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Persistence in reaction diffusion models with weak allee effect

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Abstract. We study the positive steady state distributions and dynamical behavior of reaction-diffusion equation with weak Allee effect type growth, in which the growth rate per capita is not monotonic as in logistic type, and the habitat is assumed to be a heterogeneous bounded region. The existence of multiple steady states is shown, and the global bifurcation diagrams are obtained. Results are applied to a reaction-diffusion model with type II functional response, and also a model with density-dependent diffusion of animal aggregation.

1. Introduction

Reaction diffusion equations can be used to model the spatiotemporal distribution and abundance of organisms. A typical form of reaction-diffusion population model is

$$\frac{\partial u}{\partial t} = \mathcal{D}\Delta u + uf(x,u), \tag{1.1}$$

where $u(x,t)$ is the population density, $\mathcal{D} > 0$ is the diffusion constant, Δu is the Laplacian of u with respect to the x variable, and $f(x,u)$ is the growth rate per capita, which is affected by the heterogeneous environment. Such an ecological model was first considered by Skellam [41], and similar reaction-diffusion biological models were also studied by Fisher [18] and Kolmogoroff, Petrovsky, and Piscounoff [25] earlier. Since then reaction-diffusion models have been used to describe various spatiotemporal phenomena in biology, physics, chemistry and ecology, see Fife [17], Okubo and Levin [32], Smoller [42], Murray [31], and Cantrell and Cosner [7].

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Since the pioneering work by Skellam [41], the logistic growth rate $f(x,u) = m(x) - b(x)u$ has been used in population dynamics to model the crowding effect. A more general logistic type can be characterized by a declining growth rate per capita function, *i.e.* $f(x,u)$ is decreasing with respect to u (see Figure 1-a.) However it has been increasingly recognized by population ecologists that the growth rate per capita may achieve its peak at a positive density, which is called an *Allee effect* (see Allee [1], Dennis [15], Lewis and Kareiva [28].) An Allee effect can be caused by shortage of mates (Hopf and Hopf [22], Veit and Lewis [48]), lack of effective pollination (Groom [19]), predator saturation (de Roos et. al. [14]), and cooperative behaviors (Wilson and Nisbet [51].)

If the growth rate per capita $f(x,u)$ is negative when u is small, we call such a growth pattern a *strong Allee effect* (see Figure 1-c); if $f(x,u)$ is smaller than the maximum but still positive for small u, we call it a *weak Allee effect* (see Figure 1-b.) In Clark [9], a strong Allee effect is called a *critical depensation* and a weak Allee effect is called a *noncritical depensation.* A population with a strong Allee effect is also called *asocial* by Philip [36]. Most people regard the strong Allee effect as the Allee effect, but population ecologists have started to realize that Allee effect may be weak or strong (see Wang and Kot [49], Wang, Kot and Neubert [50].) The possible growth rate per capita functions were also discussed in Conway [10,11].

In this paper we consider the dispersal and evolution of a species on a bounded heterogeneous habitat Ω, and the inhomogeneous growth rate $f(x,u)$ is either logistic or has an Allee effect. We assume the exterior of the habitat is completely hostile, thus $u = 0$ on the boundary of the habitat $\partial\Omega$. Hence we consider the model

$$\begin{cases} \dfrac{\partial u}{\partial t} = \mathcal{D}\Delta u + uf(x,u), & x \in \Omega, \quad t > 0, \\ u(x,t) = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in \Omega. \end{cases} \tag{1.2}$$

We assume the growth rate per capita $f(x,u)$ satisfies

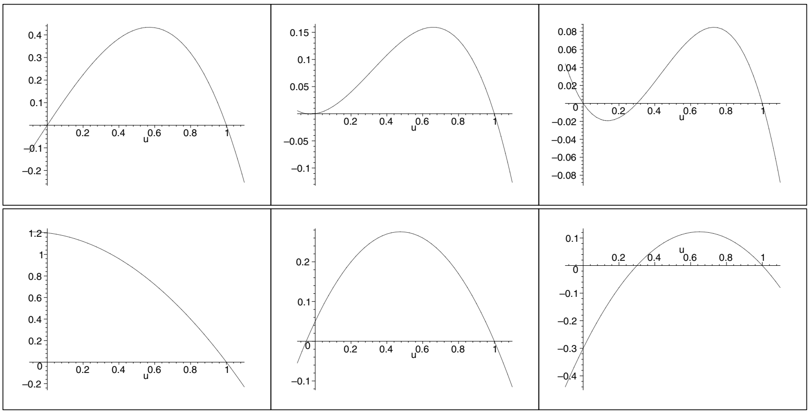

Fig. 1. (a) logistic; (b) weak Allee effect; (c) strong Allee effect; the graphs on top row are growth rate $uf(u)$, and the ones on lower row are growth rate per capita $f(u)$.

- (f1) For any $u \geq 0$, $f(\cdot, u) \in C^{\alpha}(\overline{\Omega})$ for $\alpha \in (0,1)$, and for any $x \in \overline{\Omega}$, $f(x, \cdot) \in C^1(\mathbf{R}^+)$;
- (f2) For any $x \in \overline{\Omega}$, there exists $u_2(x) \geq 0$ such that $f(x,u) \leq 0$ for $u > u_2(x)$, and there exists $M > 0$ such that $u_2(x) \leq M$ for all $x \in \overline{\Omega}$;
- (f3) For any $x \in \overline{\Omega}$, there exists $u_1(x) \geq 0$ such that $f(x, \cdot)$ is increasing in $[0, u_1(x)]$, $f(x, \cdot)$ is decreasing in $[u_1(x), \infty)$, and there exists $N > 0$ such that $N \geq f(x, u_1(x))$ for all $x \in \overline{\Omega}$.

The function $u_2(x)$ (carrying capacity at x) indicates the crowding effects on the population, which may vary by location, but it has a uniform upper bound M. The function $u_1(x)$ is where $f(x,u)$ achieves the maximum value. Here we still allow logistic growth in which case $u_1(x) = 0$. The constant N is the uniform upper bound of the growth rate per capita. We assume that $f(x,u)$ can take one of the following three forms:

- (f4a) **Logistic**. $f(x,0) > 0$, $u_1(x) = 0$, and $f(x, \cdot)$ is decreasing in $[0, \infty)$ (Figure 1-a);
- (f4b) **Weak Allee effect**. $f(x,0) \geq 0$, $u_1(x) > 0$, $f(x, \cdot)$ is increasing in $[0, u_1(x)]$, $f(x, \cdot)$ is decreasing in $[u_1(x), \infty)$ (Figure 1-b);
- (f4c) **Strong Allee effect**. $f(x,0) < 0$, $u_1(x) > 0$, $f(x, u_1(x)) > 0$, $f(x, \cdot)$ is increasing in $[0, u_1(x)]$, $f(x, \cdot)$ is decreasing in $[u_1(x), \infty)$ (Figure 1-c).

The main goal here is to determine the long time dynamical behavior of the population: whether the population will persist or become extinct in long time. From the mathematical theory of dynamical systems, the long time behavior of the solutions of (1.2) is usually determined by the steady state solutions. Thus we will answer the aforementioned questions by a careful analysis of steady state solutions of (1.2).

The dynamical behavior of (1.2) without an Allee effect is well-known. When the species has a logistic growth, there is a critical value $\mathcal{D}_1 > 0$ such that, when $0 < \mathcal{D} < \mathcal{D}_1$ (diffusion is slow), there is a unique positive steady state solution $u_{\mathcal{D}}$ which is the asymptotic limit for any non-negative initial distribution except $u_0 \equiv 0$, thus the persistence of the population is achieved; and when $\mathcal{D} > \mathcal{D}_1$ (diffusion is fast), the only nonnegative steady state solution is $u = 0$, thus the extinction is inevitable (see Figure 2-a.) Here the constant $\mathcal{D}_1 = 1/\lambda_1(f, \Omega)$, and $\lambda_1(f, \Omega)$ is the principal eigenvalue of

$$\Delta\psi + \lambda f(x,0)\psi = 0, \ x \in \Omega, \quad \psi = 0, \ x \in \partial\Omega. \tag{1.3}$$

The eigenvalue $\lambda_1(f, \Omega)$ is determined by the geometry and size of the habitat, as well as the heterogeneity of the habitat. A transcritical bifurcation occurs at $\lambda = \lambda_1(f, \Omega)$ and is related to the concept of the *critical patch size*. For simplicity, we assume that the domain is homogeneous, thus $f(x,0)$ is a constant. Then under a dilation $\Omega_k = \{kx : x \in \Omega\}$ of Ω, $\lambda_1(f, \Omega_k) = k^{-2}\lambda_1(f, \Omega)$. If the diffusion constant $\mathcal{D}$ is determined by the nature of the species and the environment, and if the geometry of the habitat is fixed (say a rectangle, a circular disk, or an interval), the persistence/extinction will solely depend on the size of domain which can

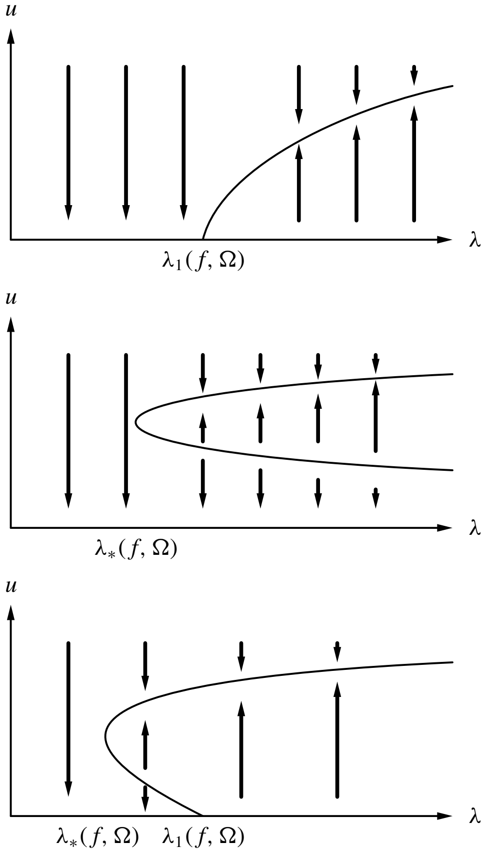

Fig. 2. Bifurcation diagrams: (a) logistic (upper); (b) strong Allee effect (middle); (c) weak Allee effect (lower). Here $\lambda = \mathcal{D}^{-1}$, where $\mathcal{D}$ is the diffusion constant.

be represented by parameter k. The critical patch size k_0 can be determined by $\lambda_1(f, \Omega)$, and the population will persist on Ω_k if and only if $k > k_0$. For example, if the patch is a square $(0, k) \times (0, k)$, then $k_0 = \sqrt{2\mathcal{D}m^{-1}}\pi$ (here eigenfunction $\psi_1 = \sin(k^{-1}\pi x)\sin(k^{-1}\pi y)$ can be obtained by separation of variables.) Note that in logistic growth, the persistence/extinction does not depend on the initial population distribution, and the fate of any initial distribution is the same, thus the persistence when $\lambda > \lambda_1(f, \Omega)$ (or $k > k_0$) is *unconditional persistence*. More general and more detailed discussions for diffusive logistic population models are given in the monograph by Cantrell and Cosner [7], based on their earlier works [4–6]. Similar results were also obtained in Henry [20], Taira [45] and many others.

When an Allee effect is present, the structure of the set of the steady state solutions is more complicated. In Ouyang and Shi [33], the bifurcation diagram of the steady state solutions of (1.2) when $f(x, u) \equiv f(u) = (u - b)(c - u)$ with $0 < 2b < c$ or similar type was considered, and when Ω is a ball of any dimension, it was shown that the bifurcation diagram is exactly like Figure 2-b. (Earlier the exact bifurcation diagram for the one-dimensional problem was obtained by

Smoller and Wasserman [43].) Note that this growth rate per capita function corresponds to a strong Allee effect. In this case, the above definition of critical patch size is no longer valid, since there is no bifurcation occurring along the line of trivial solutions $u = 0$. Nevertheless, a critical value $\mathcal{D}_*$ exists; the population becomes extinct when $\mathcal{D} > \mathcal{D}_*$, and when $\mathcal{D} < \mathcal{D}_*$, there exist two steady state solutions $u_1 > u_2 > 0$, and u_1 is a stable one which is the asymptotic limit of the population dynamics for "large" initial distributions. This is similar to the kinetic case: $u' = u(u-b)(c-u)$ with $0 < b < c$, in which the unstable equilibrium point $u = b$ serves as a threshold between the persistence and extinction. Thus for the reaction-diffusion case, such a *conditional persistence* occurs for all $\mathcal{D} < \mathcal{D}_*$. But the threshold between the persistence and extinction is much more complicated than the scalar ODE case, since the phase space here is infinite-dimensional. It can be shown that the threshold set is a co-dimension one manifold in the cone of all positive functions (in an appropriate function space), the threshold manifold is homomorphic to the unit sphere of the positive cone, and it contains the unstable steady state u_2. This threshold manifold separates the set of all initial distributions into two disconnected subsets, which we can call "above threshold" (A) and "below thresold" (B) sets. For any initial distribution in A, the asymptotic state is the stable steady state u_1; for any initial distribution in B, the asymptotic state is the stable steady state 0; and the limit would be u_2 if the orbit starts on the threshold manifold (see Theorem 7.) An abstract threshold manifold theorem is recently proved by Jiang, Liang and Zhao [23].

In this paper, we obtain the bifurcation diagram of the steady state solutions of (1.2) when $f(x, u)$ is of weak Allee effect type. A representative bifurcation diagram is like Figure 2-c. In a sense, this bifurcation diagram is a combination of the two former cases (logistic and strong Allee effect.) There are two critical values $\mathcal{D}_1 < \mathcal{D}_*$ which divide the parameter space into three parts: *extinction regime* $\mathcal{D} > \mathcal{D}_*$, *conditional persistence regime* $\mathcal{D}_1 < \mathcal{D} < \mathcal{D}_*$, and *unconditional persistence regime* $0 < \mathcal{D} < \mathcal{D}_1$. We note that the bifurcation diagram could be more complicated than Figure 2-c (see Figure 3 in Section 2.) But at least for some special domains like intervals and circular disks, we are able to show that the exact bifurcation diagram is like Figure 2-c. The bifurcation diagrams for one-dimensional problems with weak Allee effect have been obtained by Conway [10,11] and Logan [29] with quadrature methods, and here we consider the higher space dimensional case with totally different methods.

In applications, we consider an example where the Allee effect is due to a type-II functional response given by:

$$f(u) = k\left(1 - \frac{u}{N}\right) - \frac{A}{1 + Bu}. \tag{1.4}$$

We also apply the results to a nonlinear diffusion model with logistic growth proposed by Turchin [47] and Cantrell and Cosner [5,6]:

$$\frac{\partial u}{\partial t} = \mathcal{D}\Delta\phi(u) + m(x)u - b(x)u^2, \tag{1.5}$$

where $\phi(u) = u^3 - Bu^2 + Cu$ for $B, C > 0$. The nonlinear diffusion models the aggregative movement of the animals, and although the growth rate is logistic, the dynamics of the equation is more like the one with weak Allee effect. The bifurcation diagram of the steady state solutions for (1.5) have been studied in [5,6] (see also [7]) by applying bifurcation theory to (1.5). We use a transformation of the variable to convert the steady state equation into a semilinear one, thus we can directly apply the results from this paper.

We will give the mathematical details of the bifurcation diagrams in Section 2; in Section 3, we discuss the persistence/extinction dynamics, and we partially describe the attracting regions of the two stable steady state solutions; in Section 4, we consider the applications to type-II functional response and nonlinear diffusion models. We conclude the paper with some discussions of biological implications of our mathematical results in Section 5.

2. Global Bifurcation

Let $\lambda = \mathcal{D}^{-1}$. The steady state solutions of (1.2) satisfy

$$\begin{cases} \Delta u + \lambda u f(x,u) = 0, & x \in \Omega, \\ u \geq 0, & x \in \Omega, \\ u = 0, & x \in \partial\Omega. \end{cases} \tag{2.1}$$

We establish an abstract framework for (2.1). Let $X = W^{2,p}(\Omega) \cap W_0^{1,p}(\Omega)$, and let $Y = L^p(\Omega)$ where $p > n$. Then $F: \mathbf{R} \times X \to Y$ defined by $F(\lambda, u) = \Delta u + \lambda u f(x,u)$ is a continuously differentiable mapping (see [7].) We denote the set of non-negative solutions of the equation by $S = \{(\lambda, u) \in \mathbf{R}^+ \times X : u \geq 0, F(\lambda, u) = 0\}$. From the strong maximum principle of elliptic equations, either $u \equiv 0$ or $u > 0$ on Ω. We define the set of solutions to (2.1) $S = S_0 \cup S_+$, where $S_0 = \{(\lambda, 0) : \lambda > 0\}$, and $S_+ = \{(\lambda, u) \in S : u > 0\}$. S_0 is a ray of trivial solutions of (2.1). The stability of a solution (λ, u) of (2.1) when viewed as an equilibrium solution to (1.2) can be determined by the eigenvalue problem:

$$\Delta\psi + \lambda[f(x,u) + u f_u(x,u)]\psi = -\mu\psi, \ x \in \Omega, \ \ \psi = 0, \ x \in \partial\Omega. \tag{2.2}$$

(2.2) has a smallest eigenvalue $\mu_1(u)$, then the solution u is *stable* if $\mu_1(u) > 0$, otherwise it is *unstable*. The destabilization of the zero equilibrium results in bifurcation of non-constant steady state solutions. From the results of [13], [4], the bifurcation point for positive solutions is defined by

$$\frac{1}{\lambda_1(f,\Omega)} = \sup_{u \in H_0^1(\Omega)} \left\{ \int_\Omega f(x,0) u^2(x) dx : \int_\Omega |\nabla u(x)|^2 dx = 1 \right\}. \tag{2.3}$$

$\lambda_1 \equiv \lambda_1(f,\Omega)$ is a bifurcation point where nontrivial solutions of (2.1) bifurcate from the line of trivial solutions $\{(\lambda, 0)\}$, and the local and global bifurcation pictures of (2.1) are shown in the following theorem:

Theorem 1. *Suppose that $f(x,u)$ satisfies (f1)–(f3), and*

$$\{x \in \overline{\Omega} : f(x,0) > 0\} \text{ is a set of positive measure.} \tag{2.4}$$

Then

1. $\lambda = \lambda_1$ *is a bifurcation point for* (2.1) *and there is a connected component* S_+^1 *of the set of positive solutions whose closure includes the point* $(\lambda, u) = (\lambda_1, 0)$*;*
2. *Near* $(\lambda_1, 0)$*,* S_+^1 *can be written as a curve* $(\lambda(s), u(s))$ *with* $s \in (0, \delta)$*,* $\lambda(s) \to \lambda_1$ *and* $u(s) = s\varphi_1 + o(s)$ *as* $s \to 0^+$*;*
3. *For any* $(\lambda, u) \in S_+^1$, $0 \leq u(x) \leq M$*, where* M *are defined in (f2);*
4. *When* $f(x,u)$ *is of logistic type for almost all* $x \in \overline{\Omega}$*, then the bifurcation at* $(\lambda_1, 0)$ *is supercritical, i.e.* $\lambda(s) > \lambda_1$ *for* $s \in (0, \delta)$*;*
5. *When* $f(x,u)$ *is of weak or strong Allee effect type for almost all* $x \in \overline{\Omega}$*, then the bifurcation at* $(\lambda_1, 0)$ *is subcritical, i.e.* $\lambda(s) < \lambda_1$ *for* $s \in (0, \delta)$.

The proof of Theorem 1 is mostly known, but there is no a single reference covering all proofs. We give a proof in the Appendix for the sake of completeness. When f is of logistic type for almost all $x \in \overline{\Omega}$, a much clear picture of the structure of the steady state solutions can be drawn (see Figure 2-a):

Theorem 2. *Suppose that $f(x,u)$ satisfies (f1)–(f3), and $f(x,u)$ is of logistic type for almost all $x \in \overline{\Omega}$. Then in addition to Theorem 1,*

1. *For each* $\lambda > \lambda_1$*, there exists a unique solution* $u(\lambda, x)$ *of* (2.1)*;*
2. S_+ *can be parameterized as* $S_+^1 = \{(\lambda, u(\lambda, x)) : \lambda > \lambda_1\}$*,* $\lim_{\lambda \to \lambda_1^+} u(\lambda) = 0$*, and* $\lambda \mapsto u(\lambda, \cdot)$ *is differentiable;*
3. *For any* $\lambda > \lambda_1$*,* $u(\lambda, x)$ *is stable, and* $u(\lambda, x)$ *is strictly increasing in* λ.
4. *For any initial value* $u_0(x) \geq (\not\equiv) 0$*,* $\lim_{t\to\infty} u(x,t) = u(\lambda, x)$ *in* $H_0^1(\Omega)$*, where* $u(x,t)$ *is the solution of* (1.2).

Theorem 2 is also well-known, see for example, Henry [20], Cantrell and Cosner [4], Shi and Shivaji [39] and many other papers, thus we will omit the proof here. But we recall Lemma 3 in [40], which will be used later.

Lemma 1. *Suppose that* $f : \Omega \times \mathbf{R}^+ \to \mathbf{R}$ *is a continuous function such that* $f(x,s)$ *is decreasing for* $s > 0$ *at almost all* $x \in \overline{\Omega}$*. Let* $w, v \in C(\overline{\Omega}) \cap C^2(\Omega)$ *satisfy*
(a) $\Delta w + wf(x,w) \leq 0 \leq \Delta v + vf(x,v)$ *in* Ω,
(b) $w, v > 0$ *in* Ω *and* $w \geq v$ *on* $\partial\Omega$*,*
(c) $\Delta v \in L^1(\Omega)$*.*
Then $w \geq v$ *in* $\overline{\Omega}$*.*

Our main result this section is on the global bifurcation diagram when f is of a weak Allee effect type:

Theorem 3. *Suppose that $f(x,u)$ satisfies (f1)–(f3), and $f(x,u)$ is of a weak Allee effect type for almost all $x \in \overline{\Omega}$. Then in addition to Theorem 1,*

1. *There exists* $\lambda_* \equiv \lambda_*(f, \Omega)$ *satisfying* $\lambda_1 > \lambda_* > 0$ *such that* (2.1) *has no solution when* $\lambda < \lambda_*$, *and when* $\lambda \geq \lambda_*$, (2.1) *has a maximal solution* $u_m(\lambda, x)$ *such that for any solution* $v(\lambda, x)$ *of* (2.1), $u_m(\lambda, x) \geq v(\lambda, x)$ *for* $x \in \Omega$*;*
2. *For* $\lambda > \lambda_*$, $u_m(\lambda, x)$ *is increasing with respect to* λ, *the map* $\lambda \mapsto u_m(\lambda, \cdot)$ *is right continuous for* $\lambda \in [\lambda_*(f, \Omega), \infty)$, *i.e.* $\lim_{\eta \to \lambda^+} ||u_m(\eta, \cdot) - u_m(\lambda, \cdot)||_X = 0$, *and all* $u_m(\lambda, \cdot)$ *are on the global branch* S^1_+.
3. (2.1) *has at least two solutions when* $\lambda \in (\lambda_*, \lambda_1)$ *(see Fig. 3.)*

Proof. Recall that S^1_+ is the connected component of S_+ whose closure contains $(\lambda_1, 0)$. From Theorem 1, near $(\lambda_1, 0)$, S^1_+ is a smooth curve and the bifurcation is subcritical. Thus $\lambda_*(f, \Omega) = \inf\{\lambda > 0 : (\lambda, u) \in S^1_+\} < \lambda_1$. On the other hand, let Λ_1 be the principal eigenvalue of the problem

$$\Delta\phi + \Lambda\phi = 0,\ x \in \Omega,\quad \phi = 0,\ x \in \partial\Omega, \tag{2.5}$$

and let ϕ_1 be the corresponding positive eigenfunction. Then from (2.1) and (2.5), we obtain

$$\int_\Omega [\lambda f(x, u(x)) - \Lambda_1] u(x)\phi_1(x) dx = 0. \tag{2.6}$$

Thus $\lambda_* > \Lambda_1/N > 0$, where N is the maximum carrying capacity defined in (f3). From Theorem 1, (2.1) has at least one solution for each $\lambda > \lambda_*$.

Next we show that for each $\lambda > \lambda_*$, (2.1) has a maximal solution. We define

$$\overline{f}(x, u) = \begin{cases} f(x, u_1(x)), & 0 \leq u \leq u_1(x); \\ f(x, u), & u > u_1(x), \end{cases} \tag{2.7}$$

where $u_1(x)$ is defined in (f3). Then $\overline{f}$ satisfies (f1)–(f3), and $\overline{f}$ is of logistic type for all $x \in \overline{\Omega}$. In particular, $\overline{f}$ is non-increasing with respect to u. From Theorem 2, for each $\lambda > \lambda_1(\overline{f}, \Omega)$, (2.1) with f replaced by $\overline{f}$ has a unique solution $\overline{u}(\lambda, x)$. Notice here $\overline{f}$ is not C^1 in u at $u = u_1(x)$, but $\overline{f}_u(x, u)$ is still a measurable function on $\overline{\Omega} \times \mathbf{R}$, hence the results in Theorem 2 still hold (see Theorem 2.3 of [4].) For $\lambda \leq \lambda_1(\overline{f}, \Omega)$, (2.1) has no solution. Indeed if there is such a solution $(\lambda, u(x))$, then

$$\int_\Omega [\lambda f(x, u(x)) - \lambda_1(\overline{f}, \Omega)\overline{f}(x, 0)] u(x)\overline{\phi}_1(x) dx = 0, \tag{2.8}$$

where $\overline{\phi}_1$ is the positive eigenfunction which corresponds to $\lambda_1(\overline{f}, \Omega)$. But if $\lambda \leq \lambda_1(\overline{f}, \Omega)$, $\lambda f(x, u(x)) - \lambda_1(\overline{f}, \Omega)\overline{f}(x, 0) \leq (\not\equiv) 0$, which contradicts with (2.8). Thus $\lambda_*(f, \Omega) > \lambda_1(\overline{f}, \Omega)$.

Suppose that $v(\lambda, x)$ is a solution of (2.1) for $\lambda > \lambda_*(f, \Omega)$, then $\Delta v + \lambda v\overline{f}(x, v) \geq \Delta v + \lambda v f(x, v) = 0$. On the other hand, $\Delta\overline{u} + \lambda\overline{u}\overline{f}(x, \overline{u}) = 0$, and $\overline{u} = v = 0$ on $\partial\Omega$. Thus by Lemma 1, $\overline{u}(\lambda, x) \geq v(\lambda, x)$ for all $x \in \Omega$. Thus $\overline{u}(\lambda, \cdot)$ and $v(\lambda, \cdot)$ is a supersolution and subsolution pair of (2.1). By the well-known comparison method, there is a solution $u_m(\lambda, x)$ (which may equal to v) of (2.1) obtained by iterating the supersolution $\overline{u}$. Since each function in the iteration sequence is greater than $v(\lambda, x)$, then $u_m(\lambda, x) \geq v(\lambda, x)$, and $v(\lambda, x)$

is an arbitrary solution, so $u_m(\lambda, x)$ is the maximal solution. When $f(x, u) \geq 0$ for almost all (x, u), $\overline{u}(\lambda, \cdot)$ is increasing with respect to λ. Hence so is $u_m(\lambda, x)$. This also shows that $\lim_{\lambda \to (\lambda_*)^+} u_m(\lambda, x) = u_m(\lambda_*, x) \geq 0$ exists. $u_m(\lambda_*, x) \not\equiv 0$ since $\lambda_* < \lambda_1$ and λ_1 is the only bifurcation point along the trivial solutions. On the other hand, from elliptic estimates, $u_m(\lambda_*, x)$ is a classical solution of (2.1), and from the maximum principle, $u_m(\lambda_*, x) > 0$ in Ω. This proves the existence of a positive solution at $\lambda = \lambda_*$.

We show that when $u_m(\lambda, x)$ is increasing on λ, then $u_m(\lambda, x)$ is right continuous. Since $f(x, u)$ is bounded, then from standard elliptic estimates, $u_m(\lambda, \cdot)$ is bounded in $W^{2,p}(\Omega)$ for $p > 1$ and $u_m(\lambda, \cdot)$ is decreasing when $\lambda \to \lambda_a^+$ for some λ_a. Then for a subsequence $\lambda^n \to \lambda_a$, $u_m(\lambda, \cdot)$ converges to a function $w(\lambda_a, \cdot)$ in $W^{1,p}(\Omega)$, and $w(\lambda_a, \cdot)$ is a weak solution of (2.1). By definition, $w(\lambda_a, \cdot) \leq u_m(\lambda_a, \cdot)$. But $u_m(\lambda_a, \cdot) \leq u_m(\lambda, \cdot)$ for $\lambda > \lambda_a$, then $u_m(\lambda_a, \cdot) \leq \lim_{\lambda \to \lambda_a^+} u_m(\lambda, \cdot) = w(\lambda_a, \cdot)$. Thus $w(\lambda_a, \cdot) = u_m(\lambda_a, \cdot)$, and by standard elliptic estimates, we can show the convergence of $u_m(\lambda, \cdot)$ can be in X. Thus $u_m(\lambda, \cdot)$ is right continuous with respect to λ. The proof of that u_m must be on the global branch can be found in Proposition 3.3 of Du and Shi [16].

Finally we prove that for $\lambda \in (\lambda_*(f, \Omega), \lambda_1(f, \Omega))$, (2.1) has at least two solutions. We use a variant of Mountain-Pass Lemma. As in the standard setup, we define

$$I(\lambda, u) = \int_\Omega \left[\frac{1}{2} |\nabla u(x)|^2 - \lambda G(x, u(x)) \right] dx, \tag{2.9}$$

where $u \in H_0^1(\Omega)$, $G(x, u) = \int_0^u tf(x, t)dt$ when $u \geq 0$, and $G(x, u) = 0$ when $u < 0$. It is well-known that a critical point u of $I(\lambda, u)$ is a classical solution of (2.1) from the smoothness of $f(x, u)$ in u. When $\lambda \in (\lambda_*(f, \Omega), \lambda_1(f, \Omega))$, by using the sub and super-solutions in the last paragraph, and [44] Theorem I.2.4 at page 17, one can show that (2.1) has a solution $u_1(\lambda, \cdot)$ such that $\overline{u}(\lambda, x) \geq u_1(\lambda, x) \geq v(\lambda, x)$, which is a relative minimizer of $I(\lambda, \cdot)$ in the set $U = \{u \in H_0^1(\Omega) : \overline{u} \geq u \geq v \text{ almost everywhere}\}$, and v is an arbitrary solution of (2.1). From the proof in [44] page 148, $u_1(\lambda, \cdot)$ is also a relative minimizer of $I(\lambda, \cdot)$ in $H_0^1(\Omega)$ if v is a strict subsolution (note that $\overline{u}(\lambda, \cdot)$ is always a strict supersolution.) But $u_m(\lambda_a, \cdot)$ for $\lambda_a < \lambda$ is a strict subsolution from the last paragraph, thus we can take $v = u_m(\lambda_a, \cdot)$. On the other hand, when $\lambda < \lambda_1(f, \Omega)$, $u = 0$ is also a relative minimizer of $I(\lambda, \cdot)$ in $H_0^1(\Omega)$. Now from [44] Theorem II.10.3 at page 144, either $I(\lambda, \cdot)$ has a critical point u_2 which is not of minimum type, or $I(\lambda, \cdot)$ has a continuum of relative minimizers, which connect u_1 and 0, with $I(\lambda, u) = 0$ for all u on the continuum. The latter case can not occur since $u = 0$ is a strict local minimizer. Therefore (2.1) has at least two solutions u_1 and u_2 for $\lambda \in (\lambda_*(f, \Omega), \lambda_1(f, \Omega))$, u_1 is a local minimizer, and u_2 is of mountain-pass type. □

The existence of two positive steady state solutions can also be proved using global bifurcation theory, see [16] Proposition 3.3. It is also possible to show that (2.1) has exactly two solutions when $\lambda \in (\lambda_*(f, \Omega), \lambda_1(f, \Omega))$ and the domain Ω is a ball. Exact multiplicity of solutions to (2.1) with homogeneous spherical habitat has been studied in Ouyang and Shi [33,34], and Korman and Shi [26]. We recall

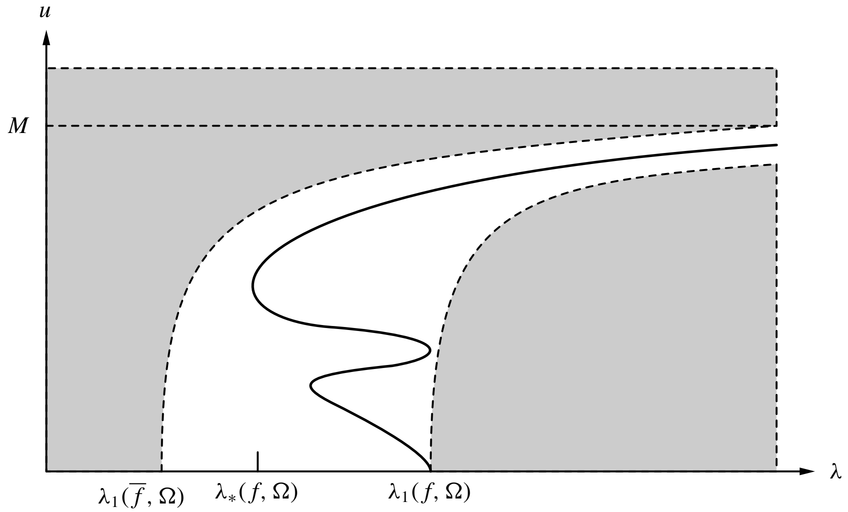

Fig. 3. Bifurcation diagram for weak Allee effect. Notice that it is possible that the equation possesses more than two steady state solutions in (λ_*, λ_1); the two dotted curves denote the bifurcation curves for $\overline{f}$ and $\underline{f}$ respectively; the shaded area denotes the regions where (2.1) cannot have a solution.

some related results here. We consider the case when $f(u)$ is of weak Allee effect type. Since f is now independent of x, conditions (f1)–(f4) become

(ff) There exist u_1 and u_2 such that $u_2 > u_1 > 0$, $f(u) > 0$ for $u \in [0, u_2)$, $f(u_2) = 0$, f is increasing on $(0, u_1)$ and f is decreasing on (u_1, u_2).

When the spatial dimension is one, we obtain the following result on the precise bifurcation diagram: (see Figure 2-c)

Theorem 4. *Suppose that $f(u)$ satisfies (ff) and*

(f5) $f \in C^2(\mathbf{R}^+)$, there exists $u_3 \in (0, u_2)$ such that $(uf(u))''$ is non-negative on $(0, u_3)$, and $(uf(u))''$ is non-positive on (u_3, u_2).

Then the equation

$$\begin{aligned} &u'' + \lambda u f(u) = 0, \quad r \in (-1, 1), \\ &u > 0, \quad r \in (-1, 1), \quad u(-1) = u(1) = 0, \end{aligned} \tag{2.10}$$

has no solution when $\lambda < \lambda_*(f)$, has exactly one solution when $\lambda = \lambda_*$ and $\lambda \geq \lambda_1(f)$, and has exactly two solutions when $\lambda_*(f) < \lambda < \lambda_1(f)$, where $\lambda_*(f) = \lambda_*(f, I)$ and $\lambda_1(f) = \lambda_1(f, I)$, $I = (-1, 1)$, are same as the constants defined in Theorem 3. Moreover

1. *All solutions lie on a single smooth curve which bifurcates from $(\lambda, u) = (\lambda_1(f), 0)$;*
2. *The solution curve can be parameterized by $d = u(0) = \max_{x \in I} u(x)$ and it can be represented as $(\lambda(d), d)$, where $d \in (0, u_2)$;*

3. *Let* $\lambda(d_1) = \lambda_*(f)$*, then for* $d \in (0, d_1)$*,* $\lambda'(d) < 0$ *and the corresponding solution* $(\lambda(d), u)$ *is unstable, and for* $d \in (d_1, u_2)$*,* $\lambda'(d) > 0$ *and the corresponding solution* $(\lambda(d), u)$ *is stable.*

When the habitat is a multi-dimensional ball, the following result is proved in proved in Korman and Shi [26].

Theorem 5. *Suppose that* $f(u)$ *satisfies (ff), (f5) and*

(f6) $2[(uf(u))']^2 - nuf(u)(uf(u))'' \geq 0$ *for* $u \in (0, u_2)$*,*

where n is the spatial dimension. Then all the conclusions in Theorem 4 hold for

$$\Delta u + \lambda u f(u) = 0, \quad x \in B^n, \quad u > 0, \quad x \in B^n, \quad u = 0, \quad x \in \partial B^n, \tag{2.11}$$

where $B^n = \{x \in \mathbf{R}^n : |x| < 1\}$.

3. Dynamical Behavior and attracting regions

For diffusive logistic equations, the extinction or persistence of population depends on the diffusion constant, and is unconditional for any initial distribution u_0 (see Theorem 2). But we have shown that in the presence of an Allee effect, (1.2) could have multiple steady state solutions, and extinction and persistence are both possible depending on the initial value u_0. Mathematically the maximal steady state u_m and the extinction steady state 0 are both locally stable. In this section, we partially describe the attraction regions of the two stable steady states. For a general set up of the dynamics of semilinear parabolic equation, see Henry [20].

First we show that bounds of the solution set S_+ in the Allee effect case can be described in terms of two logistic systems. Suppose that $f(x, u)$ is of weak Allee effect type for almost all $x \in \overline{\Omega}$. Recall that $\overline{f}$ is defined in (2.7), we also define

$$\underline{f}(x, u) = \begin{cases} f(x, 0), & 0 \leq u \leq u_3(x); \\ f(x, u), & u > u_3(x), \end{cases} \tag{3.1}$$

where $u_3(x) \in (u_1(x), u_2(x))$ such that $f(x, u_3(x)) = f(x, 0)$. Then both $\overline{f}$ and $\underline{f}$ are non-increasing on $[0, u_2(x)]$, thus Theorem 2 can be applied to (2.1) with f replaced by $\overline{f}$ or $\underline{f}$ (see the remark on the smoothness of $\overline{f}$ or $\underline{f}$ in the proof of Theorem 3.) When $f = \overline{f}$, the solution set of (2.1) has the form:

$$\overline{S_+} = \{(\lambda, \overline{u}(\lambda, x)) : \lambda_1(\overline{f}, \Omega) < \lambda < \infty\}, \tag{3.2}$$

and when $f = \underline{f}$, the solution set of (2.1) has the form:

$$\underline{S_+} = \{(\lambda, \underline{u}(\lambda, x)) : \lambda_1(\underline{f}, \Omega) < \lambda < \infty\}, \tag{3.3}$$

Proposition 1. *The solution set* S_+ *of* (2.1) *lies between* $\overline{S_+}$ *and* $\underline{S_+}$*, i.e.,*

$$S_+ \subset \{(\lambda, u) : \lambda_1(\overline{f}, \Omega) < \lambda < \infty, \max\{\underline{u}(\lambda, \cdot), 0\} < u < \overline{u}(\lambda, \cdot)\}, \tag{3.4}$$

(see Figure 3, where two dotted curves represent $\underline{S_+}$ *and* $\overline{S_+}$*.)*

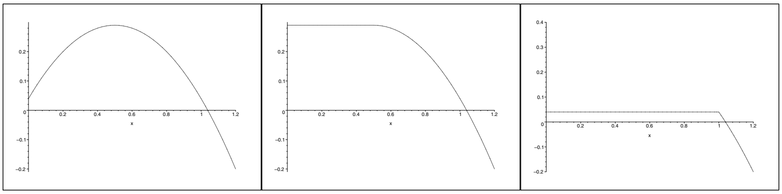

Fig. 4. (a) weak Allee effect f; (b) upper logistic $\overline{f}$; (c) lower logistic $\underline{f}$.

Proof. Since $\overline{f}$ and $\underline{f}$ are non-increasing on $[0, u_2(x)]$, then we can apply Lemma 1 in the same way as in the proof of Theorem 3 to prove this result. The strict inequality can be proved by the strong maximum principle. □

Next we consider the attracting region of the maximal solution u_m.

Theorem 6. *Suppose that $f(x, u)$ satisfies (f1)–(f3), and $f(x, u)$ is of weak Allee effect type for almost all $x \in \overline{\Omega}$. Let $u_m(\lambda, x)$ be the maximal solution of* (2.1)*, and let $u(x, t)$ be the solution of* (1.2)*. Then*

1. *If $\lambda < \lambda_*(f, \Omega)$, for any $u_0(x) \geq 0$, the population extinguishes and $\lim_{t\to\infty} u(x, t) = 0$ uniformly for $x \in \overline{\Omega}$;*
2. *If $\lambda \geq \lambda_*(f, \Omega)$, for $u_0(x) \geq u_m(\lambda_*, x)$, the population persists and*
$$u_m(\lambda, x) \geq \overline{\lim}_{t\to\infty} u(x, t) \geq \underline{\lim}_{t\to\infty} u(x, t) \geq u_m(\lambda_*, x); \tag{3.5}$$
if $u_0(x) \geq u_m(\lambda, x)$, then $\lim_{t\to\infty} u(x, t) = u_m(\lambda, x)$ uniformly for $x \in \overline{\Omega}$.
3. *If $\lambda > \lambda_1(f, \Omega)$, for any $u_0(x) \geq 0$, the population persists and*
$$u_m(\lambda, x) \geq \overline{\lim}_{t\to\infty} u(x, t) \geq \underline{\lim}_{t\to\infty} u(x, t) \geq \underline{u}(\lambda, x), \tag{3.6}$$
where $\underline{u}$ is the unique solution of (2.1) *with $f = \underline{f}$.*

Proof. From the maximum principle, $u(x, t) \geq 0$ for any $x \in \overline{\Omega}$ and $t > 0$. For Part 1, it is well-known (see [20]) that the ω-limit set of $\{u(x, t)\}$ is the union of steady state solutions, but $u = 0$ is the unique non-negative steady state, so the limit must be $u = 0$. Next we prove Part 2. Since $f(x, u) \geq 0$ for almost all x and $u_2 \geq u \geq 0$, then for $v = u_m(\lambda_*, x)$, (recall that $\lambda_* = \mathcal{D}_*^{-1}$ and $\lambda = \mathcal{D}^{-1}$)

$$\begin{aligned} 0 &= \mathcal{D}_* \Delta v - f(x, v) = \mathcal{D}(\Delta v - \lambda_* f(x, v)) \\ &\geq \mathcal{D}(-\Delta v - \lambda f(x, v)) = v_t - \mathcal{D}\Delta v - f(x, v). \end{aligned} \tag{3.7}$$

Thus $v = u_m(\lambda_*, \cdot)$ is a subsolution of (1.2), and the solution $v(x, t)$ of (1.2) with $u_0 = u_m(\lambda_*, \cdot)$ is increasing in t, thus from the comparison principle of parabolic equation, $u(x, t) \geq v(x, t) \geq u_m(\lambda_*, x)$. On the other hand, $\overline{\lim}_{t\to\infty} u(x, t) \leq u_m(\lambda, x)$, so we obtain (3.7). If $u_0 \geq u_m(\lambda, x)$, then $u(x, t) \geq u_m(\lambda, x)$ for all $t > 0$ since u_m is a steady state. Therefore we must have $\lim_{t\to\infty} u(x, t) = u_m(\lambda, x)$. For Part 3, the lower bound of $u(x, t)$ can be obtained from the comparison principle, Theorem 2 and the fact that $f(x, u) \geq \underline{f}(x, u)$. □

When the habitat Ω is one dimensional or a n-dimensional ball, the exact bifurcation diagram is known under some convexity conditions on f (see Theorems 4 and 5), we have a much better understanding of dynamical behavior. In the following, we define the positive cone $C = \{u \in C(\overline{\Omega}) : u(x) \geq 0,\ x \in \Omega;\ u(x) = 0, x \in \partial\Omega\}$.

Theorem 7. *Suppose that the assumptions on $f(u)$ and Ω in Theorems 4 and 5 are satisfied. Then in addition to Theorem 6,*

1. *If $\lambda > \lambda_1(f, \Omega)$, then $\lim_{t\to\infty} u(x,t) = u_m(\lambda, x)$ uniformly for $x \in \overline{\Omega}$.*
2. *If $\lambda_* \leq \lambda < \lambda_1$, then there exists a co-dimension one manifold $M \subset C$ such that $C \backslash M$ has exactly two connected components X_1 and X_2, such that if $u_0 \in X_1$, $\lim_{t\to\infty} u(x,t) = u_m(\lambda, x)$; if $u_0 \in X_2$, $\lim_{t\to\infty} u(x,t) = 0$; and if $u_0 \in M$, $\lim_{t\to\infty} u(x,t) = u_s(\lambda, x)$, which is the unique non-maximal positive steady state solution.*

Proof. Part 1 is clear since $u_m(\lambda, x)$ is the unique positive steady state, and it can be proved that $u = 0$ is unstable (see [20].) For part 2, the existence of manifold M follows from Theorem 2.2 of [23], and the verification of the assumptions is similar to the proof of Theorem 3.1 in [23]. Then the convergence of the flow to u_m in X_1 and to 0 in X_2 also follows from Theorem 2.2 of [23]. Then for $u_0 \in M$, the limit must be u_s since it is the only other steady state. □

The results in this section show that in the diffusive equation with weak Allee effect, there are two important threshold diffusion constants $\mathcal{D}_* = \lambda_*^{-1}$ and $\mathcal{D}_1 = \lambda_1^{-1}$. When $\mathcal{D} > \mathcal{D}_*$, the species always becomes extinct; and when $\mathcal{D} < \mathcal{D}_1$, then the species always persists (although maybe not tend to the maximum steady state). In the intermediate range $\mathcal{D}_1 < \mathcal{D} < \mathcal{D}_*$, a bistable structure exists in the sense that there exist at least two stable non-negative steady states and one unstable positive steady state (see Theorem 6.) When the exact structure of the steady states is known, then the dynamical system has an exact saddle point structure as described in Theorem 7 (see details in [23].) We remark that the results in [23] only hold for monotone dynamical systems (the scalar reaction diffusion belongs to that category). In [16], the bistability in a diffusive predator-prey system (which is not a monotone system) was proved, but the exact saddle point structure is not known.

4. Biological Applications

4.1. Diffusive Logistic Model with Predation

A simple population model with Allee effect (without diffusion) is

$$\frac{du}{dt} = Ku\left(1 - \frac{u}{N}\right) - \frac{Au}{1 + Bu}, \tag{4.1}$$

where u is the size of a population, and $k, N, A, B > 0$ are constants. The extra negative term in the equation can be interpreted as the search of a mate, or the impact of a satiating generalist predator (see for example, Holling [21], and Thieme [46] page 65).

In this subsection, we consider the diffusive logistic equation with predation, which causes the Allee effect:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \mathcal{D}\Delta u + Ku\left(1 - \dfrac{u}{N}\right) - \dfrac{Au}{1+Bu}, & t > 0,\ x \in \Omega, \\ u(t,x) = 0, & t > 0,\ x \in \partial\Omega, \\ u(0,x) = u_0(x) \geq 0, & x \in \Omega, \end{cases} \tag{4.2}$$

Here we assume that $\mathcal{D} > 0$ and $K, N, A, B > 0$ are constants. The nondimensionalized steady state equation of (4.2) can be written as

$$\Delta u + \lambda\left(ku - u^2 - \frac{u}{1+mu}\right) = 0,\ x \in \Omega,\quad u > 0,\ x \in \Omega,\quad u = 0,\ x \in \partial\Omega, \tag{4.3}$$

where $\lambda, k, m > 0$. Here $\lambda^{-1} = \mathcal{D}A^{-1}$ is the (rescaled) diffusion rate, $k = KA^{-1}$ is the (rescaled) maximum growth rate per capita, and $m = BN$ is the (rescaled) prey handling time. From simple algebra and definitions in Section 1, we have

Proposition 2. *Let* $g(u) = ku - u^2 - u/(1+mu) \equiv uf(u)$.

1. *If* $0 \leq m < 1$ *and* $k > 1$, *then* $f(u)$ *is of logistic type;*
2. *If* $m > 1$ *and* $k > 1$, *then* $f(u)$ *is of weak Allee effect type;*
3. *If* $0 < k < 1$, $m > 1$ *and* $f((-1+\sqrt{m})/m) > 0$, *then* $f(u)$ *is of strong Allee effect type.*

By applying Theorems 2 and 3, we now obtain

Theorem 8. *Suppose that* Ω *is a connected smooth bounded region in* $\mathbf{R}^n$, $n \geq 1$, *and* $f(u) = k - u - 1/(1+mu)$.

1. *If* $0 \leq m < 1$ *and* $k > 1$, *then* (4.3) *has no solution when* $\lambda \leq \lambda_1(f,\Omega)$, *and has a unique solution* $u(\lambda, x)$ *when* $\lambda > \lambda_1(f,\Omega)$, *where* $\lambda_1(f,\Omega) = \Lambda_1/(k-1)$ *and* Λ_1 *is the principal eigenvalue defined in* (2.5)*;* $(\lambda, u(\lambda,\cdot))$ *is a smooth curve in* $\mathbf{R} \times X$, *and* $u(\lambda,\cdot)$ *is increasing with respect to* λ*;*
2. *If* $m > 1$ *and* $k > 1$, *then there exists* $\lambda_* < \lambda_1(f,\Omega)$ *such that* (4.3) *has no solution when* $\lambda < \lambda_*$, *has at least one solution when* $\lambda \geq \lambda_1(f,\Omega)$, *and has at least two solutions when* $\lambda_* < \lambda < \lambda_1(f,\Omega)$.

We remark that in [26], an exact multiplicity result for the spherical habitat is obtained for the case of weak and strong Allee effect. The dynamical behavior of (4.2) is now rather clear in term of parameters k and m, and the results in Theorems 6 and 7. The parameter ranges of (k, m) so that $f(u)$ belonging to logistic, weak or strong Allee effect are shown in Fig. 5. Two boundary lines are given by $k = 1$ and $m = 1$, and the boundary between strong Allee effect and $f(u) < 0$ regions is given by a curve $F(u_+(m,k)) = 0$ where $F(u) = \int_0^u tf(t)dt$ and $u_+(m,k)$ is the larger zero of $f(u) = 0$.

If we fix $k > 1$ (strong growth rate), then a bifurcation point $\lambda_1 = \Lambda/(k-1)$ is also fixed; when the handling time m is small, the population has an unconditional persistence if $\lambda > \lambda_1$; when $m > 1$, a conditional persistence interval

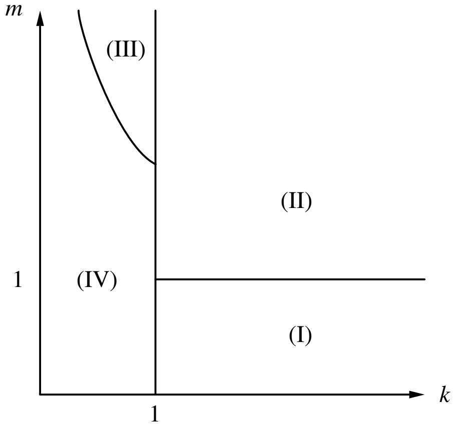

Fig. 5. Parameter regions on (k, m) space. (I): logistic; (II): weak Allee effect; (III): strong Allee effect; and (IV): $f(u) \leq 0$.

$(\lambda_*(m), \lambda_1)$ exists. By using $\overline{f}$ in Section 3, we can show that $\lambda_*(m)$ has a lower bound Λ/k. Hence for m large, the conditional persistence interval for λ is roughly $(\Lambda/k, \Lambda/(k-1))$. So when the handling time is larger, the prey species could still survive under a faster diffusion rate. On the other hand, if $k < 1$ (weak growth rate), then $u = 0$ is always a stable steady state, and small initial distribution will always lead to extinction; when m is small, the predator consumes the prey population in a faster pace than the prey can tolerate, then the prey is destined for extinction; when m is larger, the system has the character of strong Allee effect, hence bistability holds for all small diffusion rates. And using the same argument above, the conditional persistence interval for λ is roughly $(\Lambda/k, \infty)$. In [8], the persistence and extinction of prey population under predator subsidies was considered, in which the dispersal and growth of the prey is governed by an equation similar to (4.2) but a more complicated boundary condition.

4.2. Logistic equation with nonlinear diffusion: model of aggregative movement

In this subsection, we consider a model of aggregative animal movement proposed by Turchin [47] and Cantrell and Cosner [5,6]:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \mathcal{D}\Delta\phi(u) + m(x)u - b(x)u^2, & t > 0,\ x \in \Omega, \\ u(t,x) = 0, & t > 0,\ x \in \partial\Omega, \\ u(0,x) = u_0(x) \geq 0, & x \in \Omega. \end{cases} \tag{4.4}$$

Here we assume that $\mathcal{D} > 0$, $\phi(u) = u^3 - Bu^2 + Cu$ for $B, C > 0$ as in [47], $m(x), b(x) \in C^\alpha(\overline{\Omega})$ for $\alpha \in (0, 1)$, and $b(x) \geq b_0 > 0$ for all $x \in \overline{\Omega}$. We shall limit ourselves to only the weakly aggregative case, which requires $\phi'(u) > 0$ for all $u \geq 0$, and it is equivalent to $B^2 - 3C < 0$. The steady state solutions of (4.4) satisfy

$$\Delta\phi(u)+\lambda[m(x)u-b(x)u^2]=0,\ x\in\Omega,\quad u>0,\ x\in\Omega,\quad u=0,\ x\in\partial\Omega, \tag{4.5}$$

where $\lambda=\mathcal{D}^{-1}>0$.

We show that (4.5) can be converted into (2.1) with an appropriate $f(x,u)$. Let

$$v=\phi(u),\quad \text{and } u=\phi^{-1}(v)\equiv G(v). \tag{4.6}$$

Since $\phi'>0$, then ϕ and G are invertible mappings on $\mathbf{R}^+$, and (4.5) becomes

$$\Delta v+\lambda[m(x)G(v)-b(x)[G(v)]^2]=0,\ x\in\Omega,\quad v>0,\ x\in\Omega,\quad v=0,\ x\in\partial\Omega. \tag{4.7}$$

We define

$$f(x,v)=\begin{cases}\dfrac{m(x)G(v)-b(x)[G(v)]^2}{v} & \text{when } v>0,\\ m(x)G'(0)=\lim\limits_{v\to 0}\dfrac{m(x)G(v)-b(x)[G(v)]^2}{v} & \text{when } v=0.\end{cases} \tag{4.8}$$

Then the equation in (4.7) becomes $\Delta v+\lambda vf(x,v)=0$. For fixed $x\in\overline{\Omega}$, the function $f(\cdot,v)$ has the same monotonicity on v as the function

$$g(x,u)=\frac{m(x)u-b(x)u^2}{\phi(u)}=\frac{m(x)-b(x)u}{u^2-Bu+C} \tag{4.9}$$

on u since

$$\frac{\partial f(x,v)}{\partial v}=\frac{\partial g(x,u)}{\partial u}G'(v), \tag{4.10}$$

and $G'(v)=[\phi'(G(v))]^{-1}>0$. The following proposition shows that the qualitative properties of $f(x,v)$ fall into the categories which we defined earlier:

Proposition 3. *Suppose that* $f(x,v)$ *is defined as in* (4.8).

1. *If* $m(x)>0$, $Bm(x)-Cb(x)\le 0$, *then* $f(x,v)$ *is of logistic type;*
2. *If* $m(x)>0$, $Bm(x)-Cb(x)>0$, *then* $f(x,v)$ *is of weak Allee effect type.*

Proof. We have $f(x,0)=m(x)/C$, and

$$\frac{\partial g}{\partial u}(x,u)=\frac{b(x)u^2-2m(x)u+Bm(x)-Cb(x)}{(u^2-Bu+C)^2}. \tag{4.11}$$

Then the conclusions can be easily drawn from the definitions of these growth types, (4.10) and the elementary algebraic properties of $\partial g/\partial u$. □

From results in previous sections, we now obtain

Theorem 9. *Suppose that* $\phi(u)=u^3-Bu^2+Cu$, *where* $0<B^2<3C$, $m(x),b(x)\in C^\alpha(\overline{\Omega})$, *and* $m(x)>0$, $b(x)\ge b_0>0$ *for all* $x\in\overline{\Omega}$.

1. *$\lambda = \lambda_1 \equiv \lambda_1(f, \Omega)$ is a bifurcation point, where λ_1 is defined by*

$$\frac{1}{\lambda_1(f,\Omega)} = \sup_{u \in H_0^1(\Omega)} \left\{ C^{-1} \int_\Omega m(x)u^2(x)dx : \int_\Omega |\nabla u(x)|^2 dx = 1 \right\}; \tag{4.12}$$

there is a connected component T_+^1 of the solution set of (4.5) *whose closure includes* $(\lambda_1, 0)$*, and the projection of T_+^1 onto $\mathbf{R}^+ = \{\lambda\}$ covers at least* (λ_1, ∞)*; near the bifurcation point, T_+^1 can be written as a curve* $(\lambda(s), u(s))$*, with $\lambda(0) = \lambda_1$, $u(s) = \phi^{-1}(s\varphi_1) + o(s)$, and*

$$\lambda'(0) = -\frac{2[\lambda_1]^2}{C^3} \frac{\int_\Omega [Bm(x) - Cb(x)]\varphi_1^3(x)dx}{\int_\Omega |\nabla \varphi_1(x)|^2 dx}, \tag{4.13}$$

where φ_1 is a positive solution of

$$\Delta\varphi + \frac{\lambda_1}{C} m(x)\varphi = 0, \ x \in \Omega, \quad \varphi = 0, \ x \in \partial\Omega; \tag{4.14}$$

2. *If $Bm(x) - Cb(x) \le 0$ for all $x \in \Omega_+$, then* (4.5) *has no solution when $\lambda \le \lambda_1$, and* (4.5) *has a unique solution $u(\lambda, x)$ when $\lambda > \lambda_1$; moreover, $T_+^1 = \{(\lambda, u(\lambda, x))\}$ is a smooth curve, and if Ω/Ω_+ is a zero measure set, then $u(\lambda, \cdot)$ is increasing on λ for all $x \in \Omega$;*
3. *If $Bm(x) - Cb(x) > 0$ for any $x \in \Omega_+$, then there exists $\lambda_*(f, \Omega) < \lambda_1$ such that* (4.5) *has no solution when $\lambda < \lambda_*$,* (4.5) *has a maximal solution $u_m(\lambda, x)$ when $\lambda > \lambda_*$; $u_m(\lambda, \cdot)$ is increasing on λ for all $x \in \Omega$, and* (4.5) *has at least two solutions when $\lambda \in (\lambda_*, \lambda_1)$.*

The more precise exact bifurcation diagram for radially symmetric case or $n = 1$ in Section 2 cannot be obtained for this case since for $h(v) = mG(v) - b[G(v)]^2$, (f5) is not satisfied. In [27], Lee et. al. use quadrature method to obtain exact bifurcation diagrams for this case. Similar results have also been obtained in [5,6] by different bifurcation methods, but the idea of transforming (4.5) into (4.7) was also mentioned in the introduction of [5]. We notice that to have a subcritical bifurcation from the trivial solutions, we only need $\int_\Omega [Bm(x) - Cb(x)]\varphi_1^3(x)dx > 0$ so a habitat with mixed growth rates of logistic and weak Allee effect types can also induce a subcritical bifurcation, and consequently conditional persistence and bistability.

5. Conclusions

A non-spatial model with a weak Allee effect has similar qualitative behavior as the non-spatial logistic model, which predicts unconditional persistence. A non-spatial model with strong Allee effect predicts conditional persistence, which is persistence for initial population above a threshold value, and extinction for the ones below the threshold. When the dispersal of the individuals is considered via passive diffusion, the population will always be led to extinction if the diffusion is too strong due to the hostile boundary condition, but the dynamical behaviors similar to the non-spatial models are inherited for logistic and strong Allee effect growths. For diffusion model with weak Allee effect growth, the ranges of diffusion parameters of extinction and unconditional persistence are bridged by a range of conditional persistence.

We point out that the above mentioned phenomenon is not restricted to the hostile boundary condition ($u(x) = 0$ on the boundary); most results in this paper remain basically same for the no-flux boundary condition ($\nabla u \cdot n = 0$ on the boundary), or the Robin boundary condition ($\nabla u \cdot n = -ku$ on the boundary). An example with Holling type II predation and no-flux boundary condition has recently considered in [16]. It is shown that the bifurcation diagram is roughly a reversed S-shaped, and the dynamics has a bistable structure similar to the one considered here.

Critical patch size of the habitat is introduced in the context of diffusive logistic equation, and for that case it is determined by the habitat geometry and the growth rate per capita at zero population only. In the case of conditional persistence, the critical patch size not only depends on habitat geometry and the growth rate per capita at zero population but also the the growth rate per capita at larger populations. In fact, an estimate of the critical patch size now can be can be obtained by (2.6) (see the discussions on λ_* at the end of subsection 4.1), which depends on the growth rate per capita at zero population and the maximum growth rate per capita when a weak Allee effect is present. When $\lambda < \lambda_*$ in (2.1), the population has a unconditional extinction.

The bifurcation diagram in Figure 2-c allows for the possibility of *hysteresis* as the diffusion constant $\mathcal{D}$ or the habitat size varies. Suppose we start with a large size habitat, and then slowly decrease the size. Then initially the population will stabilize at the unique steady state solution u_1. However when the habitat is too small (when $\lambda < \lambda_*$), the population collapses quickly to zero. To salvage the population, we may attempt to restore the habitat by slightly increasing λ so that $\lambda > \lambda_*$. But if the population has dropped below the threshold at that moment, then the population cannot be saved since it is now still in the basin of attraction of the stable steady state $u = 0$. A similar hysteresis phenomenon was observed for the outbreak of spruce budworm by Ludwig, Aronson and Weinberger [30] (see also [31].) Note that the growth rate per capita in [30] is $f(u) = r(1 - u/k) - u/(1 + u^2)$, which may not satisfy (f3)—it could initially decrease, but then increases to a peak before falling to zero. Thus the bifurcation diagram for that case is more complicated, and it may have two turning points on the bifurcation diagram (see [30].) This $f(u)$ is a logistic growth with a type-III functional response in which the predation in low density of prey is very small, and as we have seen in subsection 4.1, the weak Allee effect usually corresponds to a type-II functional response.

Since the hysteresis will lead a persistent population to sudden extinction, it is important to find a way to prevent it to happen. One indication of how far the population is from the critical point λ_* is the magnitude of the principal eigenvalue $\mu_1(f, \Omega)$ of (2.2). We notice that $\mu_1 > 0$ when $\lambda > \lambda_*$ and u is stabilized at the carrying capacity $u_m(\lambda, \cdot)$, and $\mu_1 = 0$ when $\lambda = \lambda_*$. Thus the closeness of μ_1 to 0 can be used as warning sign of the sudden extinction. When the current population distribution is known from observed population data, μ_1 can be calculated from variational method. Hence if μ_1 decreases toward zero, precaution should be taken on prevention of habitat size, and habitat restoration should be implemented. The authors would like to thank Professor Odo Diekmann for bringing this question to their attention.

Finally we remark on the applications of our results to biological invasions. Reaction-diffusion models have been used to predict the invasion of a foreign species into an unoccupied habitat. Mathematically traveling wave solutions are used to calculate the invasion speed and profile; thus it is necessary to study the reaction-diffusion equation on the whole Euclidean space $\mathbf{R}^n$. However all realistic habitats are bounded, and invasion often occurs in an isolated habitat which has a hostile boundary. When using a weak Allee effect type growth function, it is known that any initial population will initiate the propagation of the traveling wave similar to diffusive Fisher equation. Thus the reaction-diffusion predicts a successful invasion even with the population has a weak Allee effect growth. If the invasion is considered on a bounded habitat as in this paper, then we have shown that the success of invasion depends on the size of habitat S and the diffusion rate $\mathcal{D}$. When S (or $\mathcal{D}^{-1}$) is small, the invasion always fails (unconditional extinction); and when S (or $\mathcal{D}^{-1}$) is large, the invasion always succeeds (unconditional persistence). On the other hand, when S (or $\mathcal{D}^{-1}$) is in the intermediate range, there is a threshold profile which determines the success of the invasion. This gives another aspect of the biological invasion with Allee effect, see also [24,28,35,48].

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6. Appendix

In this appendix we show some details on the bifurcation theory which are used in proof of Theorem 1 in Section 2. First we prove

Proposition 4. *Suppose that f satisfies (f1)–(f3), and we assume that $\{x \in \overline{\Omega} : f(x,0) > 0\}$ is a set of positive measure. Then $\lambda_1(f,\Omega) > 0$ and there is a connected component S_+^1 of S_+ satisfying*

1. *the closure of S_+^1 in $\mathbf{R} \times X$ contains $(\lambda_1(f,\Omega), 0)$;*
2. *the projection of S_+^1 onto $\mathbf{R}$ via $(\lambda, u) \mapsto \lambda$ contains the interval $(\lambda_1(f,\Omega), \infty)$.*

Proof. The proof is based on the global bifurcation theorem of Rabinowitz [37]. Let H be the inverse of $-\Delta : X \to Y$. Then (2.1) can be rewritten as $u - \lambda H(f(x,0)u) + \lambda H(f(x,0)u - f(x,u)u) = 0$. Define $K_1(u) = H(f(x,0)u)$ and $K_2(u) = H(f(x,0)u - f(x,u)u)$, then the operator equation $u - \lambda K_1(u) + \lambda K_2(u) = 0$ satisfies the assumptions of Theorem 1.3 in [37]. Thus we can apply the global bifurcation theorem to conclude that the closure of a connected component S_+^1 of S_+ contains $(\lambda_1(f,\Omega), 0)$, and either S_+^1 is unbounded in $\mathbf{R} \times X$ or the closure of S_+^1 contains another $(\lambda_i(f,\Omega),0)$. The latter case cannot happen since a) from (2.6), any solution on S_+ must satisfy $\lambda > \Lambda_1/N$, thus S_+^1 cannot connect to any $(\lambda_{-n}(f,\Omega),0)$; b) all solutions on S_+^1 are positive, but the solutions bifurcating from $(\lambda_n(f,\Omega),0)$ with $n\ge 2$ are sign-changing near the bifurcation point.

Therefore S_+^1 must be unbounded in $\mathbf{R}\times X$. We show that the projection of S_+^1 onto $\mathbf{R}$ is unbounded. Indeed from maximum principle, $||u||_\infty \le M$, and thus $||u||_{L^p(\Omega)} \le M$ for any $p>1$. Then for any fixed $C_0>0$, and λ in $[0,C_0]$, from Sobolev Embedding Theorem, for $\alpha\in(0,1)$, $||u||_{C^\alpha(\overline{\Omega})}\le C_1$ for $C_1>0$ only depending on Ω, M and C_0. From the equation, we can obtain $||\Delta u||_{C^\alpha(\overline{\Omega})}\le C_2$, and hence $||u||_{C^{2,\alpha}(\overline{\Omega})}\le C_3$, where $C_2, C_3>0$ only depending on Ω, f, M and C_0. Therefore if S_+ is unbounded in $\mathbf{R}\times X$, then the projection of S_+ onto $\mathbf{R}$ must be unbounded. On the other hand, from (2.6), any solution on S_+ must satisfy $\lambda>\Lambda_1/N$. Hence the projection is a connected unbounded subset of $(\Lambda_1/N,\infty)$ which contains $(\lambda_1(f,\Omega),\infty)$. □

The structure of the solution set S_+ and S_+^1 in general is complicated, but near the bifurcation point $(\lambda,u)=(\lambda_1(f,\Omega),0)$ a better description of S_+^1 can be obtained.

Proposition 5. *There exist* $\alpha,\beta>0$ *such that for* $B=\{|\lambda-\lambda_1(f,\Omega)|<\alpha, ||u||_X<\beta, u>0\}$,

$$S_+\bigcap B = S_+^1\bigcap B = \{(\lambda(s),u(s)) : 0<s<\delta\}, \tag{6.1}$$

where $\delta>0$ *is a constant,* $\lambda(s)=\lambda_1(f,\Omega)+\eta(s)$, $u(s)=s\varphi_1+sv(s)$, $0<s<\delta$, $\eta(0)=0$ *and* $v(0)=0$, *and* $\eta(s)$ *and* $v(s)$ *are continuous. If in addition,* $f_{uu}(x,0)$ *exists for almost all* $x\in\overline{\Omega}$, *then* $\eta(s)$ *and* $v(s)$ *are also differentiable and*

$$\eta'(0) = -2[\lambda_1(f,\Omega)]^2\frac{\int_\Omega f_u(x,0)\varphi_1^3(x)dx}{\int_\Omega|\nabla\varphi_1(x)|^2dx}. \tag{6.2}$$

Proof. We apply a bifurcation theorem by Crandall and Rabinowitz [12]. Consider $F(\lambda,u)$ defined at the beginning of the section. At $(\lambda,u)=(\lambda_1(f,\Omega),0)$, $F_u((\lambda_1(f,\Omega),0))$ has a one dimensional kernel spanned by φ_1, the codimension of the range of $F_u((\lambda_1(f,\Omega),0))$ is also one, and it can be characterized as $R=\{u\in Y : \int_\Omega u\varphi_1 dx=0\}$. Also $F_{\lambda u}(\lambda_1(f,\Omega),0)\varphi_1 = f_u(\lambda_1(f,\Omega),0)\varphi_1\notin R$ since

$$\int_\Omega \lambda_1(f,\Omega)f(x,0)\varphi_1^2dx = \int_\Omega|\nabla\varphi_1|^2dx>0, \tag{6.3}$$

from the equation $\Delta\varphi_1+\lambda_1(f,\Omega)f(x,0)\varphi_1=0$. Hence the results in the proposition except (6.2) follows from Theorem 1.7 in [12]. The expression in (6.2) follows from Shi [38] page 507 and (6.3). □

In Proposition 5, when $\eta'(0)>0$, we say a *supercritical bifurcation* occurs at $(\lambda_1(f,\Omega),0)$; and when $\eta'(0)<0$, we say a *subcritical bifurcation* occurs at $(\lambda_1(f,\Omega),0)$. When f is only C^1 at $u=0$, $\eta(s)$ may not be differentiable, but the direction of the bifurcation diagram can still be determined if we define a *supercritical bifurcation* occurs at $(\lambda_1(f,\Omega),0)$ if $\eta(s)>0$ for $s\in(0,\delta)$, and a *subcritical bifurcation* occurs at $(\lambda_1(f,\Omega),0)$ if $\eta(s)<0$ for $s\in(0,\delta)$. We have the following criterion regarding the direction of $\eta(s)$ when f is only continuous:

Proposition 6. *Suppose that* $f(x,u) \leq (\not\equiv) f(x,0)$ *for* $u \in (0,\delta_1)$ *for some* $\delta_1 > 0$, *then the bifurcation at* $(\lambda_1(f,\Omega),0)$ *is supercritical. Similarly if* $f(x,u) \geq (\not\equiv)$ $f(x,0)$ *for* $u \in (0,\delta_1)$ *for some* $\delta_1 > 0$, *then the bifurcation at* $(\lambda_1(f,\Omega),0)$ *is subcritical.*

Proof. From (2.1) and

$$\Delta\varphi_1 + \lambda_1(f,\Omega)f(x,0)\varphi_1 = 0,\ x \in \Omega,\quad \varphi_1 = 0,\ x \in \partial\Omega. \tag{6.4}$$

we obtain

$$\begin{aligned}&[\lambda(s) - \lambda_1(f,\Omega)]\int_\Omega u(s)\varphi_1 f(x,0)dx\\ &+\lambda(s)\int_\Omega u(s)\varphi_1[f(x,u(s)) - f(x,0)]dx = 0.\end{aligned} \tag{6.5}$$

Here we assume that $0 < s < \delta_2$ so that $\max_{x\in\overline{\Omega}}|u(s,x)| \leq \delta_1$. If $f(x,u) \leq (\not\equiv) f(x,0)$ for $u \in (0,\delta_1)$, then the second integral in (6.5) is negative. And $u(s) = s\varphi_1 + o(s)$, then $\int_\Omega u(s)\varphi_1 f(x,0)dx = s\int_\Omega f(x,0)\varphi_1^2 dx + o(s) > 0$ from (6.3). Thus $\lambda(s) > \lambda_1(f,\Omega)$ in this case, and the proof for the second case is similar. □

Note that the conditions in Proposition 6, $f(x,u) \leq (\not\equiv) f(x,0)$ for $u \in (0,\delta_1)$ includes the logistic and degenerate logistic cases, and $f(x,u) \geq (\not\equiv) f(x,0)$ for $u \in (0,\delta_1)$ includes (weak, strong, degenerate) Allee effect cases. Summarizing the above results, we obtain Theorem 1.

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