

# Some Recent Results on Diffusive Predator-prey Models in Spatially Heterogeneous Environment <sup>\*†</sup>

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## Abstract

We present several recent results obtained in our attempts to understand the influence of spatial heterogeneity in the predator-prey models. Two different approaches are taken. The first approach is based on the observation that the behavior of many diffusive population models is very sensitive to certain coefficient functions becoming small in part of the underlying spatial region. We apply this observation to three predator-prey models to reveal fundamental differences from the classical homogeneous case in each model, and demonstrate the essential differences of these models from each other. In the second approach, we examine the influence of a protection zone in a Holling type II diffusive predator-prey model, which introduces different mathematical problems from those in the first approach, and reveals important impacts of the protection zone.

## 1 Introduction

The natural environments for most biological species are inhomogeneous in space. Therefore it is reasonable to expect the dynamics of their populations to be influenced by the heterogeneity of the environments, apart from the interactions between the species. Many scientific experiments support this view; for example, biological experiments of Huffaker [Hu] found that a predator-prey system consisting of two species of mites could collapse to extinction quickly in small homogeneous environments, but would persist longer in suitable heterogeneous environments. However, it is generally not easy to capture the influence of heterogeneous environment mathematically. Traditionally the main focus in the study of population models was on the effects of interactions between the species; so even if diffusive population models are used, the coefficients appearing in the models are chosen to be positive constants, representing a homogeneous environment. One natural way to include spatial variations of the environment in these models is to replace the constant coefficients by positive functions of the space variable  $x$ . But the mathematical techniques developed to study these models are typically either not sensitive to this change, in which case the effects of heterogeneous spatial environment are difficult to observe in the mathematical

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analysis, or the techniques are too sensitive to this change and become unapplicable when the constant coefficients are replaced by functions. (We will be more specific below.)

In this paper, we will discuss several results obtained in our recent attempts to better understand the influence of spatial heterogeneity in predator-prey models, where new ideas and techniques are used to overcome the aforementioned difficulties. Two different approaches are taken. One approach is based on the observation that the behavior of many diffusive population models is very sensitive to certain coefficient functions becoming small in part of the underlying spatial region. With the hope of providing some insights in the design of new or improvement of existing biological environments, we will show how this observation can be applied to several predator-prey models to reveal essential differences from the classical homogeneous case for each model, and demonstrate interesting differences between the models. Our second approach examines the influence of a protection zone in a diffusive predator-prey model, which introduces different mathematical problems from those in the first approach, and reveals important impacts of the protection zone; we hope our results here may shed some light on the creation and design of nature reserves.

To be more realistic, the coefficients in the diffusive population models should also be dependent on time  $t$ , but we will not consider this case here. A systematic discussion of time-periodic diffusive population models can be found in Hess [He]. It would be interesting to see how our approaches discussed here can be extended to the time-periodic case.

Much research in the directions discussed in this paper is still on-going. Moreover, what we consider here is only a small proportion of a vast area of study in population models. To put this paper into perspective, we now briefly recall some history and related research.

The first population models are ordinary differential equations. It has long been accepted that the interaction between a pair of predator and prey influences the population growth of both species. The first evidence of the interaction was provided by the population data of Canadian lynx and snowshoe hare. Hudson Bay company kept careful records of all furs from the early 1800s into the 1900s. It is often assumed that the number of furs are representative of the populations in the wild, so these data can be used to represent the relative populations of the lynx and hares in the wild. The records for the furs collected by the Hudson Bay company showed distinct oscillations (approximately 9 year periods), suggesting that these species caused almost periodic fluctuations of each other's populations. Many other ecological examples can be found in, for example, [MBN].

To describe the interactions between the species, the first ordinary differential equations (ODEs) of predator-prey type were formulated by American chemist and biologist Alfred James Lotka in 1920 [Lo1, Lo2, Lo3], and Italian mathematician Vito Volterra in 1926 [V1, V2]. The simplest form of the equation is

$$\frac{du}{dt} = \lambda u - buv, \quad \frac{dv}{dt} = -\mu v + cuv, \quad (1.1)$$

where  $\lambda, \mu, b, c > 0$ . Volterra's model of biological interaction is motivated by the statistical studies of the populations of various species of fish in the Adriatic Sea conducted by biologist U. d'Ancona (see [V1, V2]). In [V2], he proposed a more general model:

$$\frac{du}{dt} = \lambda u - au^2 - buv, \quad \frac{dv}{dt} = \mu v - dv^2 + cuv, \quad (1.2)$$

where  $\lambda, a, b, c, d \geq 0$ , and  $\mu \in \mathbf{R}$ .

The Lotka-Volterra predator-prey model (1.2) possesses a unique coexistence steady state solution  $(u_*, v_*)$  when  $d \geq 0$ , and  $(u_*, v_*)$  is globally asymptotically stable when  $d > 0$  (a complete phase plane analysis of (1.2) can be found in, for example, [BC] or [HS]). However biologists have observed that while some predator-prey interactions lead to a system with a stable equilibrium, some others do not (such as the data from the above mentioned Hudson Bay company show), and there exists ecological process which destabilizes the coexistence equilibrium. Various mechanisms are introduced by ecologists for destabilization of the equilibrium [MBN]. In consideration of the limited ability of a predator to consume its prey, a general functional response of the predator  $\phi(u)$  was introduced by Solomon [So] and Holling [H1, H2], and the classical Lotka-Volterra model is modified to

$$\frac{du}{dt} = \lambda u - au^2 - b\phi(u)v, \quad \frac{dv}{dt} = \mu v - dv^2 + c\phi(u)v. \quad (1.3)$$

Here  $\phi(u)$  is a positive and nondecreasing function of  $u$  (prey density). Among many possible choices of  $\phi(u)$ , the Holling type II functional response is most commonly used in the ecological literature, which is defined by

$$\phi(u) = \frac{u}{1 + mu}, \quad (1.4)$$

where  $m$  is a positive constant:  $m = bT_h$  and  $T_h$  is the handling time for a generic predator to kill and consume a generic prey ([H1, H2]). Hence a more realistic Holling type II predator-prey model takes the form

$$\frac{du}{dt} = \lambda u - au^2 - \frac{buv}{1 + mu}, \quad \frac{dv}{dt} = \mu v - dv^2 + \frac{cuv}{1 + mu}. \quad (1.5)$$

When  $\mu < 0$  and  $d = 0$ , (1.5) becomes the Rosenzweig-MacArthur model widely used in real-life ecological applications [RM]; when  $\mu < 0$  and  $d > 0$ , the model was used by Bazykin [Ba, Tur].

Generally speaking, the dynamical behavior of the predator-prey models is very sensitive to the changes of the reaction functions. To accommodate the various different situations in ecological applications, many other functional responses and more general interactions have been introduced, and excellent surveys can be found in recent monographs [MBN, Tur]. We list below some more examples without quoting the original references (which can be retrieved from [MBN, Tur]):

$$\text{(Yodzis)} \quad \begin{cases} \frac{du}{dt} = \lambda u - au^2 - \frac{bu^2v}{1 + mu^2}, \\ \frac{dv}{dt} = \mu v - dv^2 + \frac{cu^2v}{1 + mu^2}; \end{cases} \quad (1.6)$$

$$\text{(Beddington-DeAngelis)} \quad \begin{cases} \frac{du}{dt} = \lambda u - au^2 - \frac{buv}{1 + mu + nv}, \\ \frac{dv}{dt} = \mu v - dv^2 + \frac{cuv}{1 + mu + nv}; \end{cases} \quad (1.7)$$

$$\text{(Variable Territory)} \quad \begin{cases} \frac{du}{dt} = \lambda u - au^2 - \frac{buv}{1+mu}, \\ \frac{dv}{dt} = \mu v - \frac{dv^2}{u} + \frac{cuv}{1+mu}; \end{cases} \quad (1.8)$$

$$\text{(Leslie)} \quad \begin{cases} \frac{du}{dt} = \lambda u - au^2 - buv, \\ \frac{dv}{dt} = \mu v - \frac{dv^2}{u}; \end{cases} \quad (1.9)$$

$$\text{(Leslie-May-Tanner)} \quad \begin{cases} \frac{du}{dt} = \lambda u - au^2 - \frac{buv}{1+mu}, \\ \frac{dv}{dt} = \mu v - \frac{dv^2}{u}; \end{cases} \quad (1.10)$$

$$\text{(Ratio-dependent)} \quad \begin{cases} \frac{du}{dt} = \lambda u - au^2 - \frac{buv}{u+nv}, \\ \frac{dv}{dt} = \mu v + \frac{cuv}{u+nv}. \end{cases} \quad (1.11)$$

These ODE models are usually less difficult to understand than their reaction-diffusion counterparts to be discussed below, but there is considerable biological evidence that space can affect the dynamics of populations and the structure of communities, and such effects are not captured in this kind of ODE models. In 1937, Fisher [Fis] and Kolmogoroff, Petrovsky, and Piscounoff [KPP] used a reaction-diffusion equation to study the spread of an advantageous form (allele) of a single gene in a population of diploid individuals. In the early 1950s' Skellam [Sk], Kierstead and Slobodkin [KS] studied the application of reaction-diffusion models in population persistence when spatial dispersal is involved, and Turing [Tu] used reaction-diffusion equations to study the formation of patterns for his model of morphogenesis. These pioneering works marked the beginning of reaction-diffusion models for biological problems. Since the 1970's, the corresponding reaction-diffusion equations of an ODE population model of the form

$$\frac{du}{dt} = f(u, v), \quad \frac{dv}{dt} = g(u, v),$$

namely,

$$\frac{du}{dt} - d_1 \Delta u = f(u, v), \quad \frac{dv}{dt} - d_2 \Delta u = g(u, v),$$

together with suitable boundary conditions on the boundary of the underlying spatial domain, have been widely used to study the dynamical behavior of the same species over the given spatial domain ([St1, St2, L, Mu2, OL, CC2].) These reaction-diffusion systems are usually called diffusive population models. Such models have been successfully used to study the waves of invasion and persistence of species in mathematical ecology, but for the purpose of this paper, we only describe below their use in understanding the long-time dynamical behavior on a bounded spatial domain  $\Omega$ , especially the set of steady-state solutions and their spatial patterns.

Much progress on the study of reaction-diffusion systems had been made in the 1970's and 1980's. For example, "invariant rectangle" techniques ([CCS, W]) and Lyapunov function techniques ([A, dMR]) were successfully used to understand the long-time dynamical

behavior for such systems, especially for the case of Neumann boundary conditions. Remarkably, if the diffusion rates  $d_1$  and  $d_2$  are both very large, it was shown that the only steady-state solutions of a general reaction-diffusion system with Neumann boundary conditions are constant ones, and the attractor for the reaction-diffusion system is the same as for the corresponding ordinary differential equations ([CHS]). If the underlying domain of a single reaction-diffusion equation with Neumann boundary conditions is convex, then any stable steady-state solution must be a constant ([CH, Ma]), but stable non-constant solutions can exist if  $\Omega$  is not convex ([MaM]). Similar results were also proved for competition reaction-diffusion systems with Neumann boundary conditions ([KW]), but it is unclear whether a homogeneous diffusive predator-prey system with Neumann boundary conditions can possess stable non-constant steady states since the predator-prey system does not generate a monotone dynamical system. Considerable progress has also been made on the pattern formation and bifurcation of diffusive predator-prey systems (see, *e.g.*, [Mi, MiM, MNY, Mu1, SJ, SL]). See [Co1, Co2] for surveys of some of the earlier works on diffusive predator-prey systems.

In the 1980's various analytical and topological techniques emerged for the investigation of the set of coexistence steady-states of diffusive population models, such as local bifurcation theory (see [CGS]), monotone iteration schemes (see [Pao, KL]), global bifurcation theory [BB1, BB2], and fixed point index theory [Da1, Da2] (see also [Li1, Li2]). These methods were further refined and used from the 1990's to understand the question of uniqueness, multiplicity and stability of the steady-state solutions (see, *e.g.*, [Da3, Da4], [LP], [DD1], [LN], [DL1, DL2, DL3], [PaW, PeW], [KY]).

The techniques described in the last paragraph can be largely extended to cover the case that the constant coefficients are replaced by positive functions of the space variable  $x$ . Therefore, it seems difficult to capture the effects of heterogeneous environment on diffusive population models by exploring these techniques alone. It is also worthwhile to point out that, on the other hand, some powerful techniques involving the use of a Lyapunov functional (as used in [dMR]), and the "contracting rectangle" method (as used in [Br]), may collapse when the reaction terms are space-dependent, as they rely heavily on the existence of constant solutions of the system.

In [D1, D2], based on earlier work on the single logistic equation (see, *e.g.*, [Ou, dP, FKL, DHu]), a degenerate competition model was examined, revealing fundamental changes of dynamical behavior when the crowding effect coefficient function for one of the competing species vanishes on part of the underlying domain. This observation was further developed in [D3] to study the influence of heterogeneity on the formation of sharp spatial patterns and the stability of the sharp patterned steady-state solutions in the classical (but near degenerate) competition model.

In this paper, we will examine, along a similar line of thinking, the effects of spatial heterogeneity on several diffusive predator-prey models. We will present some recent results in [DD2, DHs, DW, DS1]. Since the predator-prey models do not have the monotonicity property enjoyed by the competition model, very different techniques from those used in [D1, D2, D3] are needed, and due to the fundamental difference between the predator-prey and competition models, very different phenomena will be revealed. We will also describe our recent results in [DS2] on the effects of a protection zone in a diffusive predator-prey model. Much work is still on-going in this direction.

The rest of this paper is organized as follows. In Section 2, we consider the Lotka-Volterra predator-prey model, where after a brief discussion of the homogeneous case, we present some recent results of Dancer and Du ([DD2, DD3]) on the inhomogeneous case. In Section 3, we consider the predator-prey model with a Holling type II response function, and present some recent results of Du and Shi ([DS1, DS2]). Section 4 is concerned with a diffusive Leslie model and some recent results of Du, Hsu and Wang ([DHs, DW]) are discussed there.

Before ending this section, we would like to mention some related research on the effect of heterogeneous environment in diffusive population models. In a series of recent papers, Hutson, Lou, Mischaikow and Polacik studied various perturbations of the special competition model

$$\begin{cases} u_t - \mu\Delta u = \alpha(x)u - u^2 - uv, & x \in \Omega, t > 0, \\ v_t - \mu\Delta v = \alpha(x)v - v^2 - uv, & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \end{cases}$$

and obtained interesting results revealing some fundamental effects of heterogeneous environment on the competition model. We refer to [HMP, HLM1, HLM2, HLMP] for details. Other related results can be found in [CC2] and [Lo, LS]. In recent years, much in-depth research on diffusive predator-prey systems has been carried out by numerical simulations; a review in that direction can be found in [MPT].

## 2 The Lotka-Volterra model

### 2.1 The homogeneous case

After some suitable rescalings, the classical homogeneous diffusive Lotka-Volterra predator-prey model over a bounded smooth domain  $\Omega \subset \mathbf{R}^n$  may be expressed in the following form:

$$\begin{cases} u_t - d_1\Delta u = \lambda u - u^2 - buv, & x \in \Omega, t > 0, \\ v_t - d_2\Delta v = \mu v - v^2 + cuv, & x \in \Omega, t > 0, \\ B_1 u = B_2 v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases} \quad (2.1)$$

where  $d_1, d_2, \lambda, \mu, c, d$  are constants, and  $d_1, d_2, c, d$  are always assumed to be positive;  $B_1$  and  $B_2$  are boundary operators of the form

$$B_1 u(x, t) = \alpha_1 \partial_\nu u(x, t) + \beta_1 u(x, t), \quad B_2 v(x, t) = \alpha_2 \partial_\nu v(x, t) + \beta_2 v(x, t),$$

where  $\nu$  denotes the unit outward normal of  $\partial\Omega$ , and  $\alpha_i, \beta_i$  are nonnegative constants with  $\alpha_i^2 + \beta_i^2 > 0$ ,  $i = 1, 2$ . Therefore  $B_1$  and  $B_2$  are the Neumann boundary operators if  $(\alpha_i, \beta_i) = (1, 0)$ , and they are Dirichlet if  $(\alpha_i, \beta_i) = (0, 1)$ .

When the Neumann boundary conditions are used, the understanding of (2.1) is rather complete. It is proved by Leung [Le] that all positive solutions of (2.1), regardless of the initial data, converge to a constant steady-state solution as time goes to infinity. This implies that (2.1) behaves similarly to the corresponding ODE model. In sharp contrast,

much less is known when Dirichlet boundary conditions are used. The techniques in [Le] rely heavily on the fact that (2.1) has constant steady-states under Neumann boundary conditions. It has been conjectured that the dynamics of (2.1) under Dirichlet boundary conditions behaves similarly to the Neumann case, *i.e.*, all the positive solutions converge to the steady-state solutions as time goes to infinity, but the conjecture remains open so far.

From now on in this section, we will only consider the Dirichlet case, and will focus on the steady-state solutions. The techniques below carry over easily to the case of general boundary conditions. For convenience of comparison to the inhomogeneous case to be discussed later, we first briefly recall some well-known results on the nonnegative steady-state solutions of (2.1), namely, nonnegative solutions of the system

$$\begin{cases} -\Delta u = \lambda u - u^2 - buv, & x \in \Omega, \\ -\Delta v = \mu v - v^2 + cuv, & x \in \Omega, \\ u = v = 0, & x \in \partial\Omega. \end{cases} \quad (2.2)$$

where for convenience of notation, we have assumed that  $d_1 = d_2 = 1$ . (One could also rescale  $u, v$  and the coefficients to reduce the original elliptic system to the form (2.2).)

In the following sections, linear eigenvalue problems will play important roles in our results. We define  $\lambda_1^D(\phi, O)$  and  $\lambda_1^N(\phi, O)$  to be the first eigenvalues of  $-\Delta + \phi$  over the region  $O$ , with Dirichlet or Neumann boundary conditions respectively. If the region  $O$  is omitted in the notation, then we understand that  $O = \Omega$ . If the potential function  $\phi$  is omitted, then we understand that  $\phi = 0$ . We recall some well-known properties of  $\lambda_1^D(\phi, O)$  and  $\lambda_1^N(\phi, O)$ :

1.  $\lambda_1^D(\phi, O) > \lambda_1^N(\phi, O)$ ;
2.  $\lambda_1^B(\phi_1, O) > \lambda_1^B(\phi_2, O)$  if  $\phi_1 \geq \phi_2$  and  $\phi_1 \not\equiv \phi_2$ , for  $B = D, N$ ;
3.  $\lambda_1^D(\phi, O_1) \geq \lambda_1^D(\phi, O_2)$  if  $O_1 \subset O_2$ .

The understanding of (2.2) relies on the diffusive logistic equation

$$-\Delta w = \lambda w - w^2, \quad x \in \Omega, \quad w = 0, \quad x \in \partial\Omega. \quad (2.3)$$

It is well-known that (2.3) has no positive solution when  $\lambda \leq \lambda_1^D \equiv \lambda_1^D(\Omega)$ , and it has a unique positive solution  $\theta_\lambda$  when  $\lambda > \lambda_1^D$ . Therefore, if  $\lambda > \lambda_1^D$ , then (2.2) has a unique semitrivial solution of the form  $(u, 0)$ , namely  $(\theta_\lambda, 0)$ . Similarly, (2.2) has a unique semitrivial solution of the form  $(0, v)$  when  $\mu > \lambda_1^D$ , namely  $(0, \theta_\mu)$ . Clearly  $(0, 0)$  is always a solution to (2.2), and we call it the trivial solution. By the strong maximum principle, any other nonnegative solution  $(u, v)$  of (2.2) must be a positive solution, *i.e.*,  $u > 0, v > 0$  in  $\Omega$ . It is proved in [Da2] that (2.2) has a positive solution if and only if

$$\lambda > \lambda_1^D(c\theta_\mu) \text{ and } \mu > \lambda_1^D(-d\theta_\lambda), \quad (2.4)$$

where we understand that  $\theta_\eta = 0$  if  $\eta \leq \lambda_1^D$ . Clearly (2.4) implies  $\lambda > \lambda_1^D$ . If we fix  $c, d > 0$  and  $\lambda > \lambda_1^D$  and use  $\mu$  as a parameter, then from the monotonicity of  $\lambda_1^D(c\theta_\mu)$  in  $\mu$  it is easily seen that there exists a unique  $\mu^0 > \lambda_1^D$  such that

$$\lambda = \lambda_1^D(c\theta_{\mu^0}).$$

Denote  $\mu_0 = \lambda_1^D(-d\theta_\lambda)$ . We find that (2.4) is equivalent to

$$\mu_0 < \mu < \mu^0. \quad (2.5)$$

It is possible to use a bifurcation argument to show that a branch of positive solutions  $\Gamma = \{(\mu, u, v)\}$  bifurcates from the semitrivial solution branch  $\Gamma_u := \{(\mu, \theta_\lambda, 0) : -\infty < \mu < \infty\}$  at  $\mu = \mu_0$ , and  $\Gamma$  then joins the other semitrivial solution branch  $\Gamma_v := \{(\mu, 0, \theta_\mu) : \mu > \lambda_1^D\}$  at  $\mu = \mu^0$ , see [BB2]. These results are illustrated by Figure 1 (left). It has been conjectured that (2.2) has at most one positive solution, but this is only proved for the case  $\Omega$  is an interval, *i.e.*, when the space dimension is 1 (see [LP], see also [DLO] for some partial uniqueness results for the radial case in high dimensions). Even in that case, it is not known whether the unique positive solution is asymptotically stable as a steady-state of the corresponding parabolic system, though it is expected that the unique positive steady-state is globally attractive, as in the case of Neumann boundary conditions.

## 2.2 The heterogeneous case

When the spatial environment is inhomogeneous, (2.1) with Dirichlet boundary conditions may be modified to the following form

$$\begin{cases} u_t - \operatorname{div}(d_1(x)\nabla u) = \lambda a_1(x)u - a(x)u^2 - b(x)uv, & x \in \Omega, t > 0, \\ v_t - \operatorname{div}(d_2(x)\nabla v) = \mu a_2(x)v - d(x)v^2 + c(x)uv, & x \in \Omega, t > 0, \\ u = v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in \Omega, \end{cases} \quad (2.6)$$

where  $\lambda, \mu$  are constants and  $d_1, d_2, a_1, a_2, a, b, c, d$  are nonnegative continuous functions on  $\bar{\Omega}$ . If all the coefficient functions are strictly positive over  $\Omega$ , it is easy to see that (2.6) behaves similarly to the homogeneous case (2.1). Thus, we may call (2.6) a *classical* predator-prey model when all the coefficient functions are strictly positive over  $\Omega$ . In order to capture the influence of the heterogeneity of environment on (2.6), we consider a limiting case, where some of the coefficient functions in (2.6) vanish partially over  $\Omega$ , which we call a degeneracy henceforth. We will show that the dynamical behavior of (2.6) with certain degeneracies may change drastically from the classical model.

Note that though a degenerate model as described above is not very realistic as a population model, it is a natural limiting problem for the classical model when some of its coefficients are very small on part of the underlying domain. Hence a better understanding of the degenerate cases provides important insight to the classical model with variable coefficients.

As a first step in this direction, we examine the effects of heterogeneous spatial environment on the set of steady-state solutions of (2.6). To be more specific, we consider such effects caused by the partial vanishing of  $a(x)$ . Let us recall that  $a(x)$  describes the intro-specific pressure of  $u$ . The partial vanishing of  $a(x)$  implies that, in the absence of  $v$ , the growth of  $u$  is governed by a degenerate logistic law, or more precisely, a mixture of the logistic and Malthusian laws over  $\Omega$ .

To avoid unnecessary complications and to simplify our notations, we assume that all the other coefficient functions are positive constants. Through some simple rescalings of

$u, v$  and the coefficients, one sees that for the steady-state solutions, we need only consider the following system,

$$\begin{cases} -\Delta u = \lambda u - a(x)u^2 - buv, & x \in \Omega, \\ -\Delta v = \mu v - v^2 + cuv, & x \in \Omega, \\ u = v = 0, & x \in \partial\Omega, \end{cases} \quad (2.7)$$

where  $b, c$  are positive constants. We assume that  $a(x) \equiv 0$  on the closure of some smooth domain  $\Omega_0$  satisfying  $\overline{\Omega_0} \subset \Omega$  and  $a(x) > 0$  over  $\overline{\Omega} \setminus \overline{\Omega_0}$ . We will show that there exists a critical value  $\lambda^* > 0$  such that (2.7) behaves largely as the homogeneous case  $a(x) \equiv 1$  when  $\lambda < \lambda^*$ , but fundamental changes occur once  $\lambda \geq \lambda^*$ .

From now on, we fix  $b, c$  and regard  $\lambda$  and  $\mu$  as varying parameters. Clearly  $v \equiv 0$  satisfies the second equation in (2.7). In this case  $u$  satisfies the so called degenerate logistic equation

$$-\Delta u = \lambda u - a(x)u^2, \quad x \in \Omega, \quad u = 0, \quad x \in \partial\Omega. \quad (2.8)$$

It is well known ([Ou, dP, FKLm]) that (2.8) has only the trivial nonnegative solution  $u \equiv 0$  when  $\lambda \notin (\lambda_1^D(\Omega), \lambda_1^D(\Omega_0))$ , and it has a unique positive solution  $u_\lambda$  when  $\lambda$  belongs to this open interval. It is easily seen that  $u_\lambda \rightarrow 0$  in  $L^\infty(\Omega)$  when  $\lambda \rightarrow (\lambda_1^D(\Omega))^+$ . Moreover, by [DHu], as  $\lambda \rightarrow (\lambda_1^D(\Omega_0))^-$ ,

$$u_\lambda \rightarrow \infty \quad \text{uniformly on } \overline{\Omega_0},$$

$$u_\lambda \rightarrow U_{\lambda_1^D(\Omega_0)} \quad \text{locally uniformly on } \overline{\Omega} \setminus \overline{\Omega_0},$$

where  $U_\lambda$  denotes the minimal positive solution of the following boundary blow-up problem

$$-\Delta U = \lambda U - a(x)U^2, \quad x \in \Omega \setminus \overline{\Omega_0}; \quad U|_{\partial\Omega} = 0, \quad U|_{\partial\Omega_0} = \infty. \quad (2.9)$$

Here  $U|_{\partial\Omega_0} = \infty$  means  $\lim_{d(x, \partial\Omega_0) \rightarrow 0} U(x) = \infty$ . By [DHu], (2.9) has a minimal and maximal positive solution for each  $\lambda \in (-\infty, \infty)$ .

To summarize, for each  $\lambda \in (\lambda_1^D(\Omega), \lambda_1^D(\Omega_0))$ , (2.7) has a unique semitrivial solution of the form  $(u, 0)$  with  $u > 0$ , namely,  $(u_\lambda, 0)$ ; there is no such semitrivial solution for other  $\lambda$  values. Similar to (2.2), (2.7) has a unique semitrivial solution  $(0, \theta_\mu)$  of the form  $(0, v)$  if  $\mu > \lambda_1^D(\Omega)$  and there is no such semitrivial solution for other  $\mu$  values. As before, the obvious solution  $(u, v) = (0, 0)$  of (2.7) is called the trivial solution.

To analyze the set of positive solutions for (2.7) we will need the following *a priori* estimates. (Similar result also holds for Neumann boundary value problems.)

**Theorem 2.1.** *Given an arbitrary positive constant  $M$  we can find another positive constant  $C$ , depending only on  $M$  and  $a(x), b, c, \Omega$  in (2.7), such that if  $(u, v)$  is a positive solution of (2.7) with  $|\lambda| + |\mu| \leq M$ , then*

$$\|u\|_\infty + \|v\|_\infty \leq C.$$

Here  $\|\cdot\|_\infty = \|\cdot\|_{L^\infty(\Omega)}$ .

We refer to [DD2] for the proof of Theorem 2.1. An important step in this proof is the following useful result.

**Lemma 2.2.** *Suppose  $\{u_n\} \subset C^2(\overline{\Omega})$  satisfies*

$$-\Delta u_n \leq \lambda u_n, \quad u_n|_{\partial\Omega} = 0, \quad u_n \geq 0, \quad \|u_n\|_\infty = 1,$$

where  $\lambda$  is a positive constant. Then, there exists  $u_\infty \in L^\infty(\Omega) \cap H_0^1(\Omega)$  such that, subject to a subsequence,  $u_n \rightarrow u_\infty$  weakly in  $H_0^1(\Omega)$ , strongly in  $L^p(\Omega)$ ,  $\forall p \geq 1$ , and  $\|u_\infty\|_\infty = 1$ .

To study the positive solution set of (2.7), we will make use of the comparison principles and adapt the bifurcation approach used by Blat and Brown in [BB2] by fixing  $\lambda$  and using  $\mu$  as the main bifurcation parameter. It turns out that our results will be fundamentally different in the following two cases:

$$(i) \quad \lambda_1^D(\Omega) < \lambda < \lambda_1^D(\Omega_0) \quad \text{and} \quad (ii) \quad \lambda \geq \lambda_1^D(\Omega_0).$$

In the first case, (2.7) can be analyzed as in the classical case (2.2). It has a unique semitrivial solution of the form  $(u, 0)$ , namely,  $(u_\lambda, 0)$ . If  $(u, v)$  is a positive solution to (2.7), then  $u$  satisfies

$$-\Delta u \leq \lambda u - a(x)u^2, \quad u|_{\partial\Omega} = 0.$$

A simple comparison argument shows

$$0 < u \leq u_\lambda, \quad \forall x \in \Omega. \tag{2.10}$$

From the equation for  $v$  we find

$$-\Delta v > \mu v - v^2, \quad v|_{\partial\Omega} = 0,$$

which implies that

$$v \geq \theta_\mu, \quad \forall x \in \Omega, \tag{2.11}$$

where we have used the convention that  $\theta_\mu \equiv 0$  whenever  $\mu \leq \lambda_1^D(\Omega)$ .

From the equation for  $v$  we also obtain

$$\mu = \lambda_1^D(v - cu) \equiv \lambda_1^D(v - cu, \Omega).$$

Therefore, by (2.10) and the well-known monotonicity property of  $\lambda_1^D(\phi)$ , we easily deduce

$$\mu > \lambda_1^D(-cu_\lambda). \tag{2.12}$$

By the equation for  $u$  and (2.11), we deduce

$$\lambda = \lambda_1^D(au + bv) > \lambda_1^D(bv) \geq \lambda_1^D(b\theta_\mu),$$

that is,

$$\lambda > \lambda_1^D(b\theta_\mu). \tag{2.13}$$

Summarizing, we have the following result.

**Theorem 2.3.** *In the case that  $\lambda_1^D(\Omega) < \lambda < \lambda_1^D(\Omega_0)$ , a necessary condition for (2.7) to possess a positive solution is that both (2.12) and (2.13) hold.*

We will see in the following that (2.12) and (2.13) are also sufficient conditions for the existence of positive solutions.

In the  $(\mu, u, v)$ -space  $X := \mathbf{R} \times C^1(\bar{\Omega}) \times C^1(\bar{\Omega})$ , we have two semitrivial solution curves

$$\Gamma_u := \{(\mu, u_\lambda, 0) : \mu \in (-\infty, \infty)\} \quad \text{and} \quad \Gamma_v := \{(\mu, 0, \theta_\mu) : \lambda_1^D < \mu < \infty\}.$$

A local bifurcation analysis along  $\Gamma_u$  shows that from  $(\lambda_1^D(-cu_\lambda), u_\lambda, 0) \in \Gamma_u$  bifurcates a smooth curve of positive solutions  $\Gamma' = \{(\mu, u, v)\}$ . A global bifurcation consideration, together with an application of the maximum principle, shows that  $\Gamma'$  is contained in a global branch (*i.e.*, connected set) of positive solutions  $\Gamma = \{(\mu, u, v)\}$  which is either unbounded or joins the semitrivial curve  $\Gamma_v$  at exactly  $(\mu_0, 0, \theta_{\mu_0}) \in \Gamma_v$ , where  $\mu_0 > \lambda_1^D(\Omega)$  is determined uniquely by

$$\lambda = \lambda_1^D(b\theta_{\mu_0}). \quad (2.14)$$

It follows from (2.13) that  $\mu < \mu_0$  whenever  $(\mu, u, v) \in \Gamma$ . Therefore, we find that  $(\mu, u, v) \in \Gamma$  implies

$$\lambda_1^D(-cu_\lambda) < \mu < \mu_0. \quad (2.15)$$

From this, and applying Theorem 2.1, we conclude that  $\Gamma$  is bounded in the space  $\mathbf{R} \times L^\infty(\Omega) \times L^\infty(\Omega)$ . By standard  $L^p$  theory for elliptic operators, we conclude that  $\Gamma$  is also bounded in  $X$ . Hence  $\Gamma$  must join  $\Gamma_v$ . A local bifurcation analysis near  $(\mu_0, 0, \theta_{\mu_0})$  shows that near this point,  $\Gamma$  consists of a smooth curve.

To summarize, we have proved the following result.

**Theorem 2.4.** *When  $\lambda_1^D(\Omega) < \lambda < \lambda_1^D(\Omega_0)$ , there is a bounded connected set of positive solutions  $\Gamma = \{(\mu, u, v)\}$  in the space  $X$  which joins the semitrivial solutions branches  $\Gamma_u$  and  $\Gamma_v$  at  $(\lambda_1^D(-cu_\lambda), u_\lambda, 0)$  and  $(\mu_0, 0, \theta_{\mu_0})$ , respectively; moreover, near these two points,  $\Gamma$  consists of smooth curves. (See Figure 1 (left).)*

Clearly, (2.15) is equivalent to (2.12) and (2.13) combined. It now follows from Theorems 2.3 and 2.4 the following result.

**Corollary 2.5.** *When  $\lambda_1^D(\Omega) < \lambda < \lambda_1^D(\Omega_0)$ , (2.7) has a positive solution if and only if (2.15) holds.*

The above discussion shows that our results for case (i) are similar to that of the classical case  $b(x) \equiv 1$ .

Let us now consider the second case where  $\lambda \geq \lambda_1^D(\Omega_0)$ . A fundamental difference to the first case now is that we no longer have a semitrivial solution of the form  $(u, 0)$ . However, the semitrivial solution curve  $\Gamma_v$  is unchanged, and the bifurcation analysis of [BB2] along  $\Gamma_v$  can still be adapted. Again, a local bifurcation analysis shows that a smooth curve of positive solutions  $\Gamma' = \{(\mu, u, v)\}$  bifurcates from  $(\mu_0, 0, \theta_{\mu_0}) \in \Gamma_v$  where  $\mu_0$  is determined by (2.14). As before, a global bifurcation analysis, together with an application of the maximum principle, shows that  $\Gamma'$  is contained in a global branch of positive solutions  $\Gamma$  which is either unbounded in  $X$  or joins a semitrivial solution of the form  $(u, 0)$ . But we already know that there is no semitrivial solution of the form  $(u, 0)$ . Therefore,  $\Gamma$  must be unbounded.

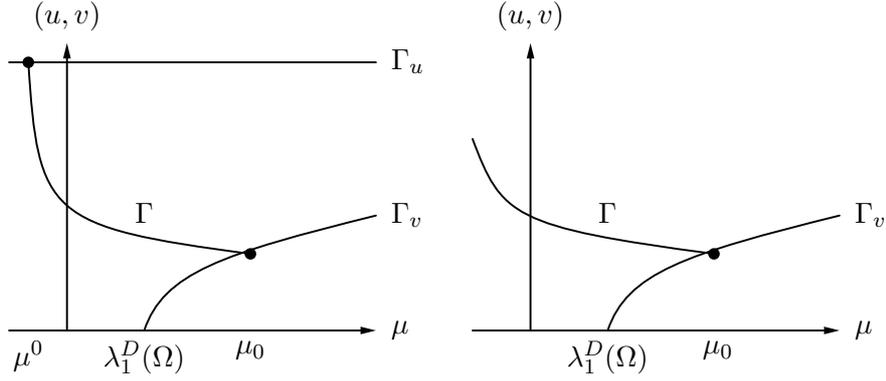


Figure 1: Bifurcation diagrams of positive steady state solutions of (2.7).  $\Gamma_u = \{(\theta_\lambda, 0) : \mu \in \mathbf{R}\}$ ;  $\Gamma_v = \{(0, \theta_\mu) : \mu \geq 0\}$ . The branch  $\Gamma$  connecting  $\Gamma_u$  and  $\Gamma_v$  consists of coexistence states. (left):  $\lambda_1^D(\Omega) < \lambda < \lambda_1^D(\Omega_0)$ ; (right):  $\lambda \geq \lambda_1^D(\Omega_0)$ .

One easily sees that the arguments leading to (2.13) still work for our present situation. Hence  $\mu < \mu_0$  whenever (2.7) has a positive solution. We now apply Theorem 2.1 and conclude that

$$\text{proj}_\mu \Gamma = (-\infty, \mu_0). \quad (2.16)$$

Summarizing the above discussion, we obtain the following result.

**Theorem 2.6.** *When  $\lambda \geq \lambda_1^D(\Omega_0)$ , (2.7) has a positive solution if and only if  $\mu < \mu_0$ . Moreover, there is an unbounded connected set of positive solutions  $\Gamma = \{(\mu, u, v)\}$  in  $X$  which joins the semitrivial solution branch  $\Gamma_v$  at  $(\mu_0, 0, \theta_{\mu_0})$  and satisfies (2.16). (See Figure 1 (right).)*

The fact that (2.7) has a positive solution for arbitrarily large negative  $\mu$  is strikingly different from the classical case. Biologically, this implies that the prey species can support a predator species of arbitrarily negative growth rate. This is due to the fact that the population of the prey would blow up in the region  $\Omega_0$  in the absence of the predator and hence one might think  $\Omega_0$  as a region where food is abundant for the predator. On the other hand, our above result indicates that the blow-up of the prey population can be avoided by introducing a predator with rather arbitrary growth rate.

We now consider the asymptotic behavior of the positive solutions of (2.7) as  $\mu \rightarrow -\infty$ . For this purpose, we consider a decreasing sequence of negative numbers  $\mu_n$  which converges to  $-\infty$ , and let  $(u_n, v_n)$  be an arbitrary positive solution of (2.7) with  $\mu = \mu_n$ . We have the following result.

**Theorem 2.7.** *Let  $(\mu_n, u_n, v_n)$  be as above. Then the following conclusions hold:*

- (i)  $\lim_{n \rightarrow \infty} \|u_n\|_\infty / |\mu_n| = 1/d$ ,  $\lim_{n \rightarrow \infty} \|v_n\|_\infty / |\mu_n| = 0$ ;
- (ii)  $u_n / |\mu_n| \rightarrow 0$  and  $v_n \rightarrow 0$  uniformly on any compact subset of  $\overline{\Omega} \setminus \overline{\Omega_0}$ ;
- (iii)  $\underline{\lim}_{n \rightarrow \infty} \|u_n\|_{L^1(\Omega)} / |\mu_n| > 0$ ,  $\overline{\lim}_{n \rightarrow \infty} \|v_n\|_{L^1(\Omega)} < \infty$ , and when  $\lambda > \lambda_1^D(\Omega_0)$ ,  $\underline{\lim}_{n \rightarrow \infty} \|v_n\|_{L^1(\Omega)} > 0$ ;

(iv)  $u_n/\|u_n\|_\infty \rightarrow \hat{u}$  weakly in  $H_0^1(\Omega)$ ,  $v_n$  weak\* converges in  $C(\Omega)^*$  to  $(\lambda/c)\chi_{\{\hat{u}=1\}}$ , where  $\hat{u} = 0$  a.e. in  $\Omega \setminus \Omega_0$  and  $\hat{u}|_{\Omega_0}$  is the unique positive solution of

$$-\Delta u = \lambda\chi_{\{u<1\}}u, \quad u|_{\partial\Omega_0} = 0, \quad \|u\|_\infty = 1. \quad (2.17)$$

We refer to [DD2, DD3] for the proof of this theorem.

*Remark 2.8.* (i) As  $\int_\Omega u dx$  and  $\int_\Omega v dx$  represent the total population of  $u$  and  $v$ , respectively, the conclusions in part (i) and part (iii) of Theorem 2.7 imply that, as  $\mu \rightarrow -\infty$ , the total population of  $u$  blows up at the rate of  $|\mu|$ , while the total population of  $v$  stays bounded. Moreover, when  $\lambda > \lambda_1^D(\Omega_0)$ , the total population of  $v$  is bounded from below by a positive constant independent of  $\mu$ .

(ii) Note that (2.17) is a kind of free boundary problem. It was proved in [DD3] that this problem has no positive solution when  $\lambda < \lambda_1^D(\Omega_0)$ , and it has a unique positive solution when  $\lambda \geq \lambda_1^D(\Omega_0)$ . Moreover, if  $\lambda > \lambda_1^D(\Omega_0)$ , it is easily seen from equation (2.17) that  $|\{\hat{u} = 1\}| > 0$  in part (iv) of Theorem 2.7; hence  $\hat{u}$  has a ‘‘flat core’’. If  $\lambda = \lambda_1^D(\Omega_0)$ , then the flat core has measure zero and  $\hat{u}$  is the first normalized eigenfunction on  $\Omega_0$ .

(iii) If  $\{\|v_n\|_{L^q}\}$  is bounded for some  $q > 1$ , then it is easy to show that  $v_n \rightarrow 0$  uniformly on any compact subset of the set  $\{\hat{u} < 1\}$ . However, we were unable to determine whether  $\{\|v_n\|_{L^q}\}$  is always bounded for some  $q > 1$ .

### 3 The Holling type II model

As mentioned in Section 1, it is generally believed that a Holling type II functional response is more reasonable than the unbounded functional response used in the Lotka-Volterra model. In this section we will examine a Holling type II diffusive predator-prey model with Neumann boundary conditions. We will see that in both the homogeneous case and the heterogeneous case, the Holling type II model exhibits much richer dynamics than the Lotka-Volterra model. In particular, we will reveal some fundamental differences caused by the spatial heterogeneity of the environment. Moreover, we will see that a similar degeneracy to that for the Lotka-Volterra model will result in very different effects for the Holling type II model. Furthermore, we will investigate the impact of a protection zone for the prey species on this model, and reveal some interesting results and problems.

#### 3.1 The homogeneous case

In a homogeneous environment with no-flux boundary conditions, a Holling type II diffusive model has the form

$$\begin{cases} u_t - d_1\Delta u = \lambda u - au^2 - \frac{buv}{1+mu}, & x \in \Omega, t > 0, \\ v_t - d_2\Delta v = \mu v - dv^2 + \frac{cuv}{1+mu}, & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases} \quad (3.1)$$

When  $m = 0$ , (3.1) reduces to (2.1). In fact, it follows from the Lyapunov functional analysis in [dMR] that the dynamics of (3.1) is essentially the same as that of (2.1) (with Neumann boundary conditions) when  $0 < m < a/\lambda$ ; namely,  $(\lambda/a, 0)$  is globally attractive when  $\mu \leq -c\lambda/(a + m\lambda)$ , the unique constant positive steady-state is globally attractive when  $-c\lambda/(a + m\lambda) < \mu < \lambda d/b$ , and  $(0, \mu/d)$  is globally attractive when  $\mu \geq \lambda d/b$ . Therefore, in such a case, the diffusive model has the same dynamical behavior as the ODE model. When  $m$  is increased, multiple constant positive steady-states can arise and periodic solutions may occur through Hopf bifurcation. We refer to [Hz] for an analysis of Hopf bifurcation for the ODE model. The constant steady-states are described in the following results (which is essentially results in [DL3] Section 2):

**Theorem 3.1.** *Suppose that  $d_1, d_2, a, b, c, d, \lambda, m > 0$  are fixed and  $\mu \in \mathbf{R}$ . Then the following hold:*

1. *The constant steady state solutions of (3.1) consist of  $(0, 0)$ ,  $(\lambda/a, 0)$ ,  $(0, \mu/d)$  and a branch of coexistence states  $(\mu(u), u, v(u))$  given by*

$$\mu(u) = \frac{d}{b}(\lambda - au)(1 + mu) - \frac{cu}{1 + mu}, \quad v(u) = \frac{(\lambda - au)(1 + mu)}{b}, \quad (3.2)$$

where  $0 < u < \lambda/a$  (see Figure 2); the bifurcation point along  $\Gamma_u = \{(\lambda/a, 0) : \mu \in \mathbf{R}\}$  is  $\mu^0 = -c\lambda/(1 + m\lambda)$ , and the bifurcation point along  $\Gamma_v = \{(0, \mu/d) : \mu \geq 0\}$  is  $\mu_0 = \lambda d/b$ .

2. *Define*

$$q = \frac{bc}{ad}, \quad m_2 = \frac{a}{\lambda}(q + 1), \quad m_1 = \begin{cases} m_2 & \text{if } q \leq 1; \\ \frac{a}{\lambda}(3q^{1/3} - 1) & \text{if } q > 1. \end{cases} \quad (3.3)$$

Let

$$\bar{\mu}_* = \min_{u \in [0, \lambda/a]} \mu(u), \quad \bar{\mu}^* = \max_{u \in [0, \lambda/a]} \mu(u). \quad (3.4)$$

Then for all  $m \geq 0$ ,  $\bar{\mu}_* = \mu^0$ ; when  $0 \leq m \leq m_2$ ,  $\bar{\mu}^* = \mu_0$ , and when  $m > m_2$ ,  $\bar{\mu}^* > \mu_0$ . Moreover when  $0 \leq m \leq m_1$ ,  $\mu(u)$  is strictly decreasing in  $(0, \lambda/a)$ ; when  $m_1 < m < m_2$ ,  $\mu(u)$  has exactly one local minimum and one local maximum point in  $(0, \lambda/a)$ ; and when  $m \geq m_2$ ,  $\mu(u)$  has exactly one local maximum point in  $(0, \lambda/a)$  (see Figure 2 left.)

3. *For all  $m \geq 0$ , when  $\mu \leq \bar{\mu}_*$ , there is no any other non-negative steady state solutions, and  $(\lambda/a, 0)$  is globally asymptotically stable. If in addition,  $0 \leq m \leq a/\lambda$ , then  $(0, \mu/d)$  is globally asymptotically stable when  $\mu > \bar{\mu}^*$ , and the unique positive steady state is globally asymptotically stable when  $\bar{\mu}_* < \mu < \bar{\mu}^*$ .*

4.  $\bar{\mu}^* = \frac{\lambda^2 dm}{4a^2 b} + o(m)$  as  $m \rightarrow \infty$ .

The existence of space dependent positive steady-state solutions was considered by Du and Lou [DL3] when  $m$  is sufficiently large, and they proved the following results (see Theorems 1.1, 1.2 and Corollary 4.6):

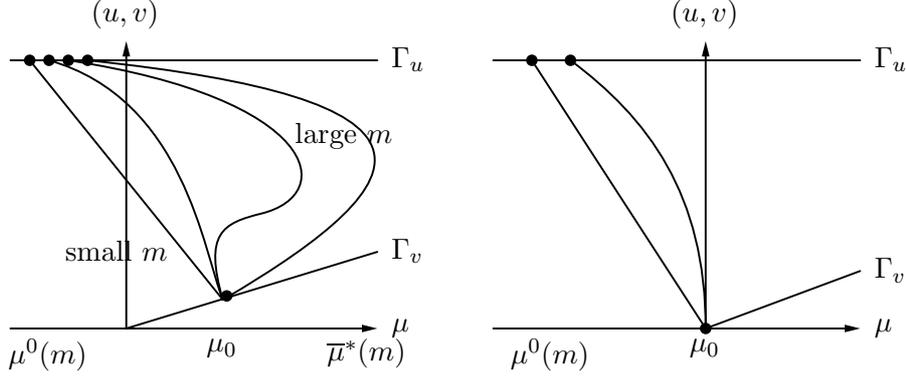


Figure 2: Bifurcation diagrams of constant non-negative steady state solutions of (3.1).  $\Gamma_u = \{(\lambda/a, 0) : \mu \in \mathbf{R}\}$ ;  $\Gamma_v = \{(0, \mu/d) : \mu \geq 0\}$ . The branch  $\Gamma$  connecting  $\Gamma_u$  and  $\Gamma_v$  consists of coexistence states. (left):  $d > 0$ , with four different values of  $m$  (0, small positive, intermediate, large), the corresponding coexistence curves move from left to right when these values are taken by  $m$  successively; (right):  $d = 0$ , with  $m = 0$  and  $m > 0$  respectively.

**Theorem 3.2.** *Suppose that  $d_1, d_2, a, b, c, d, \lambda > 0$  are fixed,  $\mu \in \mathbf{R}$ . Then there exists a large  $M > 0$  such that for  $m \geq M$ , the following hold:*

1. *If  $\mu < \mu_0 \equiv \lambda d/b$  or  $\mu > \bar{\mu}^*$ , then (3.1) has no non-constant steady state solutions.*
2. *If  $\mu \in (\mu_0 + \varepsilon_0, \bar{\mu}^* - \varepsilon_0)$ , and the equation*

$$-\Delta w + w \left( \lambda - \frac{b}{1/\mu + w} \right) = 0, \quad x \in \Omega, \quad \partial_\nu w = 0, \quad x \in \partial\Omega, \quad (3.5)$$

*has a non-degenerate solution  $w$ , then (3.1) has a non-constant positive solution  $(u, v)$ .*

Except for some special cases, the stability of the constant and non-constant positive steady state solutions of (3.1) are not known. The secondary bifurcations (including Turing and Hopf type bifurcations) from the branch of constant steady state solutions seem to be complicated, and further investigation is needed.

In Theorems 3.1 and 3.2, we have assumed that  $d > 0$ . An ecologically important case is  $d = 0$  and  $\mu < 0$  (so the predator cannot survive without the prey  $u$ ):

$$\begin{cases} u_t - d_1 \Delta u = \lambda u - au^2 - \frac{buv}{1+mu}, & x \in \Omega, t > 0, \\ v_t - d_2 \Delta v = \mu v + \frac{cuv}{1+mu}, & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases} \quad (3.6)$$

In (3.6), if  $\mu > 0$ , then it is clear that the predator will have an exponential growth and wipe out the prey population, thus the only interesting case is when  $\mu < 0$ . When  $\mu \leq \mu^0 \equiv -c\lambda/(a+m\lambda)$ , the steady state  $(\lambda/a, 0)$  is globally asymptotically stable. When

$\mu \in (\mu^0, 0)$ , (3.6) has a unique positive constant steady state solution for any positive  $m > 0$  (see Figure 2 right). Thus bistability for the ODE system never happens. However it is known that for a certain range of  $m$  and  $\mu$ , the unique positive constant steady state is not stable in the ODE model, and there exists a stable limit cycle. Numerical experiments on the diffusive model (3.6) have shown that various complicated spatiotemporal patterns can be generated in some parameter ranges (see [MPT] for a survey in that direction), but no rigorous treatments are available yet.

Finally we mention that the Dirichlet counterpart of (3.1) has been studied in [BB2, CEL, DL1, DL2]. Similar bifurcation diagrams for small  $m$  were obtained in [BB2, CEL], and the multiplicity and exact multiplicity of the steady state solutions when  $m$  is large were studied in [DL1, DL2]. In particular an exact  $S$ -shaped bifurcation diagram with large  $m$  (and under some conditions on the other parameters) was shown in [DL2].

### 3.2 The heterogeneous case

In heterogeneous environment, the diffusive predator-prey system becomes:

$$\begin{cases} u_t - \operatorname{div}(d_1(x)\nabla u) = \lambda(x)u - a(x)u^2 - \frac{b(x)uv}{1+m(x)u}, & x \in \Omega, t > 0, \\ v_t - \operatorname{div}(d_2(x)\nabla v) = \mu(x)v - d(x)v^2 + \frac{c(x)uv}{1+m(x)u}, & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases} \quad (3.7)$$

To focus our interest, again we only consider a more special model with all parameter functions in (3.7) being constant except  $a(x)$ . Moreover, for the convenience of notations, we assume that the diffusion constants  $d_1 = d_2 = 1$  and  $d \equiv 1$ :

$$\begin{cases} u_t - \Delta u = \lambda u - a(x)u^2 - \frac{buv}{1+mu}, & x \in \Omega, t > 0, \\ v_t - \Delta v = \mu v - v^2 + \frac{cuv}{1+mu}, & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in \Omega, \end{cases} \quad (3.8)$$

and for the equation of steady state solutions, now we have

$$\begin{cases} -\Delta u = \lambda u - a(x)u^2 - \frac{buv}{1+mu}, & x \in \Omega, \\ -\Delta v = \mu v - v^2 + \frac{cuv}{1+mu}, & x \in \Omega, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega. \end{cases} \quad (3.9)$$

As in subsection 2.1, we assume that the function  $a(x)$  is a nonnegative continuous function on  $\overline{\Omega}$ , and there exists a subdomain  $\Omega_0$  such that  $\overline{\Omega_0} \subset \Omega$ , and

$$a(x) \equiv 0 \quad \forall x \in \overline{\Omega_0}, \quad \text{and} \quad a(x) > 0 \quad \forall x \in \overline{\Omega} \setminus \overline{\Omega_0}. \quad (3.10)$$

Similar to the classical Lotka-Volterra case considered in subsection 2.1, the eigenvalue  $\lambda_1^D(\Omega_0)$  plays an important role in our analysis, and our results will be fundamentally different in the following two cases:

$$(a) \text{ weak prey growth: } 0 < \lambda < \lambda_1^D(\Omega_0), \quad (b) \text{ strong prey growth: } \lambda > \lambda_1^D(\Omega_0). \quad (3.11)$$

As in the Dirichlet case, it is well-known (see [Ou]) that the boundary value problem

$$-\Delta u = \lambda u - a(x)u^2, \quad x \in \Omega, \quad \partial_\nu u = 0, \quad x \in \partial\Omega, \quad (3.12)$$

has a unique positive solution  $u_\lambda(x)$  when  $0 < \lambda < \lambda_1^D(\Omega_0)$ , and it has no positive solution when  $\lambda \geq \lambda_1^D(\Omega_0)$ . Moreover,  $u_\lambda \rightarrow 0$  uniformly in  $\Omega$  as  $\lambda \rightarrow 0^+$ , and  $u_\lambda \rightarrow \infty$  uniformly on  $\overline{\Omega_0}$  as  $\lambda \rightarrow [\lambda_1^D(\Omega_0)]^-$ , and  $u_\lambda \rightarrow \underline{U}^\lambda$  uniformly on any compact subset of  $\overline{\Omega} \setminus \overline{\Omega_0}$  as  $\lambda \rightarrow [\lambda_1^D(\Omega_0)]^-$ , where  $\underline{U}^\lambda$  is the minimal positive solution of the boundary blow-up problem (see [DHu]):

$$-\Delta u = \lambda u - a(x)u^2, \quad x \in \Omega \setminus \overline{\Omega_0}, \quad \partial_\nu u = 0, \quad x \in \partial\Omega, \quad u = \infty, \quad x \in \partial\Omega_0. \quad (3.13)$$

It is shown in [DHu] that for any  $\lambda \in \mathbf{R}$ , (3.13) has a minimal positive solution  $\underline{U}^\lambda$  and a maximal positive solution  $\overline{U}^\lambda$ . Problems (3.12) and (3.13) will play essential roles in our analysis below.

### 3.2.1 Weak prey growth rate

We now consider the case that  $0 < \lambda < \lambda_1^D(\Omega_0)$ . In contrast to the homogeneous case, the set of steady-state solutions of (3.9) are now much more difficult to analyze, and the dynamical behavior of (3.8) is almost out of reach. We will use a bifurcation approach to study the steady-state solutions, and more importantly, we will make use of an auxiliary single equation (see (3.17) below) to obtain some in-depth results for the global bifurcation branch of the positive solutions of (3.9), which will enable us to obtain some partial results on the dynamical behavior of (3.8). Since a single reaction-diffusion equation enjoys the monotonicity property, we are able to obtain rather detailed understanding of our auxiliary equation, which in turn helps us to understand our diffusive predator-prey model. So we are indirectly using the monotonicity property to study a system which lacks such a property.

Under our assumptions for  $\lambda$ , for any  $\mu > 0$ , (3.9) has two semi-trivial solutions:  $(u_\lambda, 0)$  and  $(0, \mu)$ . They form two smooth curves in the  $(\mu, u, v)$ -space:

$$\Gamma_u = \{(\mu, u_\lambda, 0) : -\infty < \mu < \infty\}, \quad \Gamma_v = \{(\mu, 0, \mu) : 0 < \mu < \infty\}. \quad (3.14)$$

Despite the different boundary conditions, the bifurcation analysis for the Dirichlet boundary value problem can be carried over to (3.9). More precisely, along  $\Gamma_u$ , there is a bifurcation point  $\mu^0 = \lambda_1^N(-cp(u_\lambda))$  such that a smooth curve  $\Gamma'_1$  of positive solutions to (3.9) bifurcates from  $\Gamma_u$  at  $(\mu, u, v) = (\mu^0, u_\lambda, 0)$ . Similarly, there is another bifurcation point  $\mu_0 = \lambda/b$  such that a smooth curve of positive solutions  $\Gamma'_2$  to (3.9) bifurcates from  $\Gamma_v$  at  $(\mu, u, v) = (\mu_0, 0, \mu_0)$ . Moreover one can show that (3.9) has only the trivial or semi-trivial solutions when  $|\mu|$  is sufficiently large. Hence  $\Gamma'_1$  and  $\Gamma'_2$  are connected to each other, and we denote by  $\Gamma$  the maximal connected component of the set of positive steady state solutions which contains  $\Gamma'_1$  and  $\Gamma'_2$ . The direction of bifurcation of  $\Gamma$  at  $\mu = \mu_0$  can be determined by  $m$ . In summary we have the following rough global bifurcation picture (see subsection 3.1 of [DS1] for details):

**Theorem 3.3.** *When  $0 < \lambda < \lambda_1^D(\Omega_0)$ , there exists a continuum  $\Gamma$  of positive solutions of (3.9) satisfying*

$$\text{proj}_\mu \Gamma = (\bar{\mu}_*, \bar{\mu}^*] \text{ or } (\bar{\mu}_*, \bar{\mu}^*), \quad (3.15)$$

where

$$\bar{\mu}_* = \lambda_1^N(-cp(u_\lambda)), \quad \lambda/b \leq \bar{\mu}^* \leq \lambda b^{-1}(1 + m\|u_\lambda\|_\infty).$$

Moreover,  $\Gamma$  connects the branches  $\Gamma_u$  and  $\Gamma_v$  at  $(\mu, u, v) = (\mu^0, u_\lambda, 0)$  and  $(\mu, u, v) = (\mu_0, 0, \mu_0)$  respectively. Furthermore, the bifurcation at  $\mu = \mu^0$  is always supercritical, the bifurcation at  $\mu_0$  is supercritical if  $m > m_0$  and it is subcritical if  $0 \leq m < m_0$ , where  $m_0$  is given by

$$m_0 = \lambda^{-1} [\bar{a} + bc], \quad \text{where } \bar{a} = \frac{1}{|\Omega|} \int_\Omega a(x) dx. \quad (3.16)$$

While Theorem 3.3 provides useful information on the set of positive steady states, a more detailed description can be obtained by making use of the following auxiliary equation:

$$-\Delta u = \lambda u - a(x)u^2 - b\mu \frac{u}{1 + mu}, \quad x \in \Omega, \quad \partial_\nu u = 0, \quad x \in \partial\Omega. \quad (3.17)$$

To see the relevance of (3.17) to (3.9), let us observe that if  $(u, v)$  is a positive solution of (3.9), then a simple comparison argument shows  $\mu < v < \mu + c/m$ . Therefore  $u$  is a sub-solution to (3.17), and it is a super-solution to (3.17) with  $\mu$  replaced by  $\mu + c/m$ .

An in-depth study of the solution set of (3.17) will enable us to partially overcome the lack of comparison principle for the full system (3.8). By making extensive use of the monotonicity property of (3.17) and a global bifurcation argument, we have the following result:

**Proposition 3.4.** *Suppose that  $0 < \lambda < \lambda_1^D(\Omega_0)$ , and  $b, m > 0$  are fixed. Then  $\mu = \mu_0 \equiv \lambda/b$  is a bifurcation point for (3.17) such that a global unbounded continuum  $\Sigma$  of positive solutions of (3.17) emanates from  $(\mu, u) = (\mu_0, 0)$ , and*

$$\text{proj}_\mu \Sigma = (-\infty, \hat{\mu}^*] \text{ or } (-\infty, \hat{\mu}^*), \quad (3.18)$$

where  $\hat{\mu}^* = \sup\{\mu > 0 : (3.17) \text{ has a positive solution}\} \geq \mu_0$ . Moreover  $\Sigma$  satisfies the following:

1. Near  $(\mu, u) = (\mu_0, 0)$ ,  $\Sigma$  is a curve.
2. When  $\mu \leq 0$ , (3.17) has a unique positive solution  $\bar{U}_\mu(x)$ , and  $\{(\mu, \bar{U}_\mu) : \mu \leq 0\}$  is a smooth curve.
3. For  $\mu \in (-\infty, \hat{\mu}^*)$ , (3.17) has a maximal positive solution  $\bar{U}_\mu(x)$ ,  $\bar{U}_\mu$  is strictly decreasing with respect to  $\mu$ .
4. For  $\mu \in (-\infty, \lambda/b)$ , (3.17) has a minimal positive solution  $\underline{U}_\mu(x)$ ,  $\underline{U}_\mu(x) \equiv \bar{U}_\mu(x)$  when  $\mu \leq 0$ ,  $\underline{U}_\mu$  is strictly decreasing with respect to  $\mu$ .
5. If  $\hat{\mu}^* > \mu_0$ , then (3.17) has a maximal positive solution for  $\mu = \hat{\mu}^*$ , and has at least two positive solutions for  $\mu \in (\mu_0, \hat{\mu}^*)$ .

6. If  $\hat{\mu}^* > \mu_0$  and  $0 < m < m_0$ , then there exists  $\hat{\mu}_* \in (0, \mu_0)$  such that (3.17) has at least three positive solutions for  $\mu \in (\hat{\mu}_*, \mu_0)$  and  $\underline{U}_\mu(x) < \overline{U}_\mu(x)$  for  $\mu \in [\hat{\mu}_*, \mu_0)$ . Moreover,  $\lim_{\mu \rightarrow (\mu_0)^-} \underline{U}_\mu = 0$  uniformly for  $x \in \overline{\Omega}$ .

All these solutions mentioned above can be chosen from the unbounded continuum  $\Sigma$ .

The proof of Proposition 3.4 can be found in [DS1]. Estimates of  $\hat{\mu}^*$  in terms of the parameter  $m$  can also be deduced. Indeed, let  $M_a = \max_{x \in \overline{\Omega}} a(x)$  and  $\bar{a} = |\Omega|^{-1} \int_{\Omega} a(x) dx$ . Then

1.  $\hat{\mu}^*(m) \geq \frac{\lambda M_a + m \lambda^2}{4bM_a}$ , and in particular,  $\lim_{m \rightarrow \infty} \hat{\mu}^*(m) = \infty$ .
2.  $\hat{\mu}^*(m) > \lambda/b$  if  $m > 3M_a/\lambda$ ;  $\hat{\mu}_*(m) < \lambda/b$  if  $m < \bar{a}/\lambda$ .

We remark that  $\hat{\mu}^*(m) > \lambda/b > \hat{\mu}_*(m)$  is only possible for certain patterned  $a(x)$  (see [DS1] for a concrete example). With that possibility, Proposition 3.4 suggests three possible minimal bifurcation diagrams for the set of positive steady states of (3.17) as in Figure 3.

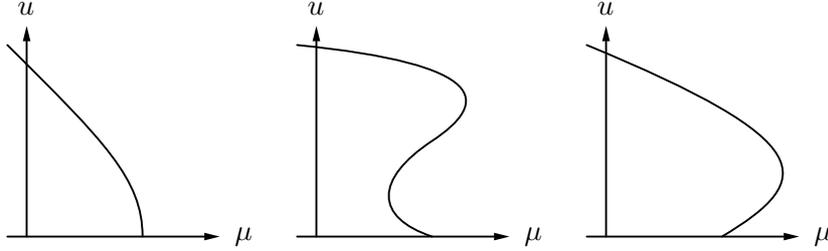


Figure 3: Possible bifurcation diagrams for (3.17)

The global bifurcation branch  $\Sigma$  of (3.17) somehow provides an estimate for the global bifurcation branch  $\Gamma$  of (3.9). A loose relationship between  $\Sigma$  and  $\Gamma$  can be rigorously established through some topological arguments, and we have the following results (see [DS1] for the proof):

**Theorem 3.5.** Suppose that  $0 < \lambda < \lambda_1^D(\Omega_0)$ , and  $b, c, m > 0$  are fixed. Let  $\hat{\mu}^*$  and  $\hat{\mu}_*$  be defined as in Proposition 3.4. Then the following hold:

1. Define

$$\mu^* = \sup\{\mu > 0 : (3.9) \text{ has a positive solution}\}, \quad (3.19)$$

and

$$\mu_* = \inf\{\mu > 0 : (3.9) \text{ has a positive solution } (u, v), \text{ and } u \not\geq \overline{U}_{\hat{\mu}^*}\}. \quad (3.20)$$

Then  $\hat{\mu}^* - c/m \leq \mu^* \leq \hat{\mu}^*$ , and  $\hat{\mu}_* \leq \mu_* \leq \hat{\mu}_* + c/m$ .

2. If  $\lambda_1^N(-cp(u_\lambda)) < \hat{\mu}^* - c/m$ , then for  $\mu \in (\lambda_1^N(-cp(u_\lambda)), \hat{\mu}^* - c/m]$ , (3.9) has a positive solution  $(u_\mu^1, v_\mu^1)$  satisfying

$$\begin{aligned} \min\{\overline{U}_\mu(x), \overline{U}_0(x)\} &> u_\mu^1(x) > \overline{U}_{\mu+c/m}(x), \quad x \in \Omega, \\ \mu + \frac{c}{m} &> v_\mu^1(x) > \max\{\mu, 0\}, \quad x \in \Omega. \end{aligned} \quad (3.21)$$

3. If  $\hat{\mu}_* + c/m < \mu_0$ , then for  $\mu \in [\hat{\mu}_* + c/m, \mu_0)$ , (3.9) has a positive solution  $(u_\mu^2, v_\mu^2)$  satisfying

$$\begin{aligned} \underline{U}_\mu(x) &> u_\mu^2(x) > \max\{\underline{U}_{\mu+c/m}(x), 0\}, \quad x \in \Omega, \\ \mu + \frac{c}{m} &> v_\mu^2(x) > \mu, \quad x \in \Omega. \end{aligned} \quad (3.22)$$

4. If  $\hat{\mu}^* > \mu_0 + c/m$ , then (3.9) has at least two positive solutions for  $\mu_0 < \mu \leq \hat{\mu}^* - c/m$ .

5. If  $\hat{\mu}^* > \mu_0 + c/m$  and  $\hat{\mu}_* < \mu_0 - c/m$ , then (3.9) has at least three positive solutions for  $\hat{\mu}_* + c/m < \mu < \mu_0$ .

All these solutions above can be chosen from the continuum  $\Gamma$ .

(Notice that  $\underline{U}_{\mu+c/m}$  is not always defined in Part 3. In that case we assume  $\underline{U}_{\mu+c/m} = 0$ . Similarly, if  $\overline{U}_{\hat{\mu}^*}$  is not defined, we understand that it equals 0.)

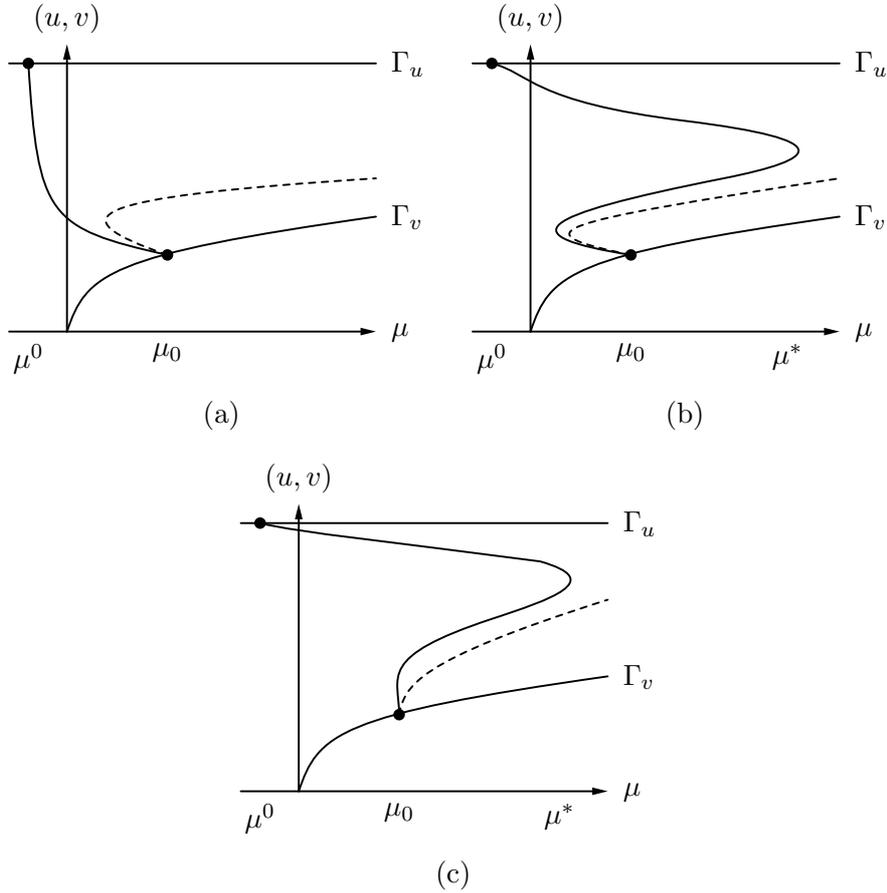


Figure 4: Bifurcation diagram of positive steady state solutions of (3.9); solid line:  $\lambda < \lambda_1^D(\Omega_0)$ , dashed line:  $\lambda > \lambda_1^D(\Omega_0)$ . (a):  $m$  is small; (b):  $m$  small but special  $a(x)$ ; (c):  $m$  is large.

In Figure 4, three possible minimal bifurcation diagrams for (3.9) are shown, and the solid curves represent the bifurcation branches in the case  $0 < \lambda < \lambda_1^D(\Omega_0)$  considered in Theorem 3.5. The diagrams in (a) and (c) are similar to those of homogeneous cases considered in subsection 3.1. The diagram in (b) shows a reversed S-shaped branch, which can happen for all small  $m$ , all  $b, c > 0$  and some particularly designed  $a(x)$ . In the homogeneous case, such reversed S-shaped curve happens when  $m$  takes intermediate values.

With the above results for the steady state solutions, and by making use of the corresponding parabolic problem of (3.17), we can prove the following partial classification of the dynamics of (3.8) (see [DS1]):

**Theorem 3.6.** *Suppose that  $0 < \lambda < \lambda_1^D(\Omega_0)$ , and  $b, c, m > 0$  are fixed. Then all solutions  $(u(x, t), v(x, t))$  of (3.8) are globally bounded, and  $v(x, t)$  satisfies*

$$\max\{\mu, 0\} \leq \underline{\lim}_{t \rightarrow \infty} v(x, t) \leq \overline{\lim}_{t \rightarrow \infty} v(x, t) \leq \max\{\mu + \frac{c}{m}, 0\}. \quad (3.23)$$

Moreover, the following hold:

1. If  $\mu < \mu^0 \equiv \lambda_1^N(-cp(u_\lambda))$ , then  $(u_\lambda, 0)$  is globally asymptotically stable.
2. If  $\mu > \hat{\mu}^*$ , then  $(0, \mu)$  is globally asymptotically stable.
3. If  $\lambda_1^N(-cp(u_\lambda)) < \mu < \hat{\mu}^* - c/m$ , and  $u_0(x) \geq \overline{U}_{\hat{\mu}^*}(x)$ , then

$$V_{\mu+c/m,1}(x) \leq \underline{\lim}_{t \rightarrow \infty} u(x, t) \leq \overline{\lim}_{t \rightarrow \infty} u(x, t) \leq \min\{\overline{U}_\mu(x), \overline{U}_0(x)\}, \quad (3.24)$$

where  $V_{\mu,1}$  is unique positive solution of

$$-\Delta u = \left( \lambda - \frac{b\mu}{1+mU} \right) u - a(x)u^2, \quad x \in \Omega, \quad \partial_\nu u = 0, \quad x \in \partial\Omega, \quad (3.25)$$

with  $U = \overline{U}_{\hat{\mu}^*}$ .

4. Suppose that  $\hat{\mu}_* < \mu_0$ , then there exists  $\hat{\mu}^\sharp \in (\lambda/b, \hat{\mu}^*)$  such that  $\lambda = \lambda_1^N(b\hat{\mu}^\sharp/(1+m\underline{U}_{\hat{\mu}_*}))$ , and for  $\hat{\mu}_* + c/m \leq \mu < \hat{\mu}^\sharp$ , if  $u_0(x) \leq \underline{U}_{\hat{\mu}_*}(x)$ , then

$$\max\{\underline{U}_{\mu+c/m}(x), 0\} \leq \underline{\lim}_{t \rightarrow \infty} u(x, t) \leq \overline{\lim}_{t \rightarrow \infty} u(x, t) \leq V_{\mu,2}(x), \quad (3.26)$$

where  $V_{\mu,2}$  is the unique positive solution of (3.25) with  $U = \underline{U}_{\hat{\mu}_*}$ , and for  $\mu \geq \hat{\mu}^\sharp$ , if  $u_0(x) \leq \underline{U}_{\hat{\mu}_*}(x)$ , then  $\lim_{t \rightarrow \infty} u(x, t) = 0$  and  $\lim_{t \rightarrow \infty} v(x, t) = \mu$  uniformly for  $x \in \overline{\Omega}$ .

The above results reveal that when the prey has a weak growth rate  $\lambda < \lambda_1^D(\Omega_0)$ , both populations stay bounded, and the bifurcation diagram and the dynamics are similar to the homogenous case. In biological terms, the above mathematical results imply that in the weak prey growth rate case, the dynamics of (3.8) has three possibilities according to the predator growth rate  $\mu$ :

1. (Weak predator growth rate) When  $\mu < \lambda_1^N(-cp(u_\lambda)) < 0$ , the predator will become extinct, while the prey will reach its carrying capacity. Thus we have unconditional persistence for the prey and unconditional extinction for the predator.

2. (Strong predator growth rate) This is when  $\mu > \hat{\mu}^*$ . Opposite to the previous case, the prey will become extinct while the predator will persist unconditionally for any initial population distribution.
3. (Intermediate predator growth rate) If  $\hat{\mu}_* + c/m < \mu < \hat{\mu}^* - c/m$  with all these constants well defined and well ordered, then a bistable phenomenon appears, where two attracting regions exist, one is defined in (3.24) for  $u$  and (3.23) for  $v$ , and the other is defined in (3.26) for  $u$  and (3.23) for  $v$ . The former one contains a coexistence steady state, but it is unclear whether that coexistence steady state is the global attractor; the latter attracting region contains a coexistence steady state with a smaller  $u$  component when  $\hat{\mu}_* + c/m < \mu < \lambda/b$ , but that coexistence steady state becomes  $(0, \mu)$  (prey extinction and predator persistence) when  $\mu > \hat{\mu}^\#$ . Though the predator population will settle in between  $\mu$  and  $\mu + c/m$ , but the fate of the prey will depend on its initial population. We notice that it is possible that  $\hat{\mu}_* = \hat{\mu}^* = \lambda/b$ , then a coexistence steady state exists for  $\lambda_1^N(-cp(u_\lambda)) < \mu < \lambda/b$ , and this is a case that the system exhibits permanence. However, bistability can happen for certain ranges of the parameters if  $a(x)$  is chosen properly.

Unfortunately, a full description of the dynamics of (3.8) is still a formidable job.

### 3.2.2 Strong prey growth rate

Now we turn to the case of  $\lambda > \lambda_1^D(\Omega_0)$ . We will only describe the results; their proofs can be found in [DS1]. Compared to the weak prey growth case, there is only one semi-trivial branch  $\Gamma_v$ , and there is still a bifurcation point  $\mu_0 = \lambda/b$  such that a smooth curve of positive solutions  $\Gamma'_2$  (contained in a global branch  $\Gamma$ ) to (3.9) bifurcates from  $\Gamma_v$  at  $(\mu, u, v) = (\mu_0, 0, \mu_0)$ . Since this is the only possible bifurcation point for positive solutions,  $\Gamma$  is unbounded in the space of  $(\mu, u, v)$ . Similar to the situation considered in subsection 2.2, we can prove the following *a priori* bound for the steady states:

**Proposition 3.7.** *Let  $\lambda > \lambda_1^D(\Omega_0)$  be fixed and  $\mu_n \leq M$ . Then there exists a positive constant  $C$  independent of  $n$  such that any positive solution  $(u_n, v_n)$  of (3.9) (with  $\mu = \mu_n$ ) satisfies*

$$\|u_n\|_\infty + \|v_n\|_\infty \leq C. \quad (3.27)$$

Combining the bifurcation analysis and the above *a priori* estimate, we have

**Theorem 3.8.** *Suppose that  $\lambda > \lambda_1^D(\Omega_0)$  is fixed. Then there exists a continuum  $\Gamma$  of positive solutions of (3.9) such that*

$$\text{proj}_\mu \Gamma = [\mu_*, \infty) \text{ or } (\mu_*, \infty), \quad -\frac{c}{m} < \mu_* \leq \frac{\lambda}{b} \quad (3.28)$$

and satisfies the following:

1.  $\Gamma$  bifurcates from  $(\mu, u, v) = (\lambda/b, 0, \lambda/b)$ , and the bifurcation there is supercritical if  $m > m_0$  and it is subcritical if  $0 \leq m < m_0$ , where  $m_0$  is defined by (3.16).
2. For any  $\mu > \mu_*$ , (3.9) has at least one positive solution.

3. If  $\mu_* < \lambda/b$ , then for  $\mu = \mu_*$ , (3.9) has a positive solution, and thus  $\text{proj}_\mu \Gamma = [\mu_*, \infty)$ .
4. All these solutions mentioned above can be chosen from the unbounded continuum  $\Gamma$ .

An illustration of the bifurcation diagrams can be seen in Figure 4 (dotted lines).

- Remark 3.9.* (i) From Theorem 3.8, one sees that a drastic change occurs when the prey growth rate  $\lambda$  increases across the threshold value  $\lambda_1^D(\Omega_0)$ . In the strong prey growth case, the system has a positive steady-state for all  $\mu > \mu_0$ ; in the weak prey growth case, the corresponding range of  $\mu$  is a bounded interval.
- (ii) This is also in sharp contrast to the  $m = 0$  case (the Lotka-Volterra model) described in Theorem 2.6, where positive steady-states exists if and only if  $\mu$  belongs to an interval of the form  $(-\infty, \tilde{\mu}_0)$ .
- (iii) Note that in the homogeneous case, we have seen that the dynamical behavior of (3.1) is similar for all  $m \in [0, a/\lambda]$ , but in the heterogeneous case, when  $\lambda > \lambda_1^D(\Omega_0)$ , a fundamental difference exists between the cases  $m = 0$  (Theorem 2.6) and  $m > 0$  (Theorem 3.8).

Next, we make use of the scalar equation (3.17) to obtain a more detailed description of the solutions of (3.8). It is clear that  $\mu = \lambda/b$  is a bifurcation point for (3.17) such that a global continuum  $\Sigma_0$  of positive solutions of (3.17) emanates from  $(\mu, u) = (\lambda/b, 0)$ , and

$$\text{proj}_\mu \Sigma_0 = [\mu_*^0, \infty) \text{ or } (\mu_*^0, \infty), \quad -\frac{c}{m} < \mu_*^0 \leq \frac{\lambda}{b}. \quad (3.29)$$

By making extensive use of the monotonicity property, one can show that  $\mu_*^0 = \inf\{\mu : (3.17) \text{ has a positive solution}\}$ . Moreover if  $\mu_*^0 < \lambda/b$ , then for  $\mu \in [\mu_*^0, \lambda/b)$ , (3.17) has a minimal positive solution  $\underline{U}_\mu$ , which is strictly decreasing with respect to  $\mu$ , and for  $\mu \in (\mu_*^0, \lambda/b)$ , (3.17) has at least two positive solutions.

By using  $\mu_*^0$  and  $\underline{U}_\mu$ , we are able to partially identify the following bitsable dynamics:

**Theorem 3.10.** *Suppose that  $\lambda > \lambda_1^D(\Omega_0)$ , and  $b, c, m > 0$  are fixed. Let  $(u(x, t), v(x, t))$  be the solution of (3.8). Then for any non-negative  $(u_0, v_0)$  with  $u_0, v_0 \not\equiv 0$  and any  $\mu \in \mathbf{R}$ ,  $v(x, t)$  satisfies*

$$\max\{\mu, 0\} \leq \underline{\lim}_{t \rightarrow \infty} v(x, t) \leq \overline{\lim}_{t \rightarrow \infty} v(x, t) \leq \max\{\mu + \frac{c}{m}, 0\}, \quad (3.30)$$

and the asymptotic behavior of  $u(x, t)$  is as follows:

1. (Blow-up) If  $\mu < \mu_*^0 - c/m$ , then  $u(x, t)$  satisfies

$$\begin{aligned} \lim_{t \rightarrow \infty} u(x, t) &= \infty \text{ uniformly on } \overline{\Omega_0}, \\ \overline{U}^\lambda(x) &\geq \overline{\lim}_{t \rightarrow \infty} u(x, t) \geq \underline{\lim}_{t \rightarrow \infty} u(x, t) \geq 0, \quad x \in \overline{\Omega} \setminus \overline{\Omega_0}. \end{aligned} \quad (3.31)$$

If in addition,  $\mu < -c/m$ , then  $\lim_{t \rightarrow \infty} v(x, t) = 0$  uniformly on  $\overline{\Omega}$ .

2. (Extinction) If  $\mu_*^0 + c/m < \lambda/b$ , and  $u_0(x) \leq \underline{U}_{\mu_*^0}(x)$ , then for  $\mu \in [\mu_*^0 + c/m, \lambda/b]$ ,

$$\underline{U}_{\mu+c/m}(x) \leq \underline{\lim}_{t \rightarrow \infty} u(x, t) \leq \overline{\lim}_{t \rightarrow \infty} u(x, t) \leq V_{\mu,5}(x), \quad (3.32)$$

where  $V_{\mu,5}$  is the solution of (3.25) with  $U = \underline{U}_{\mu^0}$ , and for  $\mu > \lambda/b$ ,

$$0 \leq \underline{\lim}_{t \rightarrow \infty} u(x, t) \leq \overline{\lim}_{t \rightarrow \infty} u(x, t) \leq \max\{V_{\mu,5}(x), 0\}. \quad (3.33)$$

Note that Part 2 of the above theorem demonstrates a bistable behavior for the dynamics of (3.8), since in that parameter range, the semitrivial steady-state  $(u_\lambda, 0)$  is asymptotically stable. It is then important to further identify the basins of attraction of the persistence and extinction behaviors. To this end, we describe in the following two criteria for the persistence (and blow-up) or extinction of  $u$ . The strategy is to first find suitable sub(sup)-solutions of (3.17), then construct suitable sub(sup)-solutions for the full system.

Suppose that  $U_{\mu_a}$  is a positive solution of (3.17) for  $\mu = \mu_a$ ; then one can show that there exists  $\mu_b < \mu_a$  such that  $U_{\mu_a}$  is a sub-solution of (3.17) for all  $\mu < \mu_b$ ; on the other hand, there exists  $\mu_c > \mu_a$  such that  $U_{\mu_a}$  is a super-solution of (3.17) for all  $\mu > \mu_c$ . To be more precise, we have the following results regarding the dynamics of the scalar equation

$$\begin{cases} w_t - \Delta w = \lambda w - a(x)w^2 - b\mu \frac{w}{1+m w}, & x \in \Omega, t > 0, \\ \partial_\nu w = 0, & x \in \partial\Omega, t > 0, \\ w(x, 0) = w_0(x) \geq 0, & x \in \Omega, \end{cases} \quad (3.34)$$

and the full system (3.8):

**Theorem 3.11.** *Suppose that  $\lambda > \lambda_1^D(\Omega_0)$ , and  $b, m > 0$  are fixed. Let  $w(x, t)$  be a solution of (3.34), and let  $(u(x, t), v(x, t))$  be a solution of (3.9). Then the following hold:*

1. (Blow-up) For any given  $\hat{\mu} > 0$  we define

$$C_{\hat{\mu}} = \sup\{\|u\|_\infty : u \text{ is a positive solution of (3.17) with } \mu \leq \hat{\mu}\} \quad (3.35)$$

(the supremum exists from Proposition 3.7). Let  $\mu_a > \hat{\mu}$  be such that

$$C_{\hat{\mu}} < (b\mu_a - \lambda)/(m\lambda)$$

and let  $U_{\mu_a}(x)$  be a positive solution of (3.17) with  $\mu = \mu_a$ . Then for  $\mu \leq \hat{\mu}$  and  $w_0(x) \geq U_{\mu_a}(x)$ , the solution  $w(x, t) \rightarrow \infty$  uniformly for  $x \in \overline{\Omega}_0$ , and  $\overline{\lim}_{t \rightarrow \infty} w(x, t) \leq \overline{U}^\lambda(x)$  for  $x \in \overline{\Omega} \setminus \overline{\Omega}_0$ ; for  $\mu < \hat{\mu} - c/m$  and  $u_0(x) \geq U_{\mu_a}(x)$ , (3.31) holds.

2. (Extinction) Let  $U_{\mu_a}(x)$  be a positive solution of (3.17) with  $\mu = \mu_a > 0$ . Define  $\tilde{\mu}^*$  to be the unique positive number such that  $\lambda = \lambda_1^N(b\tilde{\mu}^*/(1+mU_{\mu_a}))$ . Then for  $\mu > \tilde{\mu}^*$  and  $w_0(x) \leq U_{\mu_a}(x)$ ,  $\lim_{t \rightarrow \infty} w(x, t) = 0$  uniformly for  $x \in \overline{\Omega}$ ; and for  $\mu > \tilde{\mu}^*$ , if  $u_0(x) \leq U_{\mu_a}(x)$ ,  $\lim_{t \rightarrow \infty} u(x, t) = 0$  and  $\lim_{t \rightarrow \infty} v(x, t) = \mu$  uniformly for  $x \in \overline{\Omega}$ .

Theorem 3.11 provides a criterion in terms of a generic solution  $U_{\mu_a}$  of (3.17) for the persistence or extinction of  $u$ , but the profile of the steady state  $U_\mu$  is not known. For large  $\mu$ , we could determine the asymptotic behavior of  $U_\mu$ , and the following result was proved in [DS1].

**Proposition 3.12.** *Suppose that  $\lambda > \lambda_1^D(\Omega_0)$ , and  $b, m > 0$  are fixed. Let  $(\mu_n, u_n)$  be a sequence of positive solutions of (3.17) and  $\mu_n \rightarrow \infty$  as  $n \rightarrow \infty$ . Then subject to a subsequence,*

$$\lim_{n \rightarrow \infty} \mu_n \|u_n\|_\infty^{-1} = \sigma \in \left(0, \frac{m\lambda}{b}\right), \quad (3.36)$$

*and  $\sigma u_n / \mu_n \rightarrow \hat{u}$  weakly in  $H^1(\Omega)$  and strongly in  $L^p(\Omega_0)$  for any  $p > 1$ , where  $\hat{u}$  is a nonnegative function satisfying  $\hat{u}(x) = 0$  for  $x \in \Omega \setminus \overline{\Omega_0}$ , and  $\hat{u}|_{\Omega_0} \in H_0^1(\Omega_0)$  is a weak solution of the (free boundary) problem*

$$-\Delta u = \left(\lambda u - \frac{b\sigma}{m}\right) \chi_{\{u>0\}}, \quad x \in \Omega_0, \quad u(x) = 0, \quad x \in \partial\Omega_0, \quad \|u\|_\infty = 1. \quad (3.37)$$

We can now use the solution of the free boundary problem as a candidate for the sub-solution which induces blow-up:

**Proposition 3.13.** *Suppose that  $\lambda > \lambda_1^D(\Omega_0)$ , and  $b, m > 0$  are fixed. Suppose that  $U_0(x)$  is a nontrivial solution of*

$$-\Delta u = \left(\lambda_a u - \frac{b}{m}\right) \chi_{\{u>0\}}, \quad x \in \Omega_0, \quad u(x) = 0, \quad x \in \partial\Omega_0, \quad (3.38)$$

*where  $\lambda_1^D(\Omega_0) < \lambda_a < \lambda$ . We extend  $U_0$  by  $U_0(x) \equiv 0$  for  $x \in \overline{\Omega} \setminus \overline{\Omega_0}$ . Then there exists  $\sigma > 0$  such that for  $w_0(x) \geq \sigma U_0(x)$ , the solution of (3.34) satisfies  $w(x, t) \rightarrow \infty$  uniformly for  $x \in \overline{\Omega_0}$ , and  $\overline{\lim}_{t \rightarrow \infty} w(x, t) \leq \overline{U}^\lambda(x)$  for  $x \in \overline{\Omega} \setminus \overline{\Omega_0}$ ; and for  $u_0(x) \geq \sigma' U_0(x)$ , where  $\sigma' = \max\{\mu + c/m, C_{\mu+c/m}/\|U_0\|_\infty\}$ , (3.31) holds.*

For a general domain  $\Omega_0$ , the solution of the free boundary problem is not completely understood. However for a one dimensional domain, a complete solution to the free boundary problem (3.38) can be given. Indeed for  $\Omega_0 = (-\pi, \pi)$ , it can be shown (see [DS1]) that if  $1/4 < \lambda \leq 1$ , (3.38) has a unique solution

$$u(x) = \frac{b\sigma}{\lambda m} \left(1 - \frac{\cos(\sqrt{\lambda}x)}{\cos(\sqrt{\lambda}\pi)}\right),$$

where

$$\sigma = \frac{\lambda m}{b} \left(1 - \frac{1}{\cos(\sqrt{\lambda}\pi)}\right)^{-1};$$

if  $\lambda > 1$ , then the solutions are given by

$$u(x) = \sum_{i=1}^k \frac{\lambda m}{2b} \phi_\lambda(x_i + x), \quad 1 \leq k \leq [\sqrt{\lambda}],$$

where

$$\phi_\lambda(x) = \frac{b}{\lambda m} [\cos(\sqrt{\lambda}x) + 1], \quad x \in (-\pi/\sqrt{\lambda}, \pi/\sqrt{\lambda}).$$

and  $x_i$  satisfying

$$2|x_i - \pi|, 2|x_i + \pi|, |x_i - x_j| \geq \frac{2\pi}{\sqrt{\lambda}}, \quad (3.39)$$

where  $[\sqrt{\lambda}]$  denotes the largest positive integer no bigger than  $\sqrt{\lambda}$ .

Let us now explain the biological implications of our mathematical results. In the strong prey growth case ( $\lambda > \lambda_1^D(\Omega_0)$ ), no matter how large the predator growth rate is, the prey population can blow up for certain initial population distributions. Moreover from our discussions in Theorem 3.11 and Proposition 3.13, even if the prey is initially restricted to a very narrow region in the habitat (but perhaps with a high density), unbounded growth of this prey population is still possible if its growth rate  $\lambda$  is high enough. This is of particular interest for understanding the biological invasion of the prey species, since it shows that the presence of a very strong predator cannot stop the invasion if there exists an ideal environment  $\Omega_0$  which sufficiently nutrients the growth of the prey population.

Theorem 3.11 has another interesting biological explanations. These results show that for the initial population distribution  $u_0 = U_{\mu_0}$ , the prey population will become extinct when the predator is strong ( $\mu > \tilde{\mu}^*$ ), but for the same initial distribution, the prey population can also blow up if the predator is weak ( $\mu < \hat{\mu} - c/m$ ). Hence no any initial distribution is guaranteed to predict extinction or blow-up of the prey population. We remark that this idea can also be applied to the weak prey growth case considered in subsection 3.1, to show that the same initial distribution can lead to either extinction or persistence depending on the predator growth rate.

Finally we notice that in the weak prey growth case, the possibility of Allee effect (that is, bistability) depends on the value of  $m$ : when  $m$  is large, two attracting regions exist for the system, but when  $m$  is small, a unique attracting region will absorb all initial states. In sharp contrast, in the strong prey growth case, bistability is always possible no matter how small  $m$  is. Hence in the latter case the Allee effect is mainly caused by the degeneracy of  $a(x)$ , not the saturation (*i.e.*  $m > 0$ ) of the predation rate.

### 3.3 Impact of protect zones

In this subsection, we use a rather different approach to understand the effects of inhomogeneous environment on the Holling type II diffusive predator-prey model. We will examine a situation that the heterogeneity of the environment is mainly caused by the creation of a protection zone for the prey species. We refer to [DS2] for the proofs of the results to be presented below.

From our analysis in subsection 3.1, we know that in a homogeneous environment, the prey population would extinguish if the growth rate of the predator is too large, or the predation rate is too high. It is not difficult to see that this remains the case if the coefficients in the model are replaced by positive functions of  $x$ . To save an otherwise endangered prey species, a natural idea is to set up one or several protection zones for the prey, where the prey species can enter and leave freely but the predator is kept out. This create a spatial environment felt very differently by the prey and predator species. We may ask several related biological questions: Are such protection zones effective to save an endangered prey population? What are the effects of such protection zones on the predator species? Could such protection zones induce unexpected new dynamics for the species involved?

We now attempt to address these questions by examining the Holling type II diffusive predator-prey model with a single protection zone. Our model can be described by the

following system of equations:

$$\begin{cases} u_t - \operatorname{div}(d_1(x)\nabla u) = \lambda(x)u - a(x)u^2 - \frac{b(x)uv}{1+m(x)u}, & x \in \Omega, t > 0, \\ v_t - \operatorname{div}(d_2(x)\nabla v) = \mu(x)v - d(x)v^2 + \frac{c(x)uv}{1+m(x)u}, & x \in \Omega \setminus \overline{\Omega}_0, t > 0, \\ \partial_\nu u = 0, x \in \partial\Omega, t > 0, \quad \partial_\nu v = 0, x \in \partial\Omega \cup \partial\Omega_0, t > 0, \\ u(x, 0) = u_0(x) \geq 0, x \in \Omega, \quad v(x, 0) = v_0(x) \geq 0, x \in \Omega_0. \end{cases} \quad (3.40)$$

Here the protection zone is represented by  $\Omega_0$ , a subdomain of  $\Omega$  with smooth boundary  $\partial\Omega_0$ . The larger region  $\Omega$  is the habitat of the prey, but the predator species can only exist in  $\Omega \setminus \overline{\Omega}_0$ . All the coefficient functions are nonnegative in  $\overline{\Omega}$ . The function  $b(x)$  is zero when  $x \in \Omega_0$ , representing the assumption that the prey population enjoys predation-free growth in  $\Omega_0$ ; this also makes the interaction term in the equation for  $u$  well-defined over  $\Omega$ . The boundary of the protection zone does not affect the dispersal of prey, but it works as a barrier to block the predator from entering  $\Omega_0$ ; thus a no-flux boundary condition should be imposed for the predator on  $\partial\Omega_0$ . For technical reasons, we assume further that  $\overline{\Omega}_0 \subset \Omega$ . Therefore, we may call  $\Omega_0$  an interior protection zone.

To focus on the impact of the protection zone on the dynamics, we will assume that all the parameter functions in (3.40) are constant except  $b(x)$ , and  $a = d = d_1 = d_2 = 1$ . Thus we have the following system:

$$\begin{cases} u_t - \Delta u = \lambda u - u^2 - \frac{b(x)uv}{1+mu}, & x \in \Omega, t > 0, \\ v_t - \Delta v = \mu v - v^2 + \frac{cuv}{1+mu}, & x \in \Omega \setminus \overline{\Omega}_0, t > 0, \\ \partial_\nu u = 0, x \in \partial\Omega, t > 0, \quad \partial_\nu v = 0, x \in \partial\Omega \cup \partial\Omega_0, t > 0, \\ u(x, 0) = u_0(x) \geq 0, x \in \Omega, \quad v(x, 0) = v_0(x) \geq 0, x \in \Omega_0. \end{cases} \quad (3.41)$$

The steady state solutions satisfy

$$\begin{cases} -\Delta u = \lambda u - u^2 - \frac{b(x)uv}{1+mu}, & x \in \Omega, \\ -\Delta v = \mu v - v^2 + \frac{cuv}{1+mu}, & x \in \Omega \setminus \overline{\Omega}_0, \\ \partial_\nu u = 0, x \in \partial\Omega, \quad \partial_\nu v = 0, x \in \partial\Omega \cup \partial\Omega_0. \end{cases} \quad (3.42)$$

Here  $\lambda, \mu, c, m$  are positive constants,  $b(x) \in L^\infty(\Omega)$ ,  $b(x) \geq 0$  in  $\overline{\Omega}$ ,  $b(x) \equiv 0$  on  $\overline{\Omega}_0$  and for any compact subset  $A$  of  $\overline{\Omega} \setminus \overline{\Omega}_0$ , there exists  $\delta_A > 0$  such that

$$b(x) \geq \delta_A \quad \forall x \in A. \quad (3.43)$$

For simplicity, we may think of  $b(x)$  as given by  $b(x) = 0$  on  $\overline{\Omega}_0$  and  $b(x) = 1$  otherwise.

We will consider  $\lambda$  and  $\mu$  as varying parameters while fixing the other parameters. It turns out that the ranges of  $\lambda$  where the dynamics will be drastically different are as in subsection 3.2:

$$(a) \quad 0 < \lambda < \lambda_1^D(\Omega_0), \quad (b) \quad \lambda > \lambda_1^D(\Omega_0). \quad (3.44)$$

Let us now make an interesting comparison between (3.8) and (3.41): In (3.8),  $\Omega_0$  is the region where the prey could have an unbounded growth as the crowding effect is zero, but

the predator can be present in  $\Omega_0$ ; in (3.41), the prey has the same or similar living condition in  $\Omega_0$  as in other parts of the habitat  $\Omega$ , but the predator is blocked out. Hence the models (3.8) and (3.41) can be viewed as two different ways to create some ideal subregions for the prey. Indeed, our mathematical results will show that under a weak prey growth rate  $\lambda$  (which means  $0 < \lambda < \lambda_1^D(\Omega_0)$ ), the two systems (3.8) and (3.41) exhibit very similar dynamical behavior. However, these systems behave very differently when the prey growth rate is strong ( $\lambda > \lambda_1^D(\Omega_0)$ ), implying that the different strategies of designing favorable regions for the prey could lead to very different consequences.

In the following, it is more convenient for us to regard  $\lambda$  as fixed while interpreting the cases  $0 < \lambda < \lambda_1^D(\Omega_0)$  and  $\lambda > \lambda_1^D(\Omega_0)$  as caused by the change of sizes of the protect zone  $\Omega_0$ . Such a view may be best explained by the well-known diffusive logistic equation with hostile boundary condition:

$$\begin{cases} u_t - \Delta u = \lambda u - u^2, & x \in \Omega_0, t > 0, \\ u(x, t) = 0, & x \in \partial\Omega_0, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega_0. \end{cases} \quad (3.45)$$

It is known that there exists a unique  $\lambda_* = \lambda_1^D(\Omega_0) > 0$  such that when  $\lambda \leq \lambda_*$ , the population  $u$  would eventually extinguish, and when  $\lambda > \lambda_*$ , the population  $u$  will persist and settle at a unique positive steady state. Thus  $\lambda_*$  is the threshold growth rate for persistence/extinction. If one regards the growth rate  $\lambda$  as fixed, then there is a minimal patch size  $S$ , such that when the domain is smaller than  $S$ , the population will become extinct, but otherwise the population will persist. The minimal patch size is determined by the principal eigenvalue of the associated linear operator, and it depends on the geometry of the habitat (see [CC2]). (The concept of minimal patch size first appeared in the pioneering work [Sk] and [KS] as mentioned in Section 1.) Therefore, we may call  $0 < \lambda < \lambda_1^D(\Omega_0)$  the small protect zone case, and  $\lambda > \lambda_1^D(\Omega_0)$  the large protect zone case.

For the small protect zone case, the dynamical behavior of (3.41) is essentially the same as that of (3.8), hence we will not go into details for this case. In the remaining part of this subsection, we shall concentrate on the large protect zone case:  $\lambda > \lambda_1^D(\Omega_0)$ .

We start our analysis by a standard local bifurcation argument. We fix  $\lambda, c, m > 0$ , and take  $\mu$  as the bifurcation parameter. For any  $\mu > 0$ , (3.42) has two semi-trivial solutions:  $(\lambda, 0)$  and  $(0, \mu)$ . They form two smooth curves in the  $(\mu, u, v)$ -space:

$$\Gamma_u = \{(\mu, \lambda, 0) : -\infty < \mu < \infty\}, \quad \Gamma_v = \{(\mu, 0, \mu) : 0 < \mu < \infty\}. \quad (3.46)$$

Similar to before, a supercritical bifurcation occurs along the semi-trivial branch  $\Gamma_u$ . But the bifurcation along  $\Gamma_v$  now depends on the equation

$$\lambda = \lambda_1^N(b(x)\mu, \Omega). \quad (3.47)$$

It turns out that (2.1) can be satisfied by some  $\mu > 0$  only if  $0 < \lambda < \lambda_1^D(\Omega_0)$ ; when  $\lambda \geq \lambda_1^D(\Omega_0)$ ,  $\lambda > \lambda_1^N(b(x)\mu, \Omega)$  holds for all  $\mu > 0$ . Thus when  $\lambda > \lambda_1^D(\Omega_0)$ , the semi-trivial state  $(0, \mu)$  is unstable for every  $\mu > 0$ , and there is no bifurcation of positive solutions occurring along  $\Gamma_v$ . Hence we have the following global bifurcation picture (see Figure 5):

**Theorem 3.14.** *If  $\lambda \geq \lambda_1^D(\Omega_0)$ , then*

1.  $\mu^0 = -c\lambda/(1+m\lambda)$  is a bifurcation point where an unbounded continuum  $\Gamma$  of positive solutions to (3.42) bifurcates from  $\Gamma_u$  at  $(\mu, u, v) = (\mu^0, \lambda, 0)$ .
2. Near  $(\mu^0, \lambda, 0)$ ,  $\Gamma$  is a smooth curve  $(\mu(s), u(s), v(s))$  with  $s \in (0, \delta)$ , such that  $(\mu(0), u(0), v(0)) = (\mu^0, \lambda, 0)$  and  $\mu'(0) > 0$ .
3.  $\text{proj}_\mu \Gamma = (\mu^0, \infty)$ , and so (3.42) has at least one positive solution for any  $\mu > \mu^0$ , but (3.42) has no positive solution for  $\mu \leq \mu^0$ .

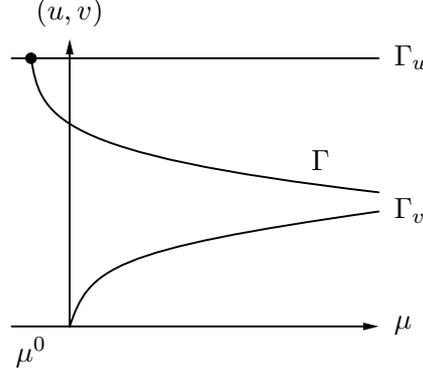


Figure 5: Bifurcation diagram of positive steady state solutions of (3.42) when  $\lambda > \lambda_1^D(\Omega_0)$ ; the diagrams when  $0 < \lambda < \lambda_1^D(\Omega_0)$  are similar to the ones with solid lines in Fig. 4.

The instability of the semi-trivial state  $(0, \mu)$  implies that the system is permanent for all  $\mu > 0$  (see [CCH]), but a better description of the dynamics can be obtained, especially when  $\mu > 0$  is large. For (3.41), the population of the predator  $v(x, t)$  still asymptotically lies between the constants  $\mu$  and  $\mu + c/m$ , i.e.  $v(x, t)$  satisfies (3.23). Hence similar to the analysis in subsection 3.2, more information on the set of coexistence states of (3.41) can be obtained if we can extract more information from the the scalar equation:

$$-\Delta u = \lambda u - u^2 - b(x)\mu \frac{u}{1+mu}, \quad x \in \Omega, \quad \partial_\nu u = 0, \quad x \in \partial\Omega. \quad (3.48)$$

The analysis of (3.48) relies on a well-known comparison lemma (see [SY] Lemma 2.3, and a more general version can be found in [DM] Lemma 2.1):

**Lemma 3.15.** *Suppose that  $f : \Omega \times \mathbf{R}^+ \rightarrow \mathbf{R}$  is a continuous function such that  $f(x, s)$  is decreasing for  $s > 0$  at almost all  $x \in \bar{\Omega}$ . Let  $w, v \in C(\bar{\Omega}) \cap C^2(\Omega)$  satisfy*

1.  $\Delta w + wf(x, w) \leq 0 \leq \Delta v + vf(x, v)$  in  $\Omega$ ,
2.  $w, v > 0$  in  $\Omega$  and  $w \geq v$  on  $\partial\Omega$ ,
3.  $\Delta v \in L^1(\Omega)$ .

Then  $w \geq v$  in  $\bar{\Omega}$ .

By using Lemma 3.15, one can construct a positive solution of (3.48) by the sub- and super-solution method:  $u = \lambda$  is a super-solution, and  $W_\lambda$  is a sub-solution, where  $W_\lambda$  is defined by  $W_\lambda(x) = 0$  in  $\Omega \setminus \overline{\Omega}_0$ ,  $W_\lambda = w_\lambda$  in  $\Omega_0$ , where  $w_\lambda$  denotes the unique positive solution of

$$-\Delta w = \lambda w - w^2, \quad x \in \Omega_0, \quad w = 0, \quad x \in \partial\Omega_0. \quad (3.49)$$

When  $\mu \rightarrow \infty$ , we could prove that each solution  $U$  of (3.48) uniformly converges to  $W_\lambda$ . Therefore for large  $\mu$ ,  $U \approx w_\lambda$  for  $x \in \Omega_0$  and  $U \approx 0$  for  $x \notin \Omega_0$ . With this explicit spatial profile of the solution, we are able to conclude that any positive solution of (3.48) is linearly stable, and we can then apply a standard fixed point index argument to show that (3.48) has a unique positive solution when  $\mu$  is sufficiently large. More precisely, we have

**Proposition 3.16.** *Suppose that  $\lambda > \lambda_1^D(\Omega_0)$ . Then*

1. *For each  $\mu \leq 0$ , (3.48) has a unique positive solution  $U_\mu$ , which is strictly decreasing in  $\mu$ , and  $\{(\mu, U_\mu) : \mu \leq 0\}$  is a smooth curve.*
2. *For each  $\mu > 0$ , (3.48) has a minimal positive solution  $\underline{U}_\mu$  and a maximal positive solution  $\overline{U}_\mu$ , and they satisfy*

$$W_\lambda(x) < \underline{U}_\mu(x) \leq \overline{U}_\mu(x) < \lambda, \quad \forall x \in \Omega. \quad (3.50)$$

3. *There exists  $\overline{\mu}^* > 0$  such that for  $\mu > \overline{\mu}^*$ ,  $\overline{U}_\mu = \underline{U}_\mu$ , and (3.48) has a unique positive solution, which we denote by  $U_\mu$ , and  $\{(\mu, U_\mu) : \mu > \overline{\mu}^*\}$  is a smooth curve. Moreover, as  $\mu \rightarrow \infty$ ,  $U_\mu \rightarrow W_\lambda$  in  $C(\overline{\Omega})$ .*

Regarding the last convergence result in Proposition 3.16, we remark that it is not difficult to show that  $U_\mu \rightarrow W_\lambda$  in  $L^p(\Omega)$  for any  $p > 1$  as  $\mu \rightarrow \infty$  from energy estimates, but the convergence in  $C(\overline{\Omega})$  requires more delicate interior and boundary estimates, see [DS2] Proposition 3.3. The uniform convergence is crucial for the later results.

The uniqueness result in Proposition 3.16 enables us to prove the uniqueness and global asymptotical stability of the positive steady state for the full system (3.41):

**Theorem 3.17.** *Suppose that  $\lambda > \lambda_1^D(\Omega_0)$ . Then*

1. *There exists  $\delta > 0$  such that (3.42) has a unique positive solution when  $\mu \in (\mu^0, \mu^0 + \delta)$ .*
2. *For any  $\mu > \mu^0$ , if  $(u, v)$  is a positive solution of (3.42), then*

$$\underline{U}_{\mu+c/m}(x) \leq u(x) \leq \overline{U}_\mu(x), \quad \max\{\mu, 0\} \leq v(x) \leq \mu + c/m, \quad (3.51)$$

where  $\underline{U}_\mu$  and  $\overline{U}_\mu$  are the minimal and maximal solutions of (3.48), respectively.

3. *There exists  $\mu^* > 0$  such that (3.42) has a unique positive solution  $(u_\mu, v_\mu)$  when  $\mu \geq \mu^*$ , and  $(u_\mu, v_\mu)$  is linearly stable in the sense that  $\text{Re}(\eta) > 0$  if  $\eta$  is an eigenvalue of the linearized eigenvalue problem at  $(u_\mu, v_\mu)$ . Moreover, when  $\mu \rightarrow \infty$ ,  $u_\mu \rightarrow W_\lambda$  uniformly in  $\overline{\Omega}$ , and  $v_\mu - \mu \rightarrow 0$  uniformly in  $\overline{\Omega} \setminus \Omega_0$ .*

4. There exists  $\mu_* > \mu^*$  such that if  $\mu \geq \mu_*$ , and if  $(u(x, t), v(x, t))$  is a solution of (3.41), then  $\lim_{t \rightarrow \infty} u(x, t) = u_\mu(x)$  and  $\lim_{t \rightarrow \infty} v(x, t) = v_\mu(x)$  uniformly for  $x \in \overline{\Omega}$  and  $x \in \Omega \setminus \overline{\Omega_0}$ , respectively.

The proof of the uniqueness of steady state is based on the linear stability analysis. For the linearized eigenvalue system, we use Kato's inequality  $(-\Delta|\phi| \leq -\text{Re}(\overline{\phi}|\phi|^{-1}\Delta\phi))$  to establish second order differential inequalities satisfied by any eigenfunction  $(\phi, \psi)$  with large  $\mu$  (thanks to the explicit asymptotic profile of the steady state), then we use energy estimates to conclude that  $\text{Re}(\eta) > 0$  for any eigenvalue  $\eta$ , which implies the linear stability of the steady state. Again the uniqueness conclusion follows from the linear stability and a standard fixed point index argument. The proof of the global asymptotic stability follows the same line, but the estimates are more involved: We first obtain careful estimates of the  $L^2$  norms of the solution  $(u(x, t), v(x, t))$  for large time  $t$ , then we apply Gronwall type inequalities to show the global asymptotic stability.

Mathematically, it is usually difficult to prove not only the uniqueness but also the global asymptotical stability of the coexistence steady state for a predator-prey model. For reaction-diffusion systems without a proper order structure, rigorous proof of global asymptotical stability has been rarely achieved. For diffusive predator-prey models, we recall that global asymptotical stability of the constant coexistence state was obtained in [dMR, Le] for the classical Lotka-Volterra system with Neumann boundary conditions. For even just slightly more complicated systems, the uniqueness is only known when the spatial dimension is 1 ([LP], see also [DLO] for partial uniqueness results for the radial case in high dimensions). Even in this special case, the local stability is still unknown (Hopf bifurcation has not been ruled out).

In biological terms, the most significant feature of our study in this subsection is the existence of a critical patch size described by the principal eigenvalue  $\lambda_1^D(\Omega_0)$  for the protection zone  $\Omega_0$ . If the protection zone is above that size (*i.e.*, if  $\lambda_1^D(\Omega_0)$  is less than  $\lambda$ , the prey growth rate), then the dynamics of the model is fundamentally changed from the usual predator-prey dynamics; in such a case, the prey population can survive regardless of the level of predation, and if the predator is strong, then the two populations stabilize at a unique coexistence state. If the protection zone is below the critical patch size, then the dynamics of the model is qualitatively similar to the usual case without protection zone, but the chances of survival of the prey species increase with the size of the protection zone, as generally expected.

The value of  $\lambda_1^D(\Omega_0)$  depends on the size as well as the shape of  $\Omega_0$ . The smaller the value of  $\lambda_1^D(\Omega_0)$ , the more protection  $\Omega_0$  provides to the prey species. For the interior protection zone case discussed here, if the volume of the zone is fixed, then it is well-known that a spherical protection zone has the smallest eigenvalue  $\lambda_1^D(\Omega_0)$  from the classical Rayleigh-Faber-Krahn inequality (see [P]). Thus if a ball of the given size can be inscribed into  $\Omega$ , then the optimal interior protection zone should be a ball. If fencing is needed to create the protection zone (for example, nets with suitable mesh sizes could be used if the prey has considerably smaller body size than its predator), then a ball shaped protection zone also uses the least fencing material as a ball has the least surface area among all regions of the same volume. This also suggests that having one big protection zone is usually better than having several protection zones that add to the same size (but this is not always so as

the shape of the protection zones matters).

It is natural to have a boundary protection zone which is built along part or all the boundary of  $\Omega$ . If  $\Omega_0$  is a ring shaped domain which has  $\partial\Omega$  as its outer boundary, that is,  $\partial\Omega \subset \partial\Omega_0$  and  $\Gamma := \partial\Omega_0 \setminus \partial\Omega$  is nonempty and is contained in  $\Omega$ , then the techniques and results here carry over easily. The critical patch size for this case is determined by  $\lambda_1^M(\Omega_0) = \lambda$ , where  $\lambda_1^M(\Omega_0)$  denotes the principal eigenvalue of the problem

$$-\Delta\phi = \lambda\phi, \quad x \in \Omega_0, \quad \partial_\nu\phi = 0, \quad x \in \partial\Omega, \quad \phi = 0, \quad x \in \Gamma.$$

From the variational characterization of eigenvalues, we have

$$\lambda_1^D(\Omega_0) > \lambda_1^M(\Omega_0) > \lambda_1^N(\Omega_0),$$

for any given region  $\Omega_0$ . Therefore, a boundary protection zone is better than a same shaped interior protection zone. We should note, however, that there are more choices for the shape of interior zones than boundary zones.

A more natural boundary protection zone is one where  $\partial\Omega_0$  splits into two parts  $\Gamma_1$  and  $\Gamma_2$ , with  $\Gamma_1 \subset \partial\Omega$ ,  $\text{int}(\Gamma_2) \subset \Omega$ , and  $\Gamma_2 \cap \partial\Omega$  is an  $(N - 2)$ -dimensional manifold. This is a mathematically challenging case, and great technical difficulties will be involved to extend our results here to this case. But we believe that similar results hold, and the critical patch size is determined by  $\lambda_1^{M'}(\Omega_0) = \lambda$ , where  $\lambda_1^{M'}(\Omega_0)$  denotes the principal eigenvalue of the problem

$$-\Delta\phi = \lambda\phi, \quad x \in \Omega_0, \quad \partial_\nu\phi = 0, \quad x \in \Gamma_1, \quad \phi = 0, \quad x \in \Gamma_2.$$

Again we have

$$\lambda_1^D(\Omega_0) > \lambda_1^{M'}(\Omega_0) > \lambda_1^N(\Omega_0).$$

If the boundary has a flat part, then a half ball  $H$  along the flat part of the boundary has the same principal eigenvalue  $\lambda_1^{M'}(H)$  as that of a whole ball of the same radius in the interior. We conjecture that if the area is fixed, then the optimal protection zone is always achieved by a boundary one. This is apparently true for some special domains. A related optimization problem is considered in [KuS].

## 4 The Leslie model

In this section, we closely examine the diffusive Leslie model. The corresponding ODE model is given by (1.9), where all the coefficients are positive constants. It is known that (1.9) has simple dynamics: the unique positive equilibrium  $(u^*, v^*)$  attracts all the positive solutions as  $t \rightarrow \infty$ ; in contrast, the slightly different Leslie-May-Tanner model (1.10) may have stable limiting cycles. See [Hz, HH1, HH2] for details.

We will consider the diffusive Leslie model with Neumann boundary conditions. Therefore in the case of homogeneous environment, the ODE solutions are also solutions to the diffusive model. We will employ a Lyapunov function technique to show that the homogeneous diffusive model has similar dynamics as the ODE model under some restriction of the parameters. We suspect that the restriction on the parameters is not necessary but are not able to remove it. In sharp contrast, we will show that when the environment is heterogeneous, the dynamics can be drastically changed.

## 4.1 The homogeneous case

If we replace  $u$  by  $u/d$ ,  $a$  by  $\alpha d$  and  $b$  by  $\beta$ , then the corresponding diffusive model of (1.9) with Neumann boundary conditions can be written in the following simpler form

$$\begin{cases} u_t - d_1 \Delta u = u(\lambda - \alpha u - \beta v), & x \in \Omega, t > 0, \\ v_t - d_2 \Delta v = \mu v(1 - \frac{v}{u}), & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \end{cases} \quad (4.1)$$

where  $d_1, d_2, \lambda, \mu, \alpha, \beta$  are positive constants. Clearly,

$$(u^*, v^*) = \left( \frac{\lambda}{\alpha + \beta}, \frac{\lambda}{\alpha + \beta} \right)$$

is the only constant positive equilibrium of (4.1).

Let  $(u(x, t), v(x, t))$  be a positive solution of (4.1). A simple comparison argument yields  $0 < u(x, t) < U(x, t)$  for all  $t > 0$  and  $x \in \Omega$ , where  $U$  is the unique solution of

$$U_t - d_1 \Delta U = \lambda U - \alpha U^2 \text{ in } \Omega \times (0, \infty), \quad U_\nu|_{\partial\Omega \times (0, \infty)} = 0, \quad U(x, 0) = u(x, 0).$$

It is well known that  $U(x, t) \rightarrow \lambda/\alpha$  as  $t \rightarrow \infty$  uniformly in  $x$ . From these facts, it follows by standard comparison arguments that  $u(x, t)$  and  $v(x, t)$  exist and remain positive for all  $t > 0$ , and

$$\overline{\lim}_{t \rightarrow \infty} u(x, t) \leq \lambda/\alpha, \quad \overline{\lim}_{t \rightarrow \infty} v(x, t) \leq \lambda/\alpha.$$

Adapting the Lyapunov function in [HH1], we define

$$\begin{aligned} V(u, v) &= \int \frac{u - u^*}{u^2} du + c \int \frac{v - v^*}{v} dv, \\ W(t) &= \int_{\Omega} V(u(x, t), v(x, t)) dx, \end{aligned}$$

where  $c > 0$  is a constant to be determined later, and  $(u(x, t), v(x, t))$  is an arbitrary positive solution of (4.1).

Denote

$$f(u, v) = u(\lambda - \alpha u - \beta v), \quad g(u, v) = \mu v(1 - v/u).$$

We have

$$\begin{aligned} & V_u(u, v)f(u, v) + V_v(u, v)g(u, v) \\ &= \frac{u - u^*}{u} (\lambda - \alpha u - \beta v) + c\mu(v - v^*)(1 - v/u) \\ &= \frac{u - u^*}{u} (\alpha u^* + \beta v^* - \alpha u - \beta v) + c\mu(v - v^*) \frac{u - u^* + v^* - v}{u} \\ &= -\alpha \frac{(u - u^*)^2}{u} + (c\mu - \beta) \frac{(u - u^*)(v - v^*)}{u} - c\mu \frac{(v - v^*)^2}{u}. \end{aligned}$$

We now choose  $c = \beta/\mu$  and obtain

$$V_u(u, v)f(u, v) + V_v(u, v)g(u, v) = -\alpha \frac{(u - u^*)^2}{u} - \beta \frac{(v - v^*)^2}{u}.$$

It follows that

$$\begin{aligned}
W'(t) &= \int_{\Omega} (V_u(u(x,t), v(x,t))u_t + V_v(u(x,t), v(x,t))v_t) dx \\
&= \int_{\Omega} \left( \frac{u-u^*}{u^2} d_1 \Delta u + c \frac{v-v^*}{v} d_2 \Delta v \right) dx - \int_{\Omega} \left( \alpha \frac{(u-u^*)^2}{u} + \beta \frac{(v-v^*)^2}{v} \right) dx \\
&= - \int_{\Omega} \left( d_1 \frac{2u^*-u}{u^3} |\nabla u|^2 + d_2 \frac{v^*}{v^2} |\nabla v|^2 + \alpha \frac{(u-u^*)^2}{u} + \beta \frac{(v-v^*)^2}{v} \right) dx.
\end{aligned}$$

Suppose that  $\alpha > \beta$ . Then  $2u^* = 2\lambda/(\alpha + \beta) > \lambda/\alpha$ . Since  $u(x, t) < U(x, t)$  and  $U(x, t) \rightarrow \lambda/\alpha$  as  $t \rightarrow \infty$ , we can find  $T > 0$  large such that  $U(x, t) < 2\lambda/(\alpha + \beta)$  for all  $t \geq T$  and all  $x \in \Omega$ . Therefore,  $w'(t) \leq 0$  for all  $t > T$  and equality holds only if  $(u, v) \equiv (u^*, v^*)$ . Together with some standard arguments based on the boundedness of  $(u, v)$  and parabolic regularity, this proves the following result.

**Proposition 4.1.** *When  $\alpha > \beta$ ,  $(u^*, v^*)$  attracts every positive solution of (4.1).*

The restriction  $\alpha > \beta$  can be relaxed by replacing  $V(u, v)$  by the following Lyapunov function

$$V^*(u, v) = \int \frac{u^2 - (u^*)^2}{u^2} du + c \int \frac{v - v^*}{v} dv,$$

with a suitable choice of  $c > 0$ , and the following result is proved in [DHs]:

**Theorem 4.2.** *There exists a constant  $s_0 \in (1/5, 1/4)$  such that if  $\alpha/\beta > s_0$ , then  $(u^*, v^*)$  attracts every positive solution of (4.1).*

*Remark 4.3.* From the proof in [DHs],  $s_0$  is the unique positive zero of the polynomial  $h(s) = 32s^3 + 16s^2 - s - 1$ . We conjecture that the conclusion of Theorem 4.2 is valid for all positive constants  $\alpha$  and  $\beta$ . Like in [dMR], the above Lyapunov function technique collapses when the diffusive system fails to have a positive constant steady-state.

## 4.2 The heterogeneous case

As before, to simplify our presentation, we only consider the case that  $\alpha$  in (4.1) is replaced by a positive continuous function  $\alpha(x)$ , while the other coefficients remain positive constants. However, with the loss of the Lyapunov function technique, we can say much less than in the homogeneous case about the global dynamical behavior, except that all the positive solutions remain bounded for all  $t > 0$ , which follows from a simple comparison argument. We will instead concentrate on the understanding of the positive steady-state solutions, namely positive solutions of the elliptic system

$$\begin{cases} -d_1 \Delta u = \lambda u - \alpha(x)u^2 - \beta uv, & x \in \Omega, \\ -d_2 \Delta v = \mu v \left(1 - \frac{v}{u}\right), & x \in \Omega, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega. \end{cases} \quad (4.2)$$

By some simple change of scales, (4.2) can be reduced to the following simpler form:

$$\begin{cases} -\Delta u = \lambda u - \alpha(x)u^2 - \beta uv, & x \in \Omega, \\ -\Delta v = \mu v \left(1 - \frac{v}{u}\right), & x \in \Omega, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega. \end{cases} \quad (4.3)$$

Here  $\Omega$  is a bounded smooth domain in  $\mathbf{R}^n$ ,  $\lambda, \mu, \beta$  are positive constants, and  $\alpha(x)$  is a continuous positive function over  $\overline{\Omega}$ .

Making use of a standard continuation and topological degree argument, it is shown in [DHs] that (4.3) always has a positive solution.

**Theorem 4.4.** *Suppose that  $\lambda, \mu, \beta$  are positive constants, and  $\alpha(x)$  is a continuous positive function over  $\overline{\Omega}$ . Then (4.3) has at least one positive solution.*

In the one spatial dimension case, that is, if  $\Omega$  is a bounded interval in  $\mathbf{R}^1$ , then the techniques in [LP] can be easily adapted to show that any possible positive solution of (4.3) is non-degenerate, namely, the linearized problem of (4.3) at any positive solution  $(u, v)$ ,

$$\begin{cases} -\Delta\phi = \lambda\phi - 2\alpha(x)u\phi - \beta v\phi - \beta u\psi, & x \in \Omega, \\ -\Delta\psi = \mu(\psi - \frac{1}{u}\phi + \frac{v}{u^2}\phi), & x \in \Omega, \\ \partial_\nu\phi = \partial_\nu\psi = 0, & x \in \partial\Omega, \end{cases} \quad (4.4)$$

has only the zero solution  $(\phi, \psi) = (0, 0)$ . It follows from this fact and a topological degree argument that (4.3) has a unique positive solution in this one dimension case. We suspect that this is true in high dimension and the unique positive solution is globally attractive to all the positive solutions of the corresponding parabolic system, but cannot find a proof for this. In fact, even in the one dimension case where uniqueness is known, we are not able to show that the unique positive solution of (4.3) is globally attractive for the corresponding parabolic system.

#### 4.2.1 The degenerate case

In order to capture the influence of the heterogeneity of the spatial environment on the behavior of (4.3), we consider in this subsection a degenerate case, where  $\alpha(x)$  is allowed to vanish on part of  $\Omega$ . For simplicity, we suppose that  $\alpha(x) = 0$  on  $\overline{\Omega}_0 \subset \Omega$ , where  $\Omega_0$  is a connected set with smooth boundary, and  $\alpha(x) > 0$  in the rest of  $\Omega$ . We will show a crucial difference in the behavior of (4.3) between the case  $\lambda < \lambda_1^D(\Omega_0)$  and the case  $\lambda > \lambda_1^D(\Omega_0)$ . Here, as before,  $\lambda_1^D(\Omega_0)$  denotes the first eigenvalue of

$$-\Delta\phi = \lambda\phi, \quad x \in \Omega, \quad \phi(x) = 0, \quad x \in \partial\Omega.$$

Let us first observe that if  $\lambda \in (0, \lambda_1^D(\Omega_0))$ , then by the main result in [Ou] (see also [FKLM]), the problem

$$-\Delta u = \lambda u - \alpha(x)u^2, \quad x \in \Omega, \quad \partial_\nu u = 0, \quad x \in \partial\Omega,$$

still has a unique positive solution  $u_\lambda^*$ . Using this fact, one easily sees that the proof of Theorem 4.4 carries over to the present degenerate case. Therefore we have the following result.

**Theorem 4.5.** *Let  $\alpha(x)$  be a continuous function as described above,  $\lambda \in (0, \lambda_1^D(\Omega_0))$ ,  $\mu > 0$  and  $\beta > 0$ . Then (4.3) has at least one positive solution.*

In sharp contrast, we will show in the following that if  $\lambda > \lambda_1^D(\Omega_0)$ , then (4.3) will no longer have a positive solution for certain  $\mu > 0$  and  $\beta > 0$ .

Let us fix  $\mu \in (0, \lambda_1^D(\Omega_0))$  and suppose  $\lambda > \lambda_1^D(\Omega_0)$ . By Lemma 2.6 in [DL], the boundary blow-up problem

$$-\Delta u = \lambda u - \alpha(x)u^2, \quad x \in \Omega \setminus \overline{\Omega_0}, \quad \partial_\nu u = 0, \quad x \in \partial\Omega, \quad u = \infty, \quad x \in \partial\Omega_0, \quad (4.5)$$

has a minimal positive solution  $U_\lambda$ . Applying Lemma 2.3 in [DL], we find that if  $(u, v)$  is a positive solution of (4.3), then

$$u(x) \leq U_\lambda(x), \quad x \in \Omega \setminus \overline{\Omega_0}.$$

Define

$$\alpha_\lambda(x) = \begin{cases} 0, & x \in \overline{\Omega_0}, \\ 1/U_\lambda(x), & x \in \Omega \setminus \overline{\Omega_0}. \end{cases}$$

Clearly  $\alpha_\lambda$  is continuous on  $\overline{\Omega}$  and  $\alpha_\lambda > 0$  on  $\Omega \setminus \overline{\Omega_0}$ .

By our choice of  $\mu$  and the main result of [Ou], the problem

$$-\Delta V = \mu V(1 - \alpha_\lambda(x)V), \quad x \in \Omega, \quad \partial_\nu V = 0, \quad x \in \partial\Omega, \quad (4.6)$$

has a unique positive solution  $V_\lambda$ .

We want to show that  $v \leq V_\lambda$  if  $(u, v)$  is a positive solution of (4.3). Indeed, we already know that  $u(x) \leq U_\lambda(x)$  on  $\Omega \setminus \overline{\Omega_0}$ . Hence

$$1/u(x) \geq \alpha_\lambda(x), \quad x \in \Omega.$$

It follows that

$$-\Delta v = \mu v(1 - v/u) \leq \mu v(1 - \alpha_\lambda(x)v), \quad x \in \Omega.$$

Thus,  $v$  is a lower solution of (4.6). It is easily checked that for any constant  $M > 1$ ,  $MV_\lambda$  is an upper solution of (4.6), and  $MV_\lambda > v$  if  $M$  is large enough. Therefore,  $v \leq V_\lambda \leq MV_\lambda$  in  $\Omega$ .

We recall that we use  $\lambda_1^N(\phi, \omega)$  to denote the first eigenvalue of the operator  $-\Delta + \phi$  over  $\omega$  under Neumann boundary conditions, and  $\lambda_1^D(\phi, \omega)$  to denote the first eigenvalue under Dirichlet boundary conditions.

If  $(u, v)$  is a positive solution of (4.3), then from the equation for  $u$  we obtain

$$\lambda = \lambda_1^N(\alpha u + \beta v, \Omega) < \lambda_1^D(\alpha u + \beta v, \Omega) < \lambda_1^D(\alpha u + \beta v, \Omega_0) = \lambda_1^D(\beta v, \Omega_0).$$

Since  $v \leq V_\lambda$ , we obtain

$$\lambda < \lambda_1^D(\beta V_\lambda, \Omega_0). \quad (4.7)$$

By the properties of the principle eigenvalue, we see that  $f(\beta) \equiv \lambda_1^D(\beta V_\lambda, \Omega_0)$  is a continuous, strictly increasing function of  $\beta$ , and  $f(0) = \lambda_1^D(\Omega_0)$ ,  $f(\infty) = \infty$ . Since  $\lambda > \lambda_1^D(\Omega_0)$ , we can find a unique  $\beta_0 = \beta_0(\lambda) > 0$  such that  $f(\beta_0) = \lambda$ . Therefore, we have

$$\lambda = \lambda_1^D(\beta_0 V_\lambda, \Omega_0), \quad \text{and} \quad \lambda \geq \lambda_1^D(\beta V_\lambda, \Omega_0), \quad \forall \beta \leq \beta_0. \quad (4.8)$$

Comparing (4.7) with (4.8), we immediately obtain the following result.

**Theorem 4.6.** *Suppose  $\mu \in (0, \lambda_1^D(\Omega_0))$  and  $\lambda \in (\lambda_1^D(\Omega_0), \infty)$ . Let  $\beta_0$  be as in (4.8). Then (4.3) has no positive solution if  $0 < \beta \leq \beta_0$ .*

Our next result shows that for the case  $\lambda > \lambda_1^D(\Omega_0)$ , (4.3) can still have a positive solution for every  $\beta > 0$  if  $\mu$  is large enough; precisely, if  $\mu > \max\{\lambda_1^D(\Omega_0), \lambda\}$ . Thus, existence of a positive solution is regained when  $\mu$  becomes large.

**Theorem 4.7.** *Suppose that  $\mu > \lambda_1^D(\Omega_0)$ , then (4.3) has a positive solution for every  $\lambda \in (0, \mu)$  and  $\beta > 0$ .*

We refer to [DHS] for the proof of Theorem 4.7, which uses a degree argument, and a key step is to obtain a priori bounds for all possible solutions of (4.3).

*Remark 4.8.* The existence problem of (4.3) in the degenerate case is not completely understood. For example, we do not know whether (4.3) has a positive solution for every  $\beta > 0$  when  $\lambda \geq \mu > \lambda_1^D(\Omega_0)$ .

## 4.2.2 Perturbation and sharp spatial patterns

Suppose that  $\alpha(x)$  is as in the last subsection, that is, it is continuous in  $\overline{\Omega}$ , vanishes on  $\overline{\Omega}_0 \subset \Omega$ , and is positive elsewhere. We now fix  $\mu \in (0, \lambda_1^D(\Omega_0))$ ,  $\lambda > \lambda_1^D(\Omega_0)$  and  $\beta \in (0, \beta_0)$ , where  $\beta_0$  is determined by (4.8). For  $\epsilon > 0$  we consider the following perturbation of (4.3):

$$\begin{cases} -\Delta u = \lambda u - [\alpha(x) + \epsilon]u^2 - \beta uv, & x \in \Omega, \\ -\Delta v = \mu v(1 - \frac{v}{u}), & x \in \Omega, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega. \end{cases} \quad (4.9)$$

By Theorem 4.4, (4.9) always has a positive solution. Denote by  $(u_\epsilon, v_\epsilon)$  an arbitrary positive solution of (4.9). Since (4.9) does not have a positive solution when  $\epsilon = 0$  (Theorem 4.6), it is interesting to see how  $(u_\epsilon, v_\epsilon)$  evolves as  $\epsilon$  shrinks to 0. We will show that as  $\epsilon \rightarrow 0$ ,  $(u_\epsilon, v_\epsilon)$  exhibits a sharp spatial pattern determined by the inhomogeneity of  $\alpha(x)$ . To this end, let  $\{\epsilon_n\}$  be an arbitrary sequence of positive numbers decreasing to 0 as  $n \rightarrow \infty$ , and denote  $(u_n, v_n) = (u_{\epsilon_n}, v_{\epsilon_n})$ .

We have the following result.

**Theorem 4.9.**  *$\{(u_n, v_n)\}$  has a subsequence, still denoted by  $(u_n, v_n)$ , such that*

- (i)  $u_n \rightarrow \infty$  uniformly on  $\overline{\Omega}_0$ ,
- (ii)  $u_n \rightarrow \tilde{u}$  in  $C^1(\overline{\omega})$  for any subdomain  $\omega$  satisfying  $\overline{\omega} \subset \overline{\Omega} \setminus \overline{\Omega}_0$ ,
- (iii)  $v_n \rightarrow \tilde{v}$  in  $C^1(\overline{\Omega})$ ,

where  $(\tilde{u}, \tilde{v})$  is a positive solution to the problem

$$\begin{cases} -\Delta \tilde{u} = \lambda \tilde{u} - \alpha(x)\tilde{u}^2 - \beta \tilde{u}\tilde{v}, & x \in \Omega \setminus \overline{\Omega}_0, \\ -\Delta \tilde{v} = \mu \tilde{v}(1 - \frac{\tilde{v}}{\tilde{u}}), & x \in \Omega, \\ \tilde{u} = \infty, x \in \partial\Omega_0, \quad \partial_\nu \tilde{u} = 0, x \in \partial\Omega, \quad \partial_\nu \tilde{v} = 0, x \in \partial\Omega, \end{cases} \quad (4.10)$$

where we use the convention that  $1/\tilde{u} = 0$  in  $\overline{\Omega}_0$ .

From Theorem 4.9 we see that for large  $n$ ,  $u_n$  exhibits a clear spatial pattern: its value is big over  $\Omega_0$ , but stays bounded away from  $\bar{\Omega}_0$ . The spatial pattern of  $u_n$  can be better observed through a rescaling.

**Theorem 4.10.** *Suppose that  $(u_n, v_n)$  converges to  $(\tilde{u}, \tilde{v})$  as in Theorem 4.9. Then  $\epsilon_n u_n \rightarrow w$  in  $C(\bar{\Omega})$ , where  $w = 0$  on  $\bar{\Omega} \setminus \Omega_0$ , and on  $\Omega_0$ ,  $w$  is the unique positive solution of*

$$-\Delta w = \lambda w - w^2 - \beta \tilde{v} w, \quad x \in \Omega_0, \quad w = 0, \quad x \in \partial\Omega_0.$$

We refer to [DHs] for the proof of Theorems 4.9 and 4.10, where a more general situation was considered.

*Remark 4.11.* In the statement of Theorem 3.16 in [DHs], equation (3.32) should be deleted. In fact, (3.32) is never satisfied. Since  $\lambda > \lambda_1^{Dj}(\beta V_\lambda)$ , we always have  $\lambda > \lambda_1^{Dj}(\beta \tilde{v})$ . Theorem 3.16 remains valid when (3.32) is deleted.

*Remark 4.12.* (i) If  $\lambda \in (0, \lambda_1^D(\Omega_0))$ , then it is easy to show that, for small  $\epsilon > 0$ , any positive solution  $(u_\epsilon, v_\epsilon)$  of (4.9) is close to a positive solution  $(u_0, v_0)$  of (4.3). Therefore,  $(u_\epsilon, v_\epsilon)$  does not develop a sharp spatial pattern as  $\epsilon \rightarrow 0$ .

(ii) Likewise, if we perturb (2.7) by replacing  $b(x)$  with  $b(x) + \epsilon$ , then the positive solution  $(u_\epsilon, v_\epsilon)$  of the perturbed equation converges to a positive solution of the original unperturbed problem, so no sharp spatial patterns for the solutions of (2.7) can be observed through this perturbation.

(iii) The above point, when compared with Theorems 4.9 and 4.10, reveals a significant difference between the diffusive Lotka-Volterra predator-prey model and the diffusive Leslie model. A key observation is that when a degeneracy occurs, the range of parameters where a positive solution exists for (2.7) is **enlarged** from the non-degenerate case, while such a range for (4.3) is **reduced** when degeneracy occurs. It is interesting to note that this difference between (2.7) and (4.3) can only be observed in the heterogeneous case.

By Theorem 4.7, (4.3) has a positive solution for every  $\beta > 0$  if  $\mu > \lambda \geq \lambda_1^D(\Omega_0)$ . In [DW], to better understand the effect of the degeneracy, the asymptotic behavior of the positive solutions of (4.3) was examined in each of the following cases:

(i)  $\beta \rightarrow 0$ , (ii)  $\beta \rightarrow \infty$ , (iii)  $\mu \rightarrow \infty$ ,

and comparison was made with the perturbed system (4.9). We refer to [DW] for the proofs of the following results.

**Theorem 4.13.** (Limiting behavior as  $\beta \rightarrow 0^+$ ) *Suppose that  $\mu > \lambda \geq \lambda_1^D(\Omega_0)$  and  $\beta > 0$ . Let  $(u_\beta, v_\beta)$  be a positive solution of (4.3). Then we have the following conclusions:*

(a)  $\lim_{\beta \rightarrow 0^+} (u_\beta(x), v_\beta(x)) = (\infty, \infty)$  uniformly on  $\bar{\Omega}_0$ ;

(b) Along any sequence of  $\beta$  decreasing to 0, there is a subsequence  $\{\beta_n\}$  such that,

$$\lim_{n \rightarrow \infty} (u_{\beta_n}, v_{\beta_n}) = (u, v) \text{ uniformly on any compact subset of } \bar{\Omega} \setminus \bar{\Omega}_0,$$

where  $(u, v)$  is a positive solution of the following system

$$\begin{cases} -\Delta u = \lambda u - a(x)u^2, & x \in \Omega \setminus \bar{\Omega}_0, \\ -\Delta v = \mu v \left(1 - \frac{v}{u}\right), & x \in \Omega \setminus \bar{\Omega}_0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, \quad u = v = \infty, \quad x \in \partial\Omega_0. \end{cases} \quad (4.11)$$

(c) If there exists  $\xi > 0$  such that  $a(x)d(x, \Omega_0)^{-\xi}$  is bounded for all  $x \in \Omega \setminus \bar{\Omega}_0$  close to  $\partial\Omega_0$ , then (4.11) has a unique positive solution  $(u, v)$  and the convergence in part (b) holds for  $\beta \rightarrow 0^+$ .

(d) If  $(u_\beta, v_\beta)$  is a positive solution of (4.9), then  $\lim_{\beta \rightarrow 0^+} (u_\beta(x), v_\beta(x)) = (U_\epsilon, V_\epsilon)$  uniformly over  $\bar{\Omega}$ , where  $U_\epsilon$  and  $V_\epsilon$  are the unique positive solutions to

$$-\Delta U = \lambda U - [a(x) + \epsilon]U^2, \quad \partial_\nu U = 0, \quad x \in \partial\Omega,$$

and

$$-\Delta V = \mu V \left(1 - \frac{V}{U_\epsilon}\right), \quad \partial_\nu V = 0, \quad x \in \partial\Omega$$

respectively.

**Theorem 4.14.** (Limiting behavior as  $\beta \rightarrow +\infty$ ) Suppose that  $\mu > \lambda \geq \lambda_1^D(\Omega_0)$  and  $\beta > 0$ . Let  $(u_\beta, v_\beta)$  be a positive solution of (4.3). Then  $\lim_{\beta \rightarrow \infty} (u_\beta, v_\beta) = (0, 0)$  uniformly on  $\bar{\Omega}$ . The same holds for positive solutions of (4.9).

**Theorem 4.15.** (Limiting behavior as  $\mu \rightarrow +\infty$ ) Suppose that  $\mu > \lambda \geq \lambda_1^D(\Omega_0)$  and  $\beta > 0$ . Let  $(u_\mu, v_\mu)$  be a positive solution of (4.3). Then  $u_\mu \rightarrow w$  in  $C^1(\bar{\Omega})$  and  $v_\mu \rightarrow w$  uniformly on any compact subset of  $\Omega$ , where  $w$  is the unique positive solution of

$$-\Delta w = \lambda w - [a(x) + \beta]w^2, \quad x \in \Omega, \quad \partial_\nu w = 0, \quad x \in \partial\Omega. \quad (4.12)$$

A similar conclusion holds for the positive solutions of (4.9) except that the limiting function is the unique positive solution of

$$-\Delta w = \lambda w - [a(x) + \epsilon + \beta]w^2, \quad x \in \Omega, \quad \partial_\nu w = 0, \quad x \in \partial\Omega. \quad (4.13)$$

Clearly Theorem 4.13 reveals a striking difference between (4.3) and (4.9): The positive solutions of (4.3) exhibit a sharp spatial pattern for small  $\beta$  while those of (4.9) do not. On the other hand, the cases considered in Theorems 4.14 and 4.15 do not seem to reveal any significant difference between (4.3) and (4.9).

*Remark 4.16.* If  $0 < \lambda < \lambda_1^D(\Omega_0)$ , then it follows from Theorem 4.5 that (4.3) has a positive solution for every  $\mu > 0$  and  $\beta > 0$ . Using the techniques in [DW], it can be shown that the corresponding limiting behaviors of (4.3) and (4.9) are the same in each of the three cases:  $\beta \rightarrow 0^+$ ,  $\beta \rightarrow \infty$ , and  $\mu \rightarrow \infty$ .

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