) in the parameter space  $(\lambda, \mu)$  looks much like the complement of the dark area in [6, Fig. 2]. Even in the most simple situations, assumption (3.1) is crucial for the validity of Theorem 3.1. Indeed, in the special case when

$$\lambda = \mu \quad \text{and} \quad b = c \quad (3.12)$$

any solution pair of the form  $(u, v) = (w, w)$ , where  $w$  is a positive solution of

$$\begin{cases} -\Delta w = \lambda w - (1 + b)w^2 & \text{in } \Omega, \\ w|_{\partial\Omega} = 0, \end{cases} \quad (3.13)$$

provides us with a coexistence state of (1.4). If  $b_M^- < 1$ , then  $(1 + b)_L > 0$  and, hence, (3.13) possesses a unique positive solution, subsequently denoted by  $\psi_\lambda$ , for each  $\lambda > \sigma$ . On the contrary, if  $b_M^- = 1$  in some nice smooth subdomain  $D_0 \subset \Omega$  around  $\partial\Omega$ , then  $1 + b = 0$  in  $D_0$  and, hence, (3.13) possesses a classical positive solution if and only if

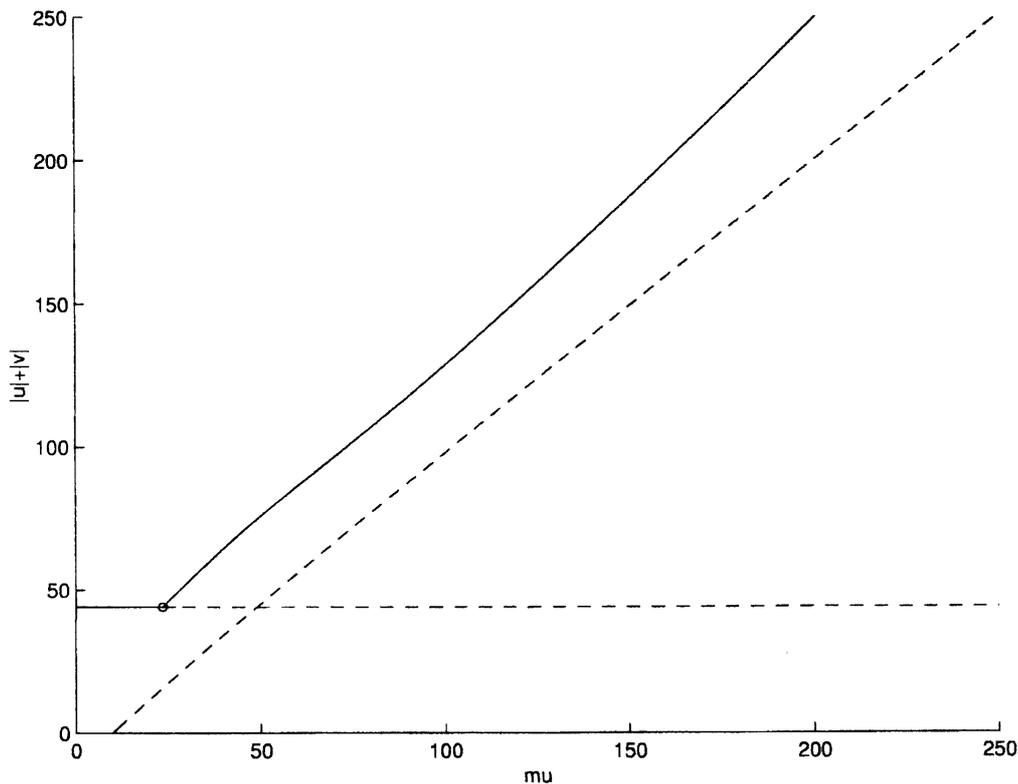
$$\sigma < \lambda < \sigma_0 := \sigma[-\Delta; D_0]$$

(cf. [7]). Moreover, it is unique, if it exists, and if we denote it by  $\psi_\lambda$ , then  $\lim_{\lambda \uparrow \sigma_0} \psi_\lambda$  provides us with the minimal classical solution of the singular boundary value problem

$$\begin{cases} -\Delta w = \lambda w - (1 + b)w^2 & \text{in } \Omega \setminus \bar{D}_0, \\ w|_{\Omega \cap \partial D_0} = \infty, \end{cases}$$

in  $\Omega \setminus \bar{D}_0$ , while  $\lim_{\lambda \uparrow \sigma_0} \psi_\lambda = \infty$  in  $\bar{D}_0 \setminus \partial\Omega$  (cf. [9]). Actually, if  $\lambda \geq \sigma_0$ , then the dynamics of the positive solutions of the parabolic counterpart of (3.13) is governed by the metasolutions of (3.13) (cf. [17]). From these features, it can be shown that the components  $\mathfrak{C}_{(\mu, \theta_\lambda, 0)}$  and  $\mathfrak{C}_{(\mu, 0, \theta_\mu)}$  have bounded parameter projections. Consequently, Theorem 3.1 cannot be true, in general, if condition (3.1) fails. Note that the behavior of the positive solutions of (3.13) is even more involved if  $b_M^- > 1$ , as a result of the fact that, in such case,  $1 + b$  changes of sign in  $\Omega$ , and, hence, (3.13) is a superlinear indefinite problem (cf. [1], [10], and the references therein). Actually in such case one can construct examples with an arbitrarily large number of coexistence states. This is a rather natural feature entailing that the increment of cooperation in competitive environments results into an increment of the complexity of the underlying dynamics. A mechanism in fully concordance and harmony with the huge bio-diversity surrounding us.

Thanks to Theorem 3.1, for the special choice (2.11), the model (2.9) possesses a coexistence state if both semi-trivial positive solutions are linearly unstable. To compute these coexistence states we have fixed  $\lambda > \sigma = \pi^2$  and used  $\mu$  as the main bifurcation parameter to compute the component  $\mathfrak{C}_{(\mu, \theta_\lambda, 0)}$  by coupling a pure spectral method with collocation and a path global continuation solver. We send to the interested reader to [11], [18] and [3] for further technical details.



**Figure 3.1.** The component  $\mathfrak{C}_{(\mu, \theta_{48.98}, 0)}$  of (2.9) in case (2.11).

Figure 3.1 shows  $\mathfrak{C}_{(\mu, \theta_\lambda, 0)}$  for the choice  $\lambda = 48.98$ . It emanates from  $(\theta_{48.98}, 0)$  at the critical value of the the parameter

$$\mu := \sigma \left[ -\frac{d^2}{dx^2} + b(x)\theta_{48.98}; (0, 1) \right] \sim 23.51$$

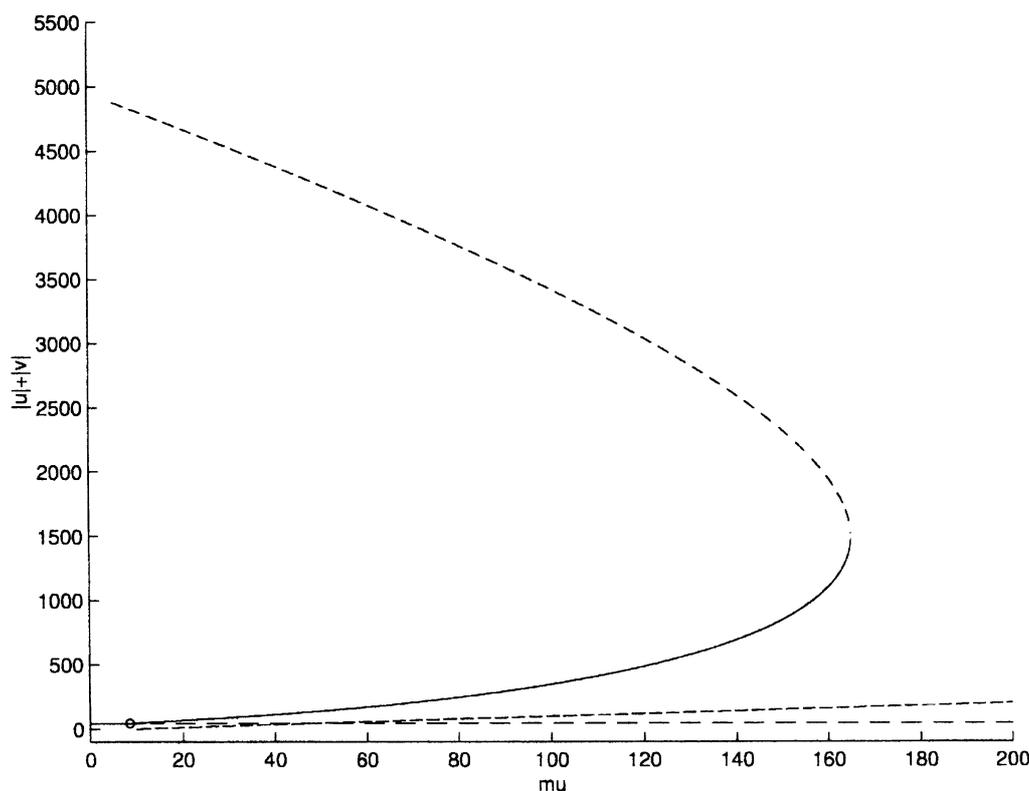
*Symbiosis in competitive environments*

and it is globally defined for any further value of  $\mu$ . All computed coexistence states has shown to be exponentially asymptotically stable and, hence, they are local attractors for the positive solutions of the parabolic counterpart of (2.9). Figure 3.1 shows four curves of special significance in describing the dynamics of the model. Stable solutions are indicated by solid lines, unstable by dashed lines. We are plotting the value of the intrinsic growth rate  $\mu$  against the norm

$$|u| + |v| := \max_{0 \leq x \leq 1} u(x) + \max_{0 \leq x \leq 1} v(x).$$

The two horizontal lines describe the trivial state  $(0, 0)$ , and the semi-trivial state  $(\theta_{48.98}, 0)$ . It should be noted that  $|\theta_{48.98}| \sim 44.02$ . Then, Figure 3.1 shows the curve of semi-trivial positive solutions  $(0, \theta_\mu)$ . This curve emanates from  $(0, 0)$  at the value of the parameter  $\mu = \pi^2$  and it grows with  $\mu$  for any further value of the parameter. Finally, Figure 3.1 shows the curve of coexistence states. It is the curve emanating super-critically from the state  $(\theta_{48.98}, 0)$  at the value of the parameter where the stability of the solution  $(\theta_\lambda, 0)$  is lost.

As already commented above, our numerical computations have confirmed, from the current perspective, that condition (3.1) is crucial for the validity of Theorem 3.1. Indeed, for the special choice (2.12), the corresponding computed component  $\mathcal{C}_{(\mu, \theta_{48.98}, 0)}$  bifurcates from  $(\theta_{48.98}, 0)$  at  $\mu \sim 8.46$  and it exhibits a sub-critical turning point at  $\mu \sim 165.1353$ , where it turns backward. The coexistence states along the lower-half curve are exponentially asymptotically stable, while the solutions along the upper-half curve are linearly unstable (cf. Figure 3.2).



**Figure 3.2.** The component  $\mathcal{C}_{(\mu, \theta_{48.98}, 0)}$  of (2.9) in case (2.12).

Strongly motivated by our numerical computations, we conjecture that, for this example,

$$\mathcal{P}_\mu \mathcal{C}_{(\mu, \theta_{48.98}, 0)} = (-\infty, 165.1353],$$

though we were not able to get a formal proof of this feature.

### 4 Limiting populations as one intrinsic growth rate blows-up

The main result of this section is the following.

**Theorem 4.1** *Suppose (3.1) and*

$$c_M^+ < \frac{1 - b_M^- c_M^-}{b_M^-}, \tag{4.1}$$

fix  $\lambda > \sigma$  and let  $\{(\mu_n, u_n, v_n)\}_{n \geq 1}$  be any sequence of coexistence states of (1.4) such that

$$\lim_{n \rightarrow \infty} \mu_n = \infty.$$

Then,

$$\lim_{n \rightarrow \infty} v_n = \infty \text{ uniformly on compact subsets of } \Omega, \tag{4.2}$$

and

$$\lim_{n \rightarrow \infty} u_n = \begin{cases} 0 & \text{in } \Omega_+^b, \\ \infty & \text{in } \Omega_-^b. \end{cases} \tag{4.3}$$

If, in addition,  $\Omega_0^b \neq \emptyset$  is a subdomain of  $\Omega$  of class  $C^{2+\nu}$  such that

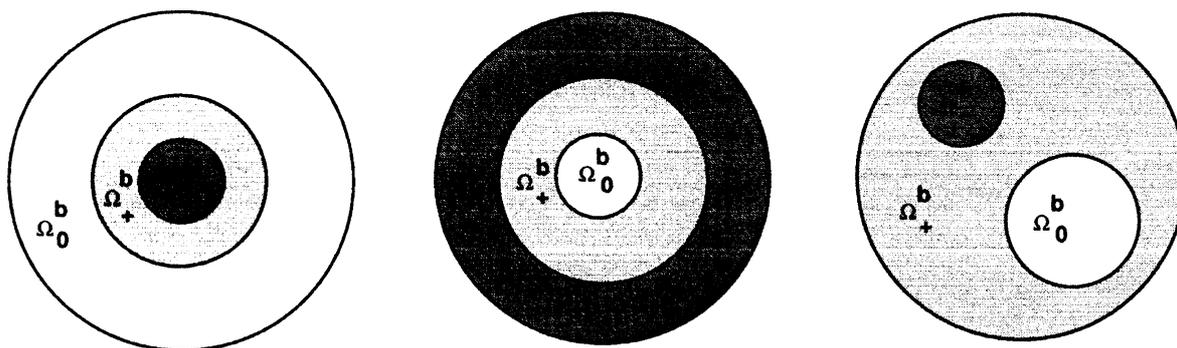
$$\bar{\Omega}_0^b \cap \bar{\Omega}_-^b = \emptyset, \tag{4.4}$$

then

$$\lim_{n \rightarrow \infty} u_n = \Theta_{[\lambda, \Omega_0^b]} \text{ uniformly in } \Omega_0^b, \tag{4.5}$$

where  $\Theta_{[\lambda, \Omega_0^b]}$  stands for the maximal non-negative solution of

$$\begin{cases} -\Delta u = \lambda u - u^2 & \text{in } \Omega_0^b, \\ u = 0 & \text{on } \partial\Omega_0^b. \end{cases} \tag{4.6}$$



**Figure 4.1.** Some admissible configurations satisfying (4.4).

Note that  $\Theta_{[\lambda, \Omega_0^b]} \gg 0$  if  $\lambda > \sigma[-\Delta; \Omega_0^b]$ , while  $\Theta_{[\lambda, \Omega_0^b]} = 0$  if  $\lambda \leq \sigma[-\Delta; \Omega_0^b]$ . Figure 4.1 shows three admissible situations where (4.4) occurs. Note that (4.4) entails

$$\partial\Omega_0^b \subset (\partial\Omega \cup \partial\Omega_+^b) \setminus \partial\Omega_-^b.$$

When  $\Omega_0^b$  consists of several separated components, say  $\Omega_{0,j}^b$ ,  $1 \leq j \leq M$ , then the second part of Theorem 4.1 holds —independently— for each  $1 \leq j \leq M$  such that  $\bar{\Omega}_{0,j}^b \cap \bar{\Omega}_-^b = \emptyset$ .

*Symbiosis in competitive environments*

If in the statement of Theorem 4.1 condition (4.4) is inter-exchanged by the following one

$$\bar{\Omega}_0^b \cap \bar{\Omega}_+^b = \emptyset, \quad (4.7)$$

then it is easy to see that

$$\lim_{n \rightarrow \infty} u_n \leq L_{[\lambda, \Omega_0^b]} \quad \text{in } \Omega_0^b, \quad (4.8)$$

where  $L_{[\lambda, \Omega_0^b]}$  stands for the unique positive solution of the problem

$$\begin{cases} -\Delta u = \lambda u - u^2 & \text{in } \Omega_0^b, \\ u = \infty & \text{on } \partial\Omega_0^b \cap \partial\Omega_-^b, \\ u = 0 & \text{on } \partial\Omega_0^b \cap \partial\Omega^b, \end{cases} \quad (4.9)$$

though, in general, it is far from clear the exact point-wise behavior of  $\lim_{n \rightarrow \infty} u_n$  (cf. [15] for further details in this direction). By symmetry, the following result holds.

**Theorem 4.2** *Suppose (3.1) and*

$$b_M^+ < \frac{1 - b_M^- c_M^-}{c_M^-}, \quad (4.10)$$

*fix  $\mu > \sigma$  and let  $\{(\lambda_n, u_n, v_n)\}_{n \geq 1}$  be any sequence of coexistence states of (1.4) such that*

$$\lim_{n \rightarrow \infty} \lambda_n = \infty.$$

*Then,*

$$\lim_{n \rightarrow \infty} u_n = \infty \quad \text{uniformly on compact subsets of } \Omega, \quad (4.11)$$

*and*

$$\lim_{n \rightarrow \infty} v_n = \begin{cases} 0 & \text{in } \Omega_+^c, \\ \infty & \text{in } \Omega_-^c. \end{cases} \quad (4.12)$$

*If, in addition,  $\Omega_0^c \neq \emptyset$  is a subdomain of  $\Omega$  of class  $C^{2+\nu}$  such that*

$$\bar{\Omega}_0^c \cap \bar{\Omega}_-^c = \emptyset, \quad (4.13)$$

*then*

$$\lim_{n \rightarrow \infty} v_n = \Theta_{[\mu, \Omega_0^c]} \quad \text{uniformly in } \Omega_0^c, \quad (4.14)$$

*where  $\Theta_{[\mu, \Omega_0^c]}$  stands for the maximal non-negative solution of*

$$\begin{cases} -\Delta v = \mu v - v^2 & \text{in } \Omega_0^c, \\ v = 0 & \text{on } \partial\Omega_0^c. \end{cases} \quad (4.15)$$

**Proof of Theorem 4.1:** Suppose (3.1) and (4.1). Pick  $\lambda > \sigma$  and a sequence  $\{(\mu_n, u_n, v_n)\}_{n \geq 1}$  of coexistence states of (1.4) with  $\lim_{n \rightarrow \infty} \mu_n = \infty$ . The existence of such a sequence is guaranteed by Theorem 3.1. Without loss of generality, we can assume that  $\mu_n \geq 0$  for each  $n \geq 1$ . Thanks to (3.11), for each  $n \geq 1$ , we have that

$$u_n \leq \frac{\lambda + \mu_n b_M^-}{1 - b_M^- c_M^-}$$

and, hence,

$$\begin{aligned} -\Delta v_n &= \mu_n v_n - v_n^2 - c^+ u_n v_n + c^- u_n v_n \geq \mu_n v_n - v_n^2 - c^+ u_n v_n \\ &\geq \left( \mu_n - c^+ \frac{\lambda + \mu_n b_M^-}{1 - b_M^- c_M^-} \right) v_n - v_n^2 \\ &= \left[ \left( 1 - \frac{b_M^-}{1 - b_M^- c_M^-} c^+ \right) \mu_n - \frac{\lambda}{1 - b_M^- c_M^-} c^+ \right] v_n - v_n^2 \\ &\geq \left[ \left( 1 - \frac{b_M^- c_M^+}{1 - b_M^- c_M^-} \right) \mu_n - \frac{\lambda}{1 - b_M^- c_M^-} c_M^+ \right] v_n - v_n^2. \end{aligned}$$

Thus, setting

$$\gamma_n := \left( 1 - \frac{b_M^- c_M^+}{1 - b_M^- c_M^-} \right) \mu_n - \frac{\lambda}{1 - b_M^- c_M^-} c_M^+, \quad n \geq 1,$$

we have that, for each  $n \geq 1$ ,  $v_n$  is a positive supersolution of

$$\begin{cases} -\Delta w = \gamma_n w - w^2 & \text{in } \Omega, \\ w = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.16}$$

Moreover, thanks to (4.1),

$$\lim_{n \rightarrow \infty} \gamma_n = \infty$$

and, in particular, there exists  $n_0 \geq 1$  such that  $\gamma_n > \sigma$  for each  $n \geq n_0$ . For such  $n$ 's, (4.16) possesses a unique positive solution,  $\theta_{\gamma_n}$ . Therefore, thanks to the strong maximum principle,

$$v_n \geq \theta_{\gamma_n}, \quad n \geq n_0.$$

Thanks to [8, Theorem 3.4] we have that

$$\lim_{n \rightarrow \infty} \theta_{\gamma_n} = \infty$$

uniformly on compact subsets of  $\Omega$  and, consequently,  $\lim_{n \rightarrow \infty} v_n = \infty$  as well.

To ascertain the limiting behaviour of  $u_n$  as  $n \rightarrow \infty$ , it suffices to observe that

$$\begin{cases} (-\Delta + b v_n) u_n = \lambda u_n - u_n^2 & \text{in } \Omega, \\ u_n = 0 & \text{on } \partial\Omega, \end{cases} \quad n \geq 1,$$

and adapt the proof of [19, Theorem 1.1] to cover our more general setting here, though those technical details together with a sharper version of [19, Theorem 1.1] will appear elsewhere.  $\square$

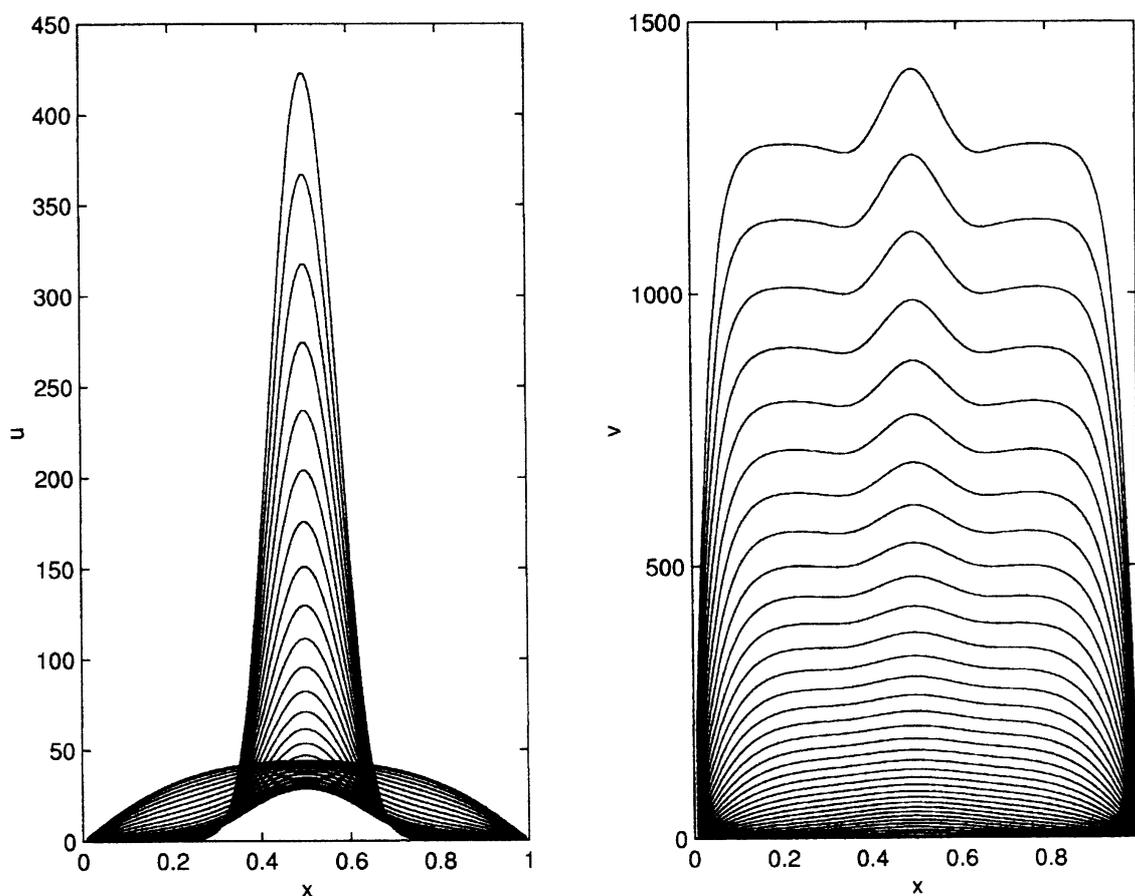
Condition (4.1) seems to be crucial for the validity of Theorem 4.1, since its proof is based upon the fact that  $\lim_{n \rightarrow \infty} v_n = \infty$  uniformly in  $\Omega$ , which, at first glance, is far from natural if  $c^+$  is sufficiently large. Indeed, for sufficiently large  $c^+$  the species  $u$  might control the growth of  $v$  within  $\Omega_+^c$  even when  $\mu \rightarrow \infty$ . Our numerical experiments have shown that the number of coexistence states of the problem might grow, as  $c^+$  increases, on increasingly large

*Symbiosis in competitive environments*

$\mu$ -intervals, so showing some of the difficulties that one might have to overcome in getting a complete picture of the dynamics for  $c^+$  large. As we plan to make a further more detailed discussion elsewhere, we will stop the current discussion here and switch to illustrate the thesis of Theorem 4.1 by means of a numerical example.

Note that problem (2.9) fits into the general setting of Theorem 4.1. Indeed, the behaviour of  $b(x)$  adjusts to the pattern described by the left picture of Figure 4.1 with  $\Omega_0^b = \emptyset$ . Moreover, for the choice (2.11), condition (4.1) is satisfied, since

$$\frac{1 - b_M^- c_M^-}{b_M^-} = \frac{1 - (0.4)^2}{0.4} = 2.1 > 2 = c_M^+.$$



**Figure 4.2.** The behavior of the coexistence states as  $\mu$  increases for the choice (2.11).

According to Theorem 4.1, the coexistence states  $(u_\mu, v_\mu)$  along the component  $\mathfrak{C}_{(\mu, \theta_{48.98}, 0)}$  plotted in Figure 3.1 must satisfy

$$\lim_{\mu \uparrow \infty} v_\mu = \infty$$

and

$$\lim_{\mu \uparrow \infty} u_\mu = \begin{cases} 0 & \text{in } \Omega_+^b := (0, 0.4) \cup (0.6, 1), \\ \infty & \text{in } \Omega_-^b := (0.4, 0.6). \end{cases}$$

This asymptotic behaviour is extremely well illustrated by simply having a glance at the sequences of plots of  $u_\mu$  and  $v_\mu$  as  $\mu$  increases separating from the critical value  $\mu \sim 23.51$ , where

$(u_\mu, v_\mu)$  bifurcates from  $(\theta_{48.98}, 0)$ . Figure 4.2 shows these sequences for a family of values of  $\mu$  ranging within the interval  $[23.51, 1276]$ . The component  $v_\mu$  always increases. It leaves zero as  $\mu$  grows approaching infinity everywhere when  $\mu \uparrow \infty$ , while  $u_\mu$  decreases from  $\theta_{48.98}$  up to reach a critical profile where it completely changes behaviour gradually increasing and approximating infinity in  $\Omega_-^b$  while decreasing to zero in  $\Omega_+^b$ , as predicted by Theorem 4.1. The peaks exhibited by  $u_\mu$  and  $v_\mu$  around 0.5 are originated by the symbiosis effects of the species within  $\Omega_-^b$ . Actually, besides the symbiosis effects within  $(0.4, 0.6)$  allow  $u$  to avoid extinction as the intrinsic growth rate of  $v$  blows up, it seems remarkable that the species  $u$  can grow up to any desired level within  $(0.4, 0.6)$  (it approaches infinity with  $(0.4, 0.6)$  as  $\mu \uparrow \infty$ ).

## 5 The profiles of the coexistence states of Figure 3.2.

Subsequently, instead of (2.11), we make the choice (2.12). As a result of the stronger symbiosis effects, we already know that the bifurcation diagram of coexistence states exhibits a sub-critical turning point at  $\mu \sim 165.1353$  (cf. Figure 3.2). In Figure 4.3 we have super-imposed a family of plots of  $u_\mu$  and  $v_\mu$  for  $\mu$  ranging in the interval  $[8.4650, 151.49]$  along the lower-half curve of Figure 3.2. All these coexistence states are exponentially asymptotically stable. Their behavior, as the intrinsic growth rate of  $v$  increases is reminiscent of the one described by Figure 4.2, though now both populations grow at a higher rate within their cooperation domain; a very natural feature from the stronger symbiotic effects inherent to (2.12).

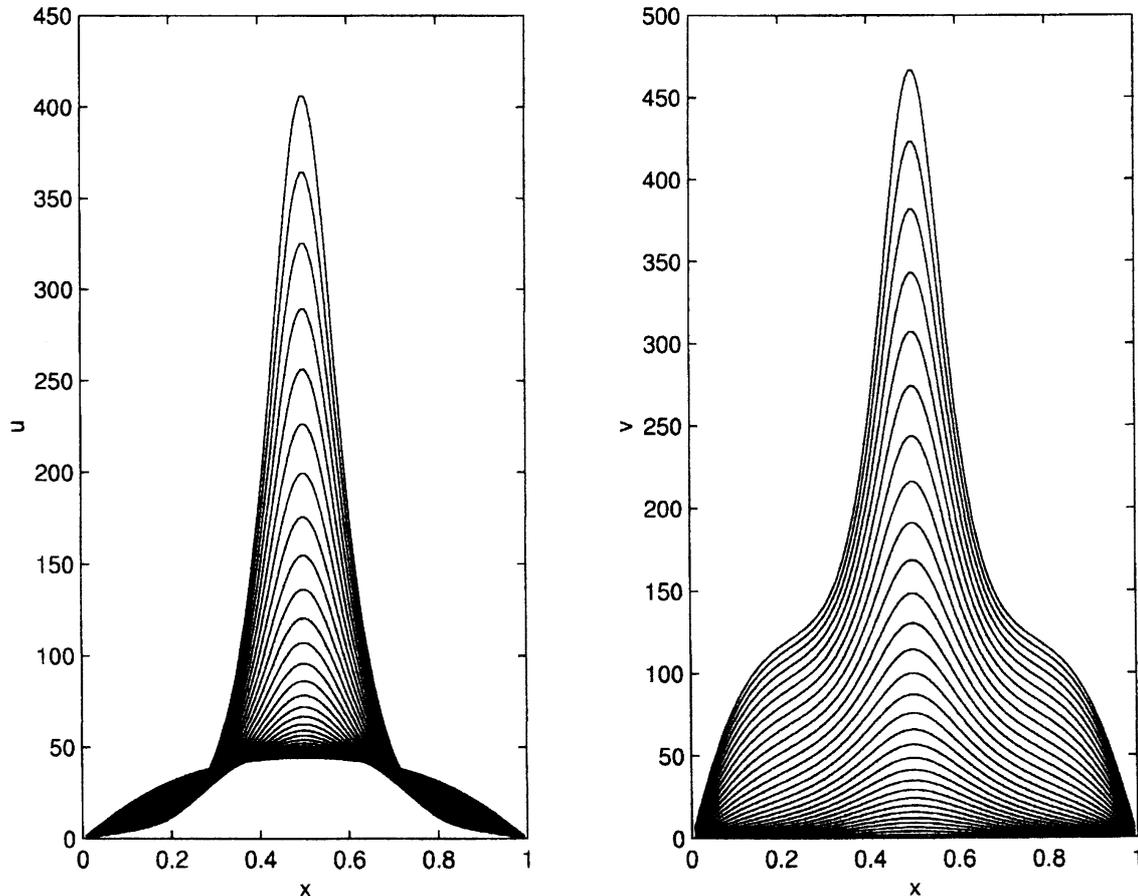
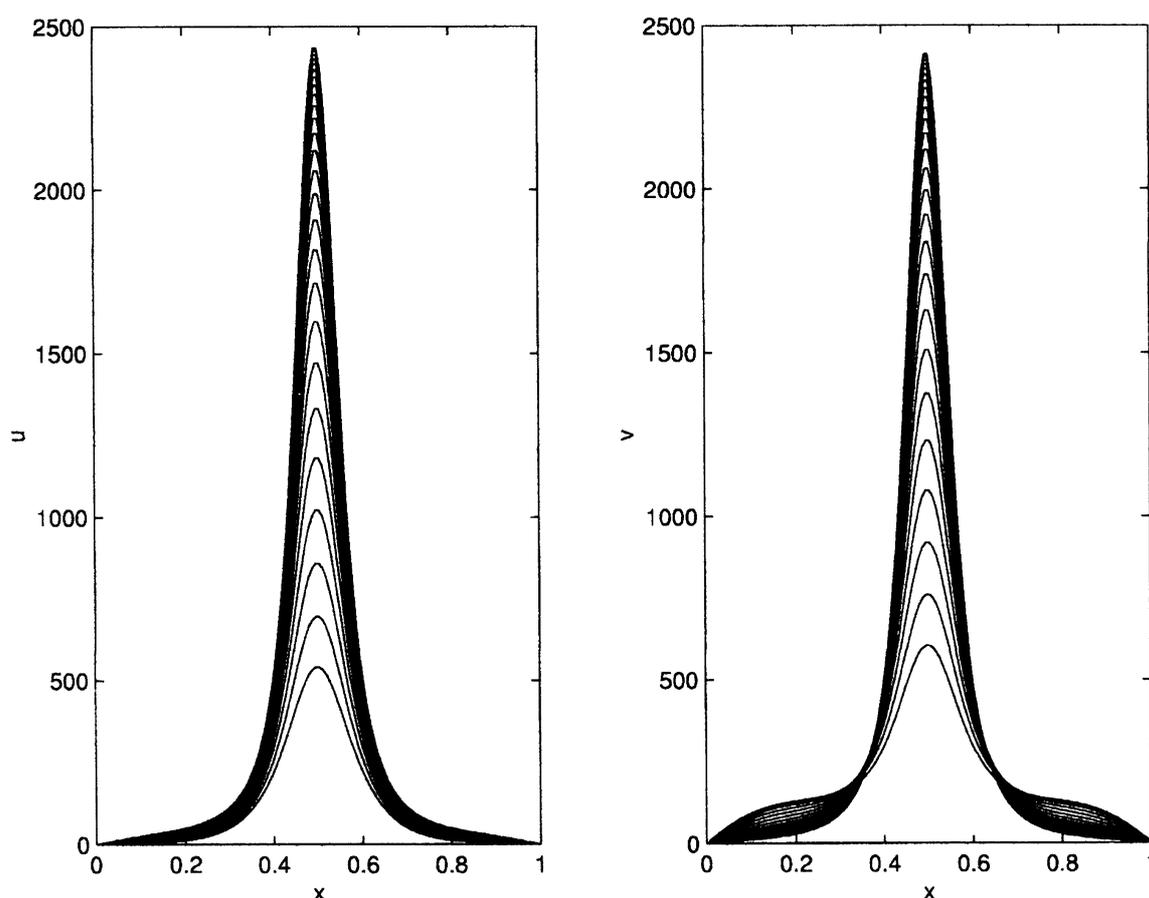


Figure 4.3. The behavior of the stable coexistence states of Figure 3.2.

### Symbiosis in competitive environments

As we pass through the turning point to the upper half-curve of coexistence states, the stability of the coexistence states along the lower half-curve get lost and all of them exhibit a genuine *superlinear behavior*, as much emphasized as smaller is  $\mu$ . Indeed, as  $\mu$  decreases from 165.1353, the populations exhibit a very strong tendency to concentrate within  $(0.4, 0.6)$ . In Figure 4.4 we have super-imposed the plots of a family among those coexistence states for  $\mu$  ranging in between 6.809 and 165.1353. As  $\mu$  decreases,  $u_\mu$  and  $v_\mu$  segregate within  $(0.4, 0.6)$ .



**Figure 4.4.** The behavior of the unstable coexistence states of Figure 3.2.

Although for sufficiently large  $\mu$  the model would not admit a coexistence state, as we actually conjecture, the limiting profiles of the solutions of the parabolic counterpart of (2.9) should blow-up within  $(0.4, 0.6)$  stabilizing towards the profile of a *meta-coexistence state* of the model, but this analysis is outside the scope of this introductory work (cf. [14] for the precise concept of meta-coexistence state). To summarize, even in the absence of coexistence states, for  $\mu$  sufficiently large the profile of the solutions after a reasonable time should not be that different from the ones exhibited by Figure 4.2, though these solutions might eventually exhibit a complete blow up within  $(0.4, 0.6)$  simultaneously stabilizing to a fixed profile within  $(0, 0.4) \cup (0.6, 1)$ , but this deeper analysis deserves further sharper attention. So, we stop our discussion here.

**Acknowledgements.** This work has been supported by the Ministry of Science and Technology of Spain under Grants BFM2000-0797 and REN2003-00707.

## References

- [1] H. Amann and J. López-Gómez, A priori bounds and multiple solutions for superlinear indefinite elliptic problems, *J. Diff. Eqns.* **146** (1998), 336-374.
- [2] S. Cano-Casanova and J. López-Gómez, Permanence under strong aggression is possible, *An. Inst. H. Poincaré, Anal. non Lin.* **20** (2003), 999-1041.
- [3] S. Cano-Casanova, J. López-Gómez and M. Molina-Meyer, Permanence through spatial segregation in heterogeneous competition, Proceedings of the 9th IEEE International Conference on Methods and Models in Automation and Robotics (R. Kaszyński Ed.), pp. 123-130, Szczecin, 2003.
- [4] M. G. Crandall and P. H. Rabinowitz, Bifurcation from simple eigenvalues, *J. Funct. Anal.* **8** (1971), 321-340.
- [5] D. Daners and P. Koch-Medina, *Abstract Evolution Equations, Periodic Problems and Applications*, Pitman Research Notes in Mathematics 279, Pitman-Longman, Essex, 1992.
- [6] M. Delgado, J. López-Gómez and A. Suárez, On the symbiotic Lotka-Volterra model with diffusion and transport effects, *J. Diff. Eqns.* **160** (2000), 175-262.
- [7] J. M. Fraile, P. Koch, J. López-Gómez and S. Merino, Elliptic eigenvalue problems and unbounded continua of positive solutions of a nonlinear elliptic problem, *J. Diff. Eqns.* **127** (1996), 295-319.
- [8] J. E. Furter and J. López-Gómez, Diffusion-mediated permanence problem for a heterogeneous Lotka-Volterra competition model, *Proc. Roy. Soc. Edinburgh* **127A** (1997), 281-336.
- [9] J. García-Melián, R. Gómez-Reñasco, J. López-Gómez and J. C. Sabina de Lis, Pointwise growth and uniqueness of positive solutions for a class of sublinear elliptic problems where bifurcation from infinity occurs, *Arch. Rat. Mech. Anal.* **145** (1998), 261-289.
- [10] R. Gómez-Reñasco and J. López-Gómez, The effect of varying coefficients on the dynamics of a class of superlinear indefinite reaction-diffusion equations, *J. Differential Equations*, **167** (2000), 36-72.
- [11] J. López-Gómez, *Estabilidad y Bifurcación Estática. Aplicaciones y Métodos Numéricos*. Cuadernos de Matemática y Mecánica, Cursos y Seminarios Nro. 4, CONICET, Santa Fé, 1988.
- [12] J. López-Gómez, Permanence under strong competition, *Dynamical Systems and Applications*, WSSAA **4** (1995), 473-488.
- [13] J. López-Gómez, The maximum principle and the existence of principal eigenvalues for some linear weighted boundary value problems, *J. Diff. Eqns.* **127** (1996), 263-294.
- [14] J. López-Gómez, Coexistence and meta-coexistence for competing species, *Houston J. of Maths.*, **29** (2003), 483-536.

*Symbiosis in competitive environments*

- [15] J. López-Gómez, The boundary blow-up rate of large solutions, *J. Diff. Eqns.* In press.
- [16] J. López-Gómez, *Spectral Theory and Nonlinear Functional Analysis*, Research Notes in Mathematics 426, CRC Press, Boca Raton, 2001.
- [17] J. López-Gómez, Dynamics of parabolic equations. From classical solutions to metasolutions, *Diff. Int. Eqns.* **16** (2003), 813–828.
- [18] J. López-Gómez, J. C. Eilbeck, M. Molina and K. N. Duncan, Structure of solution manifolds in a strongly coupled elliptic system, *IMA J. Numer. Anal.* 12 (1992), 405–428.
- [19] J. López-Gómez and M. Molina-Meyer, Singular perturbations in Economy and Ecology. The effect of strategic symbiosis in random competitive environments. *Adv. in Math. Sci. and Appns.* In press.