CHAPTER 3

Bistability Dynamics in Structured Ecological Models

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Abstract. Alternative stable states exist in many important ecosystems, and gradual change of the environment can lead to dramatic regime shift in these systems (Beisner et.al. (2003), May (1977), Klausmeier (1999), Rietkerk et.al. (2004), and Scheffer et.al. (2001)). Examples have been observed in the desertification of Sahara region, shift in Caribbean coral reefs, and the shallow lake eutrophication (Carpenter et.al. (1999), Scheffer et.al. (2003), and Scheffer et.al. (2001)). It is well-known that a social-economical system is sustainable if the life-support ecosystem is resilient (Holling (1973) and Folke et.al. (2004)). Here resilience is a measure of the magnitude of disturbances that can be absorbed before a system centered at one locally stable equilibrium flips to another. Mathematical models have been established to explain the phenomena of bistability and hysteresis, which provide qualitative and quantitative information for ecosystem managements and policy making (Carpenter et.al. (1999) and Peters et.al. (2004)). However most of these models of catastrophic shifts are non-spatial ones. A theory for spatially extensive, heterogeneous ecosystems is needed for sustainable management and recovery strategies, which requires a good understanding of the relation between system feedback and spatial scales (Folke et.al. (2004), Walker et.al. (2004) and Rietkerk et.al. (2004)). In this chapter, we survey some recent results on structured evolutionary dynamics including reaction-diffusion equations and systems, and discuss their applications to structured ecological models which display bistability and hysteresis. In Section 1, we review several classical non-spatial models with

bistability; we discuss their counterpart reaction-diffusion models in Section 2, and especially diffusion-induced bistability and hysteresis. In Section 3, we introduce some abstract results and concrete examples of threshold manifolds (separatrix) in the bistable dynamics.

3.1 Non-structured models

The logistic model was first proposed by Belgian mathematician Pierre Verhulst (Verhulst (1838)):

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{N}\right), \quad a, N > 0. \tag{3.1}$$

Here a is the maximum growth rate per capita, and N is the carrying capacity. A more general logistic growth type can be characterized by a declining growth rate per capita function. 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 (1938), Dennis (1989) and Lewis and Kareiva (1993)). An Allee effect can be caused by shortage of mates (Hopf and Hopf (1985), Veit and Lewis (1996)), lack of effective pollination (Groom (1998)), predator saturation (de Roos et.al. (1998)), and cooperative behaviors (Wilson and Nisbet (1997)).

If the growth rate per capita is negative when the population is small, we call such a growth pattern a *strong Allee effect* (see Fig.3.1-c); if $f(u)$ is smaller than the maximum but still positive for small u, we call it a *weak Allee effect* (see Fig.3.1-b). In Clark (1991), 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 (1957). Most people regard the strong Allee effect as the Allee effect, but population ecologists have started to realize that an Allee effect may be weak or strong (see Wang and Kot (2001), Wang, Kot and Neubert (2002)). Some possible growth rate per capita functions were also discussed in Conway (1983,1984). A prototypical model with Allee effect is

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{N}\right) \cdot \frac{P - M}{|M|}, \quad a, N > 0. \tag{3.2}$$

If $0 < M < N$, then the equation is of strong Allee effect type, and if $-N < M < 0$, then it is of weak Allee effect type. At least in the strong Allee effect case, M is called the sparsity constant.

The dynamics of the logistic equation is monostable with one globally asymptotically stable equilibrium, and that of strong Allee effect is bistable with two stable equilibria. A weak Allee effect is also monostable, although the growth is slower at lower density. Another example of a weak Allee effect is the equation of higher order autocatalytic chemical reaction of Gray and Scott (1990):

$$\frac{da}{dt} = -kab^p, \quad \frac{db}{dt} = kab^p, \quad k > 0, \ p \geq 1. \tag{3.3}$$

Here $a(t)$ and $b(t)$ are the concentrations of the reactant A and the autocatalyst B, k is the reaction rate, and $p \geq 1$ is the order of the reaction with respect to the

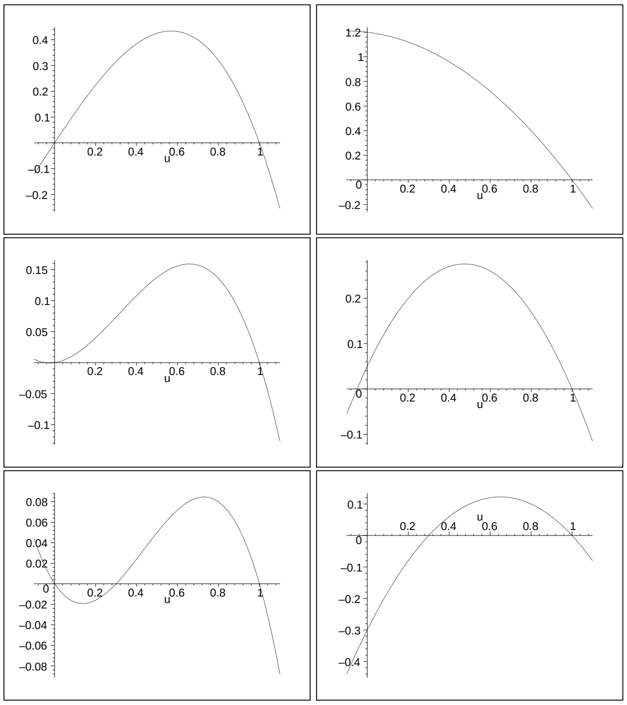

Figure 3.1 (a) logistic (top); (b) weak Allee effect (middle); (c) strong Allee effect (bottom); the graphs on the left are growth rate $uf(u)$, and the ones on the right are growth rate per capita $f(u)$.

autocatalytic species. Notice that $a(t) + b(t) \equiv a_0 + b_0$ is invariant, so that (3.3) can be reduced to

$$\frac{db}{dt} = k(a_0 + b_0 - b)b^p, \quad k, a_0 + b_0 > 0, \ p \geq 1, \tag{3.4}$$

which is of weak Allee effect type if $p > 1$, and of logistic type if $p = 1$. An autocatalytic chemical reaction has been suggested as a possible mechanism of various biological feedback controls (Murray (2003)), and the similarity between chemical reactions and ecological interactions has been observed since Lotka (1920) in his pioneer work.

The cubic nonlinearity in (3.2) has also appeared in other biological models. One prominent example is the FitzHugh-Nagumo model of neural conduction (FitzHugh (1961) and Nagumo et.al. (1962)), which simplifies the classical Hodgkin-Huxley model:

$$\epsilon\frac{dv}{dt} = v(v-a)(1-v) - w, \quad \frac{dw}{dt} = cv - bw, \quad \epsilon, a, b, c > 0, \tag{3.5}$$

where $v(t)$ is the excitability of the system (voltage), and $w(t)$ is a recovery variable representing the force that tends to return the resting state. When c is zero and $w = 0$, (3.5) becomes (3.2). Another example is a model of the evolution of fecally-orally transmitted diseases by Capasso and Maddalena (1981/82, 1982):

$$\frac{dz_1}{dt} = -a_{11}z_1 + a_{12}z_2, \quad \frac{dz_2}{dt} = -a_{22}z_2 + g(z_1), \quad a_{11}, a_{12}, a_{22} > 0. \tag{3.6}$$

Here $z_1(t)$ denotes the (average) concentration of infectious agent in the environment; $z_2(t)$ denotes the infective human population; $1/a_{11}$ is the mean lifetime of the agent in the environment; $1/a_{22}$ is the mean infectious period of the human infectives; a_{12} is the multiplicative factor of the infectious agent due to the human population; and $g(z_1)$ is the force of infection on the human population due to a concentration z_1 of the infectious agent. If $g(z_1)$ is a monotone increasing concave function, then it is known that the system is monostable with the global asymptotical limit being either an extinction steady state or a nontrivial endemic steady state. However if $g(z_1)$ is a monotone sigmoid function, *i.e.* a monotone convex-concave function with S-shape and saturating to a finite limit, then the system (3.6) possesses two nontrivial endemic steady states and the dynamics of (3.6) is bistable, which can be easily seen from the phase plane analysis.

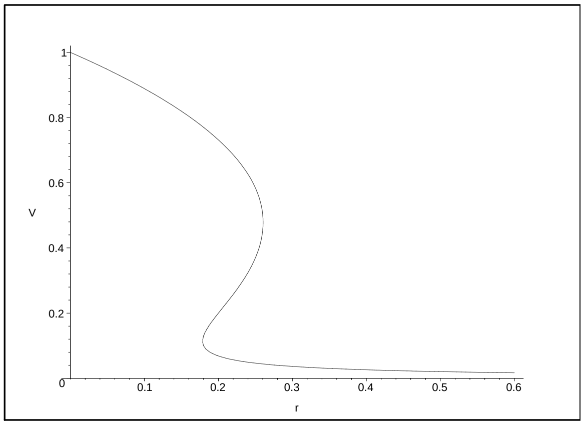

Figure 3.2 Equilibrium bifurcation diagram of (3.8) with $h = 0.1$, where the horizontal axis is r and the vertical axis is V.

Now we turn to some existing models which could lead to catastrophic shifts in ecosystems. In 1960-70s, theoretical predator-prey systems are proposed to demonstrate various stability properties in systems of populations at two or more trophic levels (Rosenzweig and MacArthur (1963) and Rosenzweig (1971)). A simplified model with such a predator-prey feature is that of a grazing system of herbivore-plant interaction as in Noy-Meir (1975), see also May (1977). Here $V(t)$ is the vegetation biomass, and its quantity changes following the differential equation:

$$\frac{dV}{dt} = G(V) - Hc(V), \tag{3.7}$$

where $G(V)$ is the growth rate of vegetation in absence of grazing, H is the herbivore population density, and $c(V)$ is the per capita consumption rate of vegetation by the herbivore. If $G(V)$ is given by the familiar logistic equation, and $c(V)$ is the Holling type II ($p = 1$) or III ($p > 1$) functional response function (Holling (1959)), then (3.7) has the form (after nondimensionalization):

$$\frac{dV}{dt} = V(1-V) - \frac{rV^p}{h^p + V^p}, \quad h, r > 0, \;\; p \geq 1. \tag{3.8}$$

This equation (with $p = 2$) also appears as the model of insect pests such as the spruce budworm (*Choristoneura fumiferana*) in Canada and northern USA (Ludwig et. al. (1978)), in which $V(t)$ is the budworm population. In either situation, the harvesting effort is assumed to be constant as the change of the predator population occurs at a much slower time scale compared to that of the prey. The function $c(V) = \dfrac{\gamma V^p}{h^p + V^p}$ with $p \geq 1$ is called the Hill function in some references. We notice that a Hill function is one of sigmoid functions which is defined in the epidemic model (3.6).

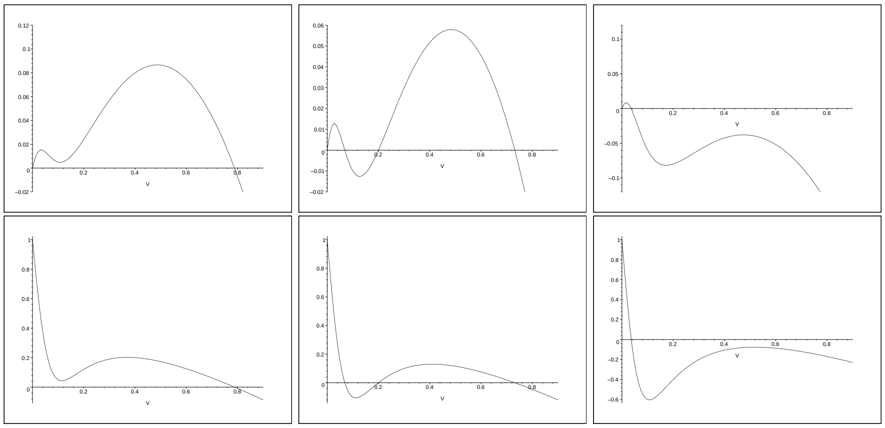

Figure 3.3 (top) Graph of the growth rate function $f(V) = V(1-V) - \dfrac{rV^p}{h^p + V^p}$ with $h = 0.1$; (bottom) Graph of the growth rate per capita $f(V)/V$. (a) $r = 0.17$ (left); (b) $r = 0.2$ (middle); (c) $r = 0.3$ (right).

To describe the catastrophic regime shifts between alternative stable states in ecosystems, a minimal mathematical model

$$\frac{dx}{dt} = a - bx + \frac{rx^p}{h^p + x^p}, \quad a, b, r, h > 0, \tag{3.9}$$

is proposed in Carpenter et.al. (1999), see also Scheffer et.al. (2001). (3.9) can be used in ecosystems such as lakes, deserts, or woodlands. For lakes, $x(t)$ is the level of nutrients suspended in phytoplankton causing turbidity, a is the nutrient loading, b is the nutrient removal rate, and r is the rate of internal nutrient recycling.

The equations (3.8) and (3.9) are examples of differential equation models which ex-

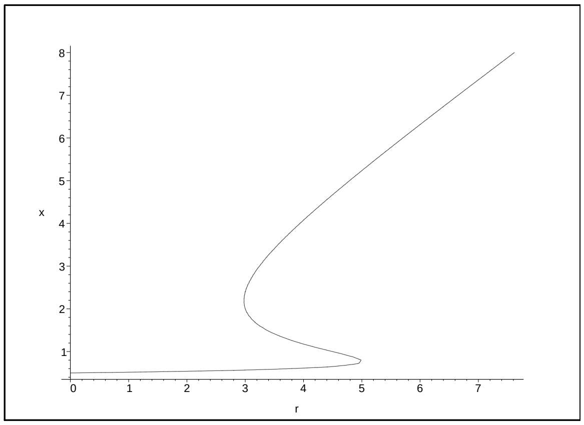

Figure 3.4 Equilibrium bifurcation diagram of (3.9) with $a = 0.5$, $b = 1$, where the horizontal axis is r and the vertical axis is x.

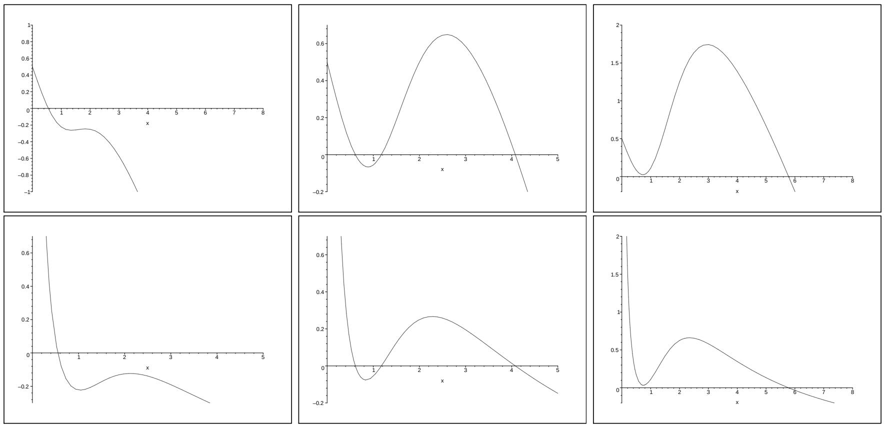

Figure 3.5 (top) Graph of the growth rate function $g(x) = a - bx + \dfrac{rx^p}{h^p + x^p}$ with $a = 0.5$, $b = 1$; (bottom) Graph of the growth rate per capita $f(x)/x$. (a) $r = 2.5$ (left); (b) $r = 4$ (middle); (c) $r = 5.5$ (right).

hibit the existence of multiple stable states and the phenomenon of hysteresis. From the bifurcation diagrams (Fig. 3.2 for (3.8), and Fig. 3.4 for (3.9)), the system has three positive equilibrium points when $r \in (r_1, r_2)$ for some $\infty > r_2 > r_1 > 0$, and the largest and smallest positive equilibrium points are stable. For the grazing system (3.8), the number of stable equilibrium points changes with the herbivore density r. For low r, the vegetation biomass tends to a unique equilibrium slightly lower than 1 (the rescaled carrying capacity); as r increases over r_1, a second stable equilibrium appears through a supercritical saddle-node bifurcation, and it represents a much lower vegetation biomass; as r continues to increases to another parameter threshold

$r_2 > r_1$, the larger stable equilibrium suddenly vanishes through a subcritical saddle-node bifurcation, and the lower stable equilibrium becomes the unique attracting one. As h increases gradually, the vegetation biomass first settles at a higher level for low h, but it collapses to a lower lever as h passes r_2; after this catastrophic shift, even if h is restored slightly, the biomass remains at the low level unless h decreases beyond r_1. This irreversibility of the hysteresis loop gives raise to a serious management problem for the grazing systems, see Noy-Meir (1975) and May (1977). Similar discussions hold for (3.9) as well as r decreases, see Scheffer et.al. (2001), where the drop from high density stable equilibrium to the low one is called “forward shift”, and the recovery from the low one to high one is a “backward shift”.

It is worth pointing out that the S-shaped bifurcation curve in Fig. 3.2 and Fig. 3.4 can also be viewed as a result of bifurcation with respect to conditions such as nutrient loading, exploitation or temperature rise (Scheffer et.al. (2001)). That is a transition from a monostable system to a bistable one, or mathematically, a cusp bifurcation from a monotone curve to a S-shaped one with two turning points (see Fig. 3.6). Such fold bifurcations have been discussed in much more general settings in Shi (1999), and Liu, Shi and Wang (2007). In general it is hard to rigorously prove the exact transition from monostable to bistable dynamics, especially for higher (including infinite) dimensional problems. In (3.8) with $p = 2$, one can show the cusp bifurcation occurs when h crosses $h_0 = \sqrt{3}/27 \approx 0.1925$. A mathematical survey on the fold and cusp type mappings (especially in infinite dimensional spaces) can be found in Church and Timourian (1997).

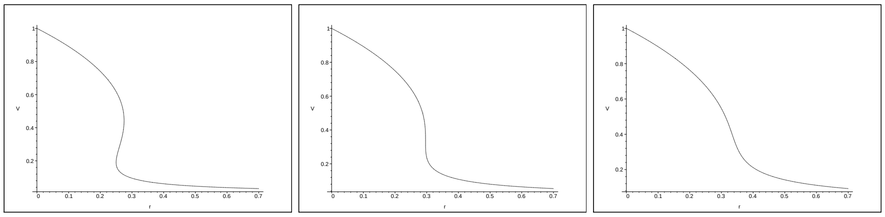

Figure 3.6 Cusp bifurcation in (3.8) with $p = 2$, where the horizontal axis is r and the vertical axis is V. (a) $h = 0.15$ (left); (b) $h = \sqrt{3}/27 \approx 0.1925$ (middle); (c) $h = 0.25$ (right).

We note that in Fig. 3.3-a and Fig. 3.5-c, the system is monostable with only one stable equilibrium point, yet the graph of “growth rate per capita”(see the lower graphs in Fig. 3.3-a and Fig. 3.5-c) has two fluctuations before turning to negative. This is similar to the weak Allee effect defined earlier where the growth rate per capita changes the monotonicity once. These geometric properties of the growth rate per capita functions motivate us to classify all growth rate patterns according to the monotonicity of the function $f(u)/u$ if $f(u)$ is the gross growth rate in a model $u' = f(u)$:

1. $f(u)$ is of *logistic* type, if $f(u)/u$ is strictly decreasing;
2. $f(u)$ is of *Allee effect* type, if $f(u)/u$ changes from increasing to decreasing when u increases;

3. $f(u)$ is of *hysteresis* type, if $f(u)/u$ changes from decreasing to increasing then to decreasing again when u increases.

In all cases, we assume that $f(u)$ is negative when u is large, thus $f(u)$ has at least one zero $u_1 > 0$. In the Allee effect case, if $f(u)$ has another zero in $(0, u_1)$, then it is a strong Allee effect, otherwise it is a weak one; in the hysteresis case, if $f(u)$ has two more zeros in $(0, u_1)$, then it is strong hysteresis, otherwise it is weak. Here we exclude the degenerate cases when $f(u_0) = f'(u_0) = 0$ (double zeros). Considering the ODE model $u' = f(u)$, the weak Allee effect or hysteresis dynamics appears to be no different from the logistic case in terms of the asymptotic behavior, since $f(u) > 0$ for $u \in (0, u_1)$ and $f(u) < 0$ for $u > u_1$. The definitions here are not only for mathematical interest. In the next section, we shall show that the addition of diffusion to the equation can dramatically change the dynamics for the weak Allee effect or hysteresis.

3.2 Diffusion induced bistability and hysteresis

Dispersal of the state variable in a continuous space can be modeled by a partial differential equation with diffusion (see Okubo and Levin (2001), Murray (2003), Cantrell and Cosner (2003)):

$$\frac{\partial u}{\partial t} = d\Delta u + f(u), \quad t > 0, \ \ x \in \Omega. \tag{3.10}$$

Here $u(x,t)$ is the density function of the state variable at spatial location x and time t, $d > 0$ is the diffusion coefficient, the habitat Ω is a bounded region in $\mathbf{R}^n$ for $n \geq 1$, $\Delta u = \sum_{i=1}^{n} \frac{\partial^2 u}{\partial x_i^2}$ is the Laplace operator, and $f(u)$ represents the non-spatial growth pattern. We assume that the habitat Ω is surrounded by a completely hostile environment, thus it satisfies an absorbing boundary condition:

$$u(x) = 0, \quad x \in \partial\Omega. \tag{3.11}$$

It is known (Henry (1981)) that for equation (3.10) with boundary condition (3.11), there is a unique solution $u(x,t)$ of the initial value problem with an initial condition $u(x,0) = u_0(x) \geq 0$, provided that $f(u), u_0(x)$ are reasonably smooth. Moreover, if the solution $u(x,t)$ is bounded, then it tends to a steady state solution as $t \to \infty$ if one of the following conditions is satisfied: (i) $f(u)$ is analytic; (ii) if all steady state solutions of (3.10) and (3.11) are non-degenerate (see for example, Polácik (2002) and references therein). Hence the asymptotical behavior of the reaction-diffusion equation can be reduced to a discussion of the structure of the set of steady state solutions and related dynamical behaviors. The steady state solutions of (3.10) and (3.11) satisfy a semilinear elliptic type partial differential equation:

$$d\Delta u(x) + f(u(x)) = 0, \ \ x \in \Omega, \quad u(x) = 0, \quad x \in \partial\Omega. \tag{3.12}$$

Since we are interested in the impact of diffusion on the extinction/persistence of population, we use the diffusion coefficient d as the bifurcation parameter. One can also use the size of the domain Ω as an equivalent parameter. To be more precise, we use the change of variable $y = x/\sqrt{d}$ to convert the equation (3.12) to:

$$\Delta u(y) + f(u(y)) = 0, \ \ y \in \Omega_d, \quad u(y) = 0, \quad y \in \partial\Omega_d, \tag{3.13}$$

where $\Omega_d = \{y : \sqrt{d}y \in \Omega\}$. This point of view fits the classic concept of critical patch size introduced by Skellam (1951). When $\Omega = (0, l)$, the one-dimensional region, the size of the domain is simply the length of the interval. In higher dimension, Ω_d is a family of domains which have the same shape but "size" proportional to $d^{-1/2}$. Here "size" can be defined as the one-dimensional scale of the domain. Size can also be defined through the principal eigenvalue of $-\Delta$ on the domain Ω with zero boundary condition, which is the smallest positive number $\lambda_1(\Omega)$ such that

$$\Delta\phi(x) + \lambda_1\phi(x) = 0, \ \ x \in \Omega, \quad \phi(x) = 0, \quad x \in \partial\Omega, \tag{3.14}$$

has a positive solution ϕ. Apparently $\lambda_1(\Omega_d) = \lambda_1(\Omega)/d$. In application a habitat slowly eroded by external influence can be approximated by such a family of domains Ω_d with similar shape but shrinking size. This is a special case of habitat fragmentation. In the following we use d as bifurcation parameter, and when d increases, the size (or the principal eigenvalue) of the domain Ω_d decreases.

The multiplicity and global bifurcation of solutions of (3.12) have been considered by many mathematicians over the last half century. Several survey papers and monographs can be consulted, see for example (Amann (1976), Cantrell and Cosner (2003), Lions (1981), and Shi (2009)) and the references therein. In this section we review some related results on that subject for the nonlinearity $f(u)$ discussed in Section 1 and their connection to ecosystem persistence/extinction.

For the Verhurst logistic model, the corresponding reaction-diffusion model was introduced by Fisher (1937) and Kolmogoroff, Petrovsky, and Piscounoff (1937) in studying the propagation of an advantageous gene over a spatial region, and the traveling wave solution was considered. The boundary value problem

$$d\Delta u + u\left(1 - \frac{u}{N}\right) = 0, \ \ x \in \Omega, \quad u = 0, \quad x \in \partial\Omega, \tag{3.15}$$

was studied by Skellam (1951) when $\Omega = (0, L)$. Indeed in this case an explicit solution and dependence of L on D can be obtained via an elliptic integral (Skellam (1951)). When Ω is a general bounded domain, it was shown (see Cohen and Laetsch (1970), Cantrell and Cosner (1989), Shi and Shivaji (2006)) that when $0 < d^{-1} < \lambda_1(\Omega) \equiv \lambda_1$, the only nonnegative solution of (3.15) is $u = 0$, and it is globally asymptotically stable; when $d^{-1} > \lambda_1$, (3.15) has a unique positive solution u_d which is globally asymptotically stable. It is also known that $u_d(x)$ is is an decreasing function of d for $d < \lambda_1^{-1}$, and $u_d(x) \to 0$ as $d^{-1} \to \lambda_1^{+}$. Hence the critical number λ_1 represents the critical patch size. When the size of habitat gradually decreases, the biomass decreases too, and when it passes the critical patch size, the biomass becomes zero through a continuous change. Hence the bifurcation diagram of (3.15) is a continuous monotone curve as shown in Fig.3.7 (a).

The bifurcation diagram in Fig.3.7 (a) changes when an Allee effect exists in the growth function $f(u)$. For the boundary value problem

$$d\Delta u + u\left(1 - \frac{u}{N}\right) \cdot \frac{u-M}{|M|} = 0, \quad x \in \Omega, \quad u = 0, \quad x \in \partial\Omega, \tag{3.16}$$

one can use M as a parameter of the bifurcation in the bifurcation diagrams. We always assume $M < N$. When $M \leq -N$, the growth rate per capita is decreasing as in logistic case, thus the bifurcation diagram is monotone as in Fig 3.7 (a). When $-N < M < 0$, the growth rate per capita is of weak Allee effect type, and a new type of bifurcation diagram appears (Fig 3.7 (b)). We notice that the nonlinearity in (3.16) is normalized so that the growth rate per capita at $u = 0$ is always 1 when $M < 0$. Rigorous mathematical results about exact multiplicity of steady state solutions and global bifurcation diagram Fig 3.7 (b) are obtained in Korman and Shi (2001), and Shi and Shivaji (2006) for a more general nonlinearity and the domain being a ball in $\mathbf{R}^n$. We also mention that if the dispersal does not satisfy a linear diffusion law but a nonlinear one, then a weak Allee effect can also occur, and the bifurcation diagram of steady state solutions is like Fig. 3.7-b, see Cantrell and Cosner (2002), and Lee et.al. (2006).

Compared to the logistic case, a backward (subcritical) bifurcation occurs at $(d^{-1}, u) = (\lambda_1, 0)$, and a new threshold parameter value $0 < \lambda_* < \lambda_1$ exists. For $d^{-1} < \lambda_*$ (*extinction regime*), the population is destined to extinction no matter what the initial population is; for $d^{-1} > \lambda_1$ (*unconditional persistence regime*), the population always survive with a positive steady state. However in the intermediate *conditional persistence regime*, $\lambda_* < d^{-1} < \lambda_1$, there are exactly two positive steady state solutions $u_{1,d}$ and $u_{2,d}$. In fact, it can be shown that the three steady state solutions (including 0) can be ordered so that $u_{1,d}(x) > u_{2,d}(x) > 0$. Here $u_{1,d}$ and 0 are both locally stable. Hence the diffusion effect induces a bistability for a monostable model of weak Allee effect. A sudden collapse of the population occurs if d increases (or the domain size decreases) when d^{-1} crosses λ_*, and the system shifts abruptly from $u_{1,d}$ to 0 and it is not recoverable. This may explain that in some ecosystems with weak Allee effect, a catastrophic shift could still occur although the corresponding ODE model predicts unconditional persistence.

For $0 < M < N$ in (3.16), a strong Allee effect means that bistability occurs even for the small diffusion case (d small). If $N/2 \leq M < N$, $u = 0$ is the unique nonnegative solution of (3.16) thus extinction is the only possibility. If $0 < M < N/2$, there exist at least two positive steady state solutions of (3.16) following a classical result of variational methods due to Rabinowitz (1973/74). When the domain is a ball in $\mathbf{R}^n$, it was shown by Ouyang and Shi (1998, 1999) that (3.16) has at most two positive solutions and the bifurcation diagram is exactly like Fig.3.7-c. Earlier the exact bifurcation diagram for the one-dimensional problem was obtained by Smoller and Wasserman (1981). It is well-known that in this case that a small initial population always leads to extinction, thus a single threshold value λ_* exists to separate the extinction and conditional persistence regimes. Earlier work on the dynamics of (3.10) and (3.11) with strong Allee effect was considered in Bradford and Philip (1970a, 1970b) and Yoshizawa (1970).

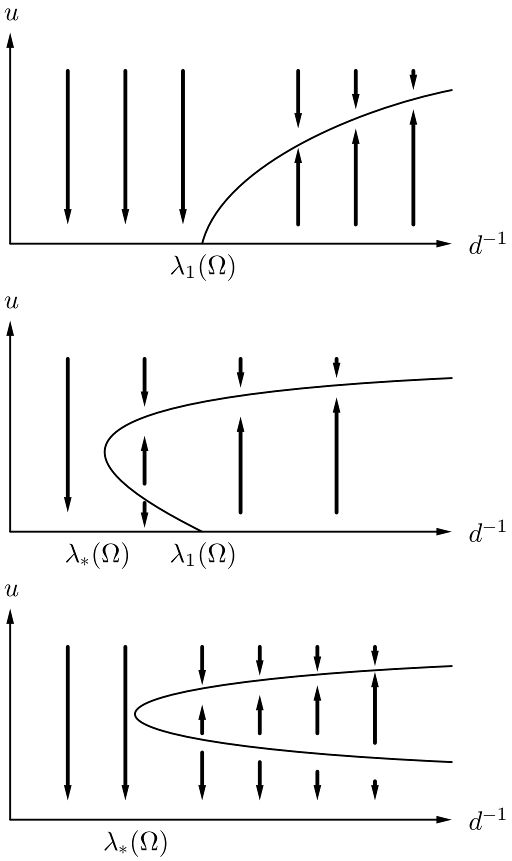

Figure 3.7 Bifurcation diagrams for (3.16): (a) logistic (upper); (b) weak Allee effect (middle); (c) strong Allee effect (lower).

The exact multiplicity results proved in Ouyang and Shi (1998, 1999) (see also Shi (2009)) hold for more general nonlinearities $f(u)$, and the criterion on $f(u)$ for the exact multiplicity are given by the shape of the function $f(u)/u$ and the convexity of $f(u)$. Another example is the border line case for (3.16) between the weak ($M < 0$) and strong Allee effect ($M > 0$), or more generally, the equation of autocatalytic chemical reaction (3.4) (assuming that $a_0 + b_0 = 1$):

$$d\Delta u + u^p(1-u) = 0, \quad x \in \Omega, \quad u = 0, \quad x \in \partial\Omega, \quad p > 1. \tag{3.17}$$

The bifurcation diagram of (3.17) is similar to Figure 3.7-c, and a proof can be found in Ouyang and Shi (1998, 1999) or Zhao, Shi and Wang (2007). Precise global bifurcation diagrams can also been given for the reaction-diffusion systems of autocatalytic chemical reaction (3.3) and epidemic model (3.6), and we will discuss them in the next section along with the associated dynamics.

The threshold value λ_* is important biologically as λ_* could give early warning of extinction for the species. Usually it is difficult to give a precise estimate of λ_* and it seems that there is no existing result on that problem. Here we only give an estimate of λ_* for the equation (3.16) with $N = 1$ and $M \in (0, 1/2)$. Hence we consider

$$d\Delta u + u(1-u)(u-M) = 0, \;\; x \in \Omega, \;\; u(x) = 0, \;\; x \in \partial\Omega. \tag{3.18}$$

Here we have $f(u) = u(1-u)(u-M)$. From an idea in Shi and Shivaji (2006), $\lambda_* > \lambda_1/f_*$, where $f_* = \max_{u\in[0,1]} f(u)/u$, or the maximal growth rate per capita. An upper bound of λ_* can be obtained if (3.18) has a nontrivial solution for that d. We define an associated energy functional

$$I(u) = \frac{d}{2}\int_\Omega |\nabla u|^2 dx - \int_\Omega F(u)dx, \tag{3.19}$$

where $F(u) = \int_0^u f(t)dt = -\dfrac{1}{4}u^4 + \dfrac{1+M}{3}u^3 - \dfrac{M}{2}u^2$. It is well-known that a solution u of (3.18) is a critical point of the functional $I(u)$ in a certain function space (see Rabinowitz (1986) or Struwe (2000) for more details.) In particular, if $\inf I(u) < 0$, then (3.18) has a nontrivial positive solution. For small d, it is apparent that $\inf I(u) < 0$ if $M \in (0, 1/2)$. Hence for largest $d = \widetilde{d}$ so that $\inf I(u) < 0$, we must have $\lambda_* < \widetilde{d}^{-1}$. For the case $\Omega = (0, L)$, we can obtain that

$$\frac{2\pi^2}{L^2(1+M)} < \lambda_* < \frac{48}{L^2(3-M)}. \tag{3.20}$$

Here the upper bound is obtained by using a test function $u(x) = x/l$ for $x \in [0, l]$, $u(x) = 1$ for $x \in [l, L/2]$ and $u(x) = u(L-x)$ for $x \in [L/2, L]$, then optimizing among all possible value of l. The estimate (3.20) is indeed quite sharp. For example, for $L = 1$ and $M = 0.2$, the estimate (3.20) becomes $16.45 < \lambda_* < 17.14$. A numerical calculation using `Maple` and the algorithm in Lee et.al. (2006) shows that $\lambda_* \approx 16.61$. The threshold value for other problems can be estimated similarly, and in general the determination of the threshold value remains an interesting open question.

Next we turn to bifurcation diagrams with hysteresis. The hysteresis diagrams in Section 1 (Fig. 3.2 and 3.4) are generated with parameter r, which is the herbivore density in (3.8) or the rate of internal nutrient recycling in (3.9). In this subsection, we consider the corresponding reaction-diffusion models. First the steady state reaction-diffusion grazing model

$$d\Delta V + V(1-V) - \frac{rV^p}{h^p + V^p} = 0, \;\; x \in \Omega, \quad V = 0, \quad x \in \partial\Omega, \tag{3.21}$$

was considered in Ludwig, Aronson and Weinberger (1979). For the case $n = 1$, by using the quadrature method, they show that the rough bifurcation diagram goes from a monotone curve with a unique large steady state, to an S-shaped curve, to a disconnected S-shaped curve, and finally a monotone curve with a unique small steady state, when r increases from near 0 to a large value (see Fig. 3.8 or the ones in Ludwig et.al. (1979)). Note that the bifurcation diagrams in Ludwig et.al. (1979) are not exact, and it is only shown that the equation has at least three positive solutions but not exactly three. An exact multiplicity result like the one in Ouyang and Shi

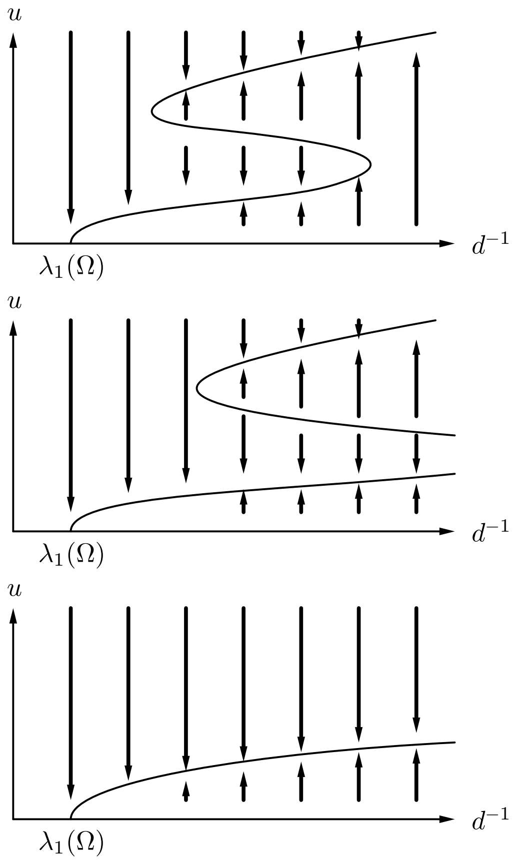

Figure 3.8 Bifurcation diagrams for (3.21): (a) weak hysteresis, r small but close to the first break point in ODE hysteresis loop, corresponding to f in Fig 3.3-a (upper); (b) strong hysteresis, corresponding to f in Fig 3.3-b (middle); (c) "collapsed", r larger than the second break point, corresponding to f in Fig 3.3-c (lower).

(1998, 1999) is not known even when $n = 1$. But it is known that in Fig. 3.8-b, the upper bound of the lower branch is the first zero of $f(u)$, and the lower bound of the upper branch is the smallest zero of $F(u) = \int_0^u f(t)dt = 0$ such that $f(u) > 0$; in Fig. 3.8-a, the lower turning point $\lambda^* \to \infty$ if the positive local minimum value of $f(u)$ tends to zero.

The transition of rough bifurcation diagrams suggests a bistable structure exists for intermediate range of r (see Fig. 3.2) when the nonlinearity is of strong hysteresis type, but a bistable structure could also exist when r is smaller when the nonlinearity is of weak hysteresis type (see Fig. 3.8-a). Indeed the S-shaped bifurcation diagram implies a hysteresis loop even though the weak hysteresis nonlinearity is positive until the zero at the "carrying capacity". Hence this is a hysteresis induced by the diffusion. Back to the context of shrinking habitat size, this suggests that for a seemingly safe ecosystem with the grazing is not too big so that the ODE model predicts a large stable equilibrium, the addition of diffusion can endanger the ecosystem if the habitat keeps shrinking, and a sudden drop to the small steady state is possible if the habitat size passes a critical value. Note that we do not exclude the possibility of catastrophic shift due to the increase of the grazing effect r, but the results in reaction-diffusion model offer another possible cause for such a sudden collapse, namely the decreasing natural vegetative habitat.

For the model (3.9) of lake turbidity, a reaction-diffusion model can also be proposed:

$$\begin{cases} u_t = d\Delta u + a - bu + \dfrac{ru^p}{h^p + u^p}, & t > 0, \;\; x \in \Omega, \\ u(x,t) = 0, & x \in \partial\Omega, \\ u(x,t) = u_0(x), & t > 0, \;\; x \in \Omega. \end{cases} \tag{3.22}$$

A similar argument can be made to offer another possible cause of the turbidity in shallow lakes, *i.e.* the shrinking that has occurred for many freshwater lakes because of the expanding of agriculture or industry. Here the bifurcation diagram of the steady state equation is not readily available in the existing literature, but similar problems with S-shaped bifurcation diagrams can be found in (Brown et.al. (1981), Du and Lou (2001), Korman and Li (1999), and Wang (1994)), to name a few. Indeed the nonlinearity $f(u)$ in (3.22) is qualitatively similar to the one in (3.21) (comparing Fig. 3.3 and Fig. 3.5), hence their bifurcation diagrams are similar.

In our discussion to this point, we have used a homogeneous Dirichlet boundary condition ($u = 0$ on the boundary). While diffusion plays an instrumental role in inducing bistability, the Dirichlet boundary condition also plays an important role. In some rough sense, a Dirichlet boundary condition is much more "spatially heterogeneous" than a Neumann boundary condition (or no flux, reflection boundary condition), and is more rigid than Neumann boundary condition. Here we also comment briefly on reaction-diffusion models with Neumann boundary condition:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\Delta u + f(u), & t > 0, \;\; x \in \Omega, \\ \dfrac{\partial u}{\partial n} = 0, & t > 0, \;\; x \in \partial\Omega, \\ u(0,x) = u_0(x) \geq 0, & x \in \Omega. \end{cases} \tag{3.23}$$

A classical result of Matano (1979), Casten and Holland (1978) is that (3.23) has no stable nonconstant equilibrium solution provided that the domain Ω is convex. A direct consequence is that the reaction-diffusion equation (3.23) has same number of stable equilibrium solutions as the ODE $u' = f(u)$, hence diffusion does not induce "more"stability. However the geometry of the domain Ω is also an important factor in the stability problem. Matano (1979) shows that if $f(u)$ is of bistable type, say $f(u) = u(1 - u^2)$, then (3.23) has a stable nonconstant equilibrium solution if Ω is dumbbell-shaped, see also Alikakos, Fusco and Kowalczyk (1996) for more intricate results in that direction. Indeed it was recently shown that the geometry of the domain is even important for the magnitude of the first non-zero eigenvalue of Laplacian operator under Neumann boundary condition, see Ni and Wang (2007). The work of Matano (1979) has been extended to two species competition models (Matano and

Mimura (1983)) for nonconvex domains and to cooperative models (Kishimoto and Weinberger (1985)) for convex domains. More results on Neumann boundary value problems can be found in Ni (1989, 1998).

To summarize, we have examined the reaction-diffusion ecological models of bistability or hysteresis in this section. When the diffusion coefficient d is small, or equivalently the habitat is large, we show the existence of multiple spatial heterogeneous steady states, so that the system possesses alternative stable spatial equilibrium solutions. Moreover, even when the non-spatial model is not bistable, the reaction-diffusion model may be bistable as we show in the weak Allee effect or weak hysteresis case. Hence diffusion enhances the stability of certain states in such systems.

The bifurcation diagrams can also be explained with habitat size as the bifurcation parameter. Indeed habitat fragmentation has been identified as one of the possible causes of the regime shift in the ecosystems [122]. The results here provide theoretical evidence to support that claim via the reaction-diffusion model approach. Other mathematical approaches concerning the implications of spatial heterogeneity in the catastrophic regime shifts have been taken. van Nes and Scheffer (2005) investigated lattice models with same nonlinearities in (3.21) and (3.22), but their numerical bifurcation diagrams have r or a as bifurcation parameters, just as in the ODE models (see Fig. 3.2 and Fig. 3.4). Bascompte and Solé (1996, 2006) consider spatially explicit metapopulation models to show the existence of extinction thresholds when a given fraction of habitat is destroyed.

Another question is as follows. When the existence of multiple steady states indicates bistability, what is the global dynamics of the system? We present some mathematical results in that direction in the following section.

3.3 Threshold manifold

For an ordinary differential equation such as (3.2) with strong Allee effect, $u = M$ is a threshold point so that the extinction and persistence depends on whether the initial value $u_0 < M$ or $> M$. Bistable dynamics in higher dimensional systems are characterized by a separatrix or threshold manifold. Sometimes such dynamics is also called saddle point behavior (Capasso and Maddalena (1982), Capasso and Wilson (1997)). This can be illustrated by considering the classical Lotka-Volterra competition model (in nondimensionalized form):

$$u' = u(1 - u - Av), v' = v(B - Cu - v), \tag{3.24}$$

where $A, B, C > 0$ satisfy $C > B > A^{-1} > 0$. The system is bistable since it possesses two locally stable equilibrium points $(1, 0)$ and $(0, B)$, and a separatrix—the stable manifold of the unstable coexistence equilibrium $(u_*, v_*) = ((AB-1)/(AC-1), (C - B)/(AC - 1))$, which separates the basins of attraction of two stable equilibria, see Fig. 3.9. We also note that (3.24) possesses another invariant manifold connecting $(1, 0)$, $(0, B)$ and (u_*, v_*), called carrying simplex, see more remarks about it in later part of this section.

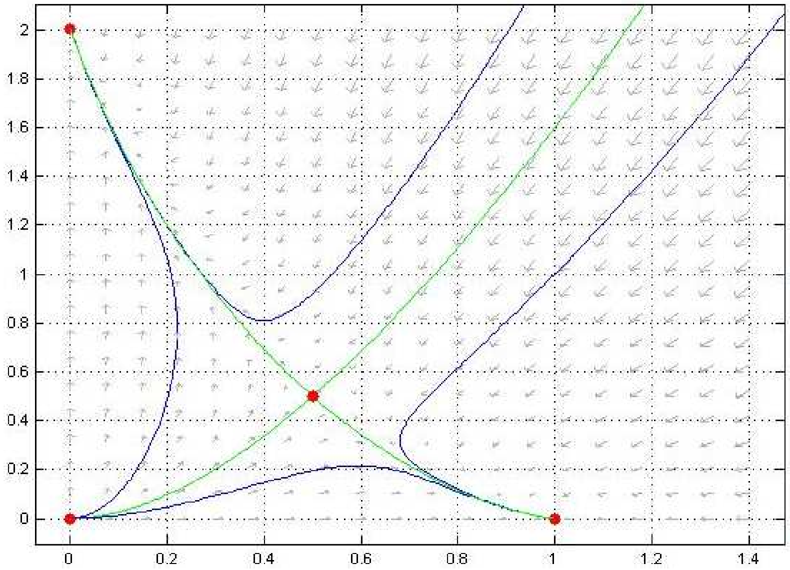

Figure 3.9 Phase portrait of the competition model (3.24). The stable manifold of (u_*, v_*) (connecting orbit from the origin) is the threshold manifold which separates the basins of attraction of two stable equilibria; and the unstable manifold of (u_*, v_*) (connecting orbits from stable equilibria) is the carrying simplex.

An abstract mathematical result about the threshold manifold has been recently given by Jiang, Liang and Zhao (2004). They prove that in a strongly order preserving or strongly monotone semiflow in a Banach space, if there are exactly two locally stable steady states, and any other possible steady state is unstable, then the set which separates the basins of attraction of two stable steady states is a codimension-one manifold (see more precise statement in Jiang et.al. (2004)). A scalar reaction-diffusion equation such as (3.10) and (3.11) generates a strongly monotone semiflow in some function space. Thus this result is immediately applicable to the scalar reaction-diffusion equation. Hence the existence of a codimension-one manifold for the Nagumo equation or all examples discussed in Section 2 with exactly two stable steady state solutions follows from Jiang et.al. (2004). The existence of the threshold manifolds relies on earlier results of Takáč (1991, 1992). We also mention that the earliest example of threshold manifold was given by McKean and Moll (1986), and Moll and Rosencrans (1990) where the Nagumo equation

$$u_t = du_{xx} + u(a-u)(u-b), \quad x \in (0, L), \quad u(0) = u(L) = 0, \tag{3.25}$$

with $0 < b < a$, was considered. They also examined the case when the cubic function is replaced by a piecewise linear function, suggested by McKean (1970) as an alternative to the FitzHugh-Nagumo model. We remark that the existence of exactly two stable steady state solutions for (3.10) and (3.11) heavily depends on the geometry of the domain Ω. Most exact multiplicity results in Section 2 hold for the ball domains but not general bounded domain Ω, as shown by Dancer (1988) in the example of dumbbell shaped domains. A similar remark can be applied to Neumann boundary value problem (3.23). For the convex domains Ω, the bistable reaction-diffusion equation (3.23) with $f(u) = u(1 - u^2)$ (Allen-Cahn equation from material science) has exactly two stable steady state solutions $u = \pm 1$ from the results of Casten and Hollnad (1978) and Matano (1979). Hence the existence of a threshold manifold follows from Jiang et.al. (2004). But for dumbbell shaped domain, it could have more stable steady state solutions from the result of Matano (1979).

The two locally stable equilibrium points in Jiang-Liang-Zhao's theorem can also be replaced by one locally stable steady state and "infinity" which is locally stable. An abstract formulation of this kind has been obtained in Lazzo and Schmidt (2005), but concrete examples have been given much earlier. For a matrix population model, Schreiber (2004) proved the existence of a threshold manifold that separates the initial values leading to extinction or unbounded growth. A more famous example in partial differential equations is the Fujita equation (Fujita (1966)):

$$u_t = d\Delta u + u^p, \quad x \in \mathbf{R}^n, \quad p > 1. \tag{3.26}$$

Fujita (1966) observed that for $p > (n+2)/(n-2)$ and $n \geq 3$, then the solution to (3.26) with certain initial values blows up in finite time, while some other solutions tend to zero as $t \to \infty$. Since the solution of the ordinary differential equation $u' = u^p$ with $p > 1$ always blows up, then the bistability in the Fujita equation is a combined effect of diffusion (stabilization) and growth (blow up). Aronson and Weinberger (1978) obtained some criteria on the extinction and blow-up of similar type equations, and they called the sensitivity of initial value between the extinction and blow-up the "hair-trigger effect". Mizoguchi (2002) proved the existence of the unique threshold between extinction and complete blow-up for radially symmetric compactly-supported initial values, although the existence of a threshold manifold cannot directly follow from Lazzo and Schmidt (2005) due to the lack of compactness when the domain is the whole space. Similar results have also been proved for bounded domain, see for example Ni, Sacks and Tavantzis (1984).

An intriguing question is whether such a precise bistable structure is still valid for systems of equations. When the system is still a monotone dynamical system, apparently this is true. For example, it holds for the reaction-diffusion counterpart of (3.24): the diffusive competition system with two competitors and no-flux boundary condition:

$$\begin{cases} u_t = d_u \Delta u + u(1 - u - Av), & t > 0, \;\; x \in \Omega, \\ v_t = d_v \Delta v + v(B - Cu - v), & t > 0, \;\; x \in \Omega, \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = 0, & t > 0, \;\; x \in \partial\Omega, \\ u(0,x) = u_0(x) \geq 0, \;\; v(0,x) = v_0(x) \geq 0, & x \in \Omega. \end{cases} \tag{3.27}$$

Here $d_u \geq 0$ and $d_v \geq 0$. The steady states of (3.24) are still (constant) equilibrium solutions of (3.27). Moreover it is known that any stable steady state of (3.27) is constant if Ω is convex from Kishimoto and Weinberger (1985). Thus a threshold manifold of codimension-one exists when Ω is convex following Jiang et.al. (2004) although the dynamics on the threshold is not clear. In a more general setting, Smith and Thieme (2001) studied abstract two species (u, v) competition systems with the origin being a repeller. Assuming that the unique nontrivial boundary steady state on each axis is stable and there is a unique positive steady state, they showed that there is an invariant threshold manifold through the positive steady state separating the attracting domains for both axis steady states. See Jiang and Liang (2006) and Castillo-Chavez, Huang and Li (1999) for more about threshold manifold of bistability in competition models. It should be noted that the results of Jiang et.al. (2004) are not valid for general competition systems with more than two competitors.

By way of contrast, for non-monotone dynamical systems, in general there is no such structure even with only two stable steady states. Some systems may however inherit threshold structure from their limiting systems or subsystems. Consider the reaction and diffusion of the two reactants A and B in an isothermal autocatalytic chemical reaction. We have the system

$$\begin{cases} a_t = D_A \Delta a - ab^p, \;\; b_t = D_B \Delta b + ab^p, & t > 0, \;\; x \in \Omega, \\ a(x,t) = a_0 > 0, \;\; b(x,t) = 0, & t > 0, \;\; x \in \partial\Omega, \\ a(x,0) = A_0(x) \geq 0, \;\; b(x,0) = B_0(x) \geq 0, & x \in \Omega. \end{cases} \tag{3.28}$$

where a and b are the concentrations of the reactant A and the autocatalyst B, $p > 1$, D_A and D_B are the diffusion coefficients of A and B respectively, and Ω is a bounded reaction zone in $\mathbf{R}^n$ (Gray and Scott (1990)). It is known that when reactor Ω is a ball in $\mathbf{R}^n$, (3.28) has either only the trivial steady state $(a_0, 0)$, or exactly three non-negative steady state solutions with two of them stable. Under the additional assumption of equal diffusion coefficients ($D_A = D_B$), Jiang and Shi (2008) shown that in the latter case, the global stable manifold for the intermediate steady state (a_2, b_2) is a codimension-one manifold which separates the basin of attraction of the two stable steady states, and moreover every solution converges to one of three steady state solutions. Here we use the fact that the asymptotic limit of (3.28) is an autonomous scalar reaction-diffusion equation, which is a monotone dynamical system, see Chen and Poláčik (1995), Mischaikow, Smith and Thieme (1995). Although rather special, this is a rare example where the complete dynamics is known for a non-monotone dynamical system in infinite dimensional space. A different bistability result for (3.28) in $\mathbf{R}^n$ is also obtained in Shi and Wang (2006) which uses some ideas from Aronson and Weinberger (1978).

Capasso and Wilson (1997) analyzed the spread of infectious diseases with a reaction-diffusion system:

$$\begin{cases} u_{1t} = d\Delta u_1 - a_{11}u_1 + a_{12}u_2, & t > 0, \;\; x \in \Omega, \\ u_{2t} = -a_{22}u_2 + g(u_1), & t > 0, \;\; x \in \Omega, \\ u_1(x,t) = u_2(x,t) = 0, & t > 0, \;\; x \in \partial\Omega, \\ u_1(x,0) = U_1(x) \geq 0, \;\; u_2(x,0) = U_2(x) \geq 0, & x \in \Omega. \end{cases} \tag{3.29}$$

This system models random dispersal of a pollutant while ignoring the small mobility of the infective human population. Here $u_1(x,t)$ denotes the spatial density of the pollutant, and $u_2(x,t)$ denotes the density of the infective human population. With $g(u)$ being the monotone sigmoid function discussed in Section 1, the steady state equation can be reduced to

$$d\Delta u_1 - a_{11}u_1 + \frac{a_{12}}{a_{22}}g(u_1) = 0, \;\; x \in \Omega, \quad u_1 = 0, \quad x \in \partial\Omega. \tag{3.30}$$

The nonlinearity here $f(u_1) = -a_{11}u_1 + \frac{a_{12}}{a_{22}}g(u_1)$ is of strong Allee effect using the term introduced in the last subsection. Hence under some reasonable conditions and Ω being a ball, the bifurcation diagram of (3.30) is the one in Fig.3.7-c. This is shown in Capasso and Wilson (1997) for the case of $n = 1$, and the general case when $n \geq 2$ can be deduced from the results in Ouyang and Shi (1998). Since (3.29) is a monotone dynamical system, then again (3.29) admits a codimension-one manifold which separates the basin of attraction of the two stable steady states (Jiang et.al. (2004)), which confirms the conjecture in Capasso and Wilson (1997). But it is still not known that whether every solution on the threshold manifold converges to the intermediate steady state solution.

Even less is known about the dynamical behavior of FitzHugh-Nagumo system:

$$\begin{cases} \epsilon v_t = d_v\Delta v + v(v-a)(1-v) - w, & t > 0, \;\; x \in \Omega, \\ w_t = d_w\Delta w + cv - bw, & t > 0, \;\; x \in \Omega, \\ v(x,t) = w(x,t) = 0, & t > 0, \;\; x \in \partial\Omega, \\ v(x,0) = V(x) \geq 0, \;\; w(x,0) = W(x) \geq 0, & x \in \Omega. \end{cases} \tag{3.31}$$

Here $d_v > 0$ and $d_w \geq 0$. When $c = 0$, it follows that $w \to 0$, and the dynamics of (3.31) is reduced to that of Nagumo equation (3.25) (in higher dimensional domain). Since (3.25) has the saddle point behavior, then (3.31) still possesses this saddle point behavior for $0 < c \ll 1$ by structural stability theory. For more general parameter ranges, the existence of multiple positive steady state solutions of (3.31) is known, see for example Matsuzawa (2005) for a nice summary. Notice that (3.31) is not a monotone dynamical system, so even the information of stable steady state solutions cannot imply the saddle point behavior.

Threshold manifolds are a class of invariant manifolds in applied dynamical systems, and they are sensitively unstable in the dynamic sense as a small perturbation will shift it to the basin of attraction of a stable equilibrium. If one reverses the time t to $-t$ to a system with threshold manifold, then the manifold becomes an attracting manifold, or vice versa. For example, in the logistic model (3.1), if time is reversed, then it has the exactly same dynamical behavior as Fujita equation or the abstract formulation in Lazzo and Schmidt (2005): both the origin and the infinity are stable and the carrying capacity N becomes a threshold point. Similarly, if one reverses the time in the classical Lotka-Volterra competition system (3.24) without diffusion, then the origin and the infinity become stable, and there is a threshold manifold containing the boundary steady state $(1,0)$, $(0,B)$ and coexistence steady state on which "hair-trigger effect" occurs, which is deduced from Hirsch (1988) or an analysis for phase pictures. Of course it is not realistic to reverse the time in logistic model or Lotka-Volterra competition system. Nevertheless, in logistic model (3.1) or Lotka-Volterra system (3.24), both the origin and the infinity are repellers, and there is a threshold manifold separating the repelling domains for the origin and the infinity. Such a threshold manifold plays the role of carrying capacity in the logistic model, so it is often called *Carrying Simplex*.

The first example of a carrying simplex was given by Hirsch (1988) in his seminal paper. For a dissipative and strongly competitive Kolmogorov system:

$$\frac{dx_i}{dt} = x_i F_i(x_1, x_2, \cdots, x_n), \quad x_i \geq 0, \quad i = 1, 2, \cdots, n, \tag{3.32}$$

Hirsch (1988) proved that if the origin is a repeller, then there exists a carrying simplex which attracts all nontrivial orbits for (3.32) and it is homeomorphic to probability simplex by radial projection. Note that dissipation implies that the infinity is also a repeller.

Smith (1986) investigated C^2 diffeomorphisms T on the nonnegative orthant K which possesses the properties (see the hypotheses in Smith (1986)) of the Poincaré map induced by C^2 strong competition system

$$\frac{dx_i}{dt} = x_i F_i(t; x_1, x_2, \cdots, x_n), \quad x_i \geq 0, \quad i = 1, 2, \cdots, n, \tag{3.33}$$

where F_i is 2π-periodic in t, $F_i(t; 0) > 0$, and (3.33) has a globally attracting 2π-periodic solution on each positive coordinate axis. This implies that the origin is a repeller for T and it has a global attractor Γ. He proved that the boundaries of the repulsion domain of the origin and the global attractor relative to the nonnegative orthant are a compact unordered invariant set homeomorphic to the probability simplex by radical projection. He conjectured both boundaries coincide, serving as a unique carrying simplex. Introducing a mild additional restriction on T, which is generically satisfied by the Poincaré map of the competitive Kolmogorov system (3.33), Wang and Jiang (2002) proved this conjecture and that the unstable manifold of $m-$periodic point of T is contained in this carrying simplex. Diekmann, Wang and Yan (2008) have showed the same result holds by dropping one of the hypotheses in Smith's original conjecture so that the result is easier to use in the setting of competitive mappings. Hirsch (2008) introduces a new condition—strict sublinearity in a neighborhood of the global attractor, to give a new existence criterion for the unique carrying simplex. The uniqueness of the carrying simplex is important in classifying the dynamics of lower dimensional competitive systems, for example the 3-dimensional Lokta-Volterra competition system (Zeeman (1993)). The classification of many three dimensional competitive mappings (see Davydova, Diekmann and van Gils (2005a, 2005b), Hirsch (2008) and references therein) are still open, and the uniqueness of the carrying simplex is one of the reasons.

Note that if one reverses the time t to $-t$ in the n-dimensional competition system (3.32), then the system becomes a monotone system with both the origin and the infinity stable (under the assumption that the origin and the infinity are repellers). However this new system is not strongly monotone as required in Jiang et.al. (2004) and Lazzo and Schmidt (2005). Thus the existence of the carrying simplex cannot follow from Jiang et.al. (2004) and Lazzo and Schmidt (2005) except in the case of

$n = 2$. Indeed this is one of the main difficulties in Hirsch (1988), Wang and Jiang (2002), and Diekmann, Wang and Yan (2008).

We conclude our discussion of threshold manifolds with a model of biochemical feedback control circuits. More details on the modeling can be found in, for example, Murray (2003) or Smith (1995). A segment of DNA is assumed to be translated to mRNA which in turn is translated to produce an enzyme and it in turn is translated to another enzyme and so on until an end product molecule is produced. This end product acts on a nearby segment of DNA to produce a feedback loop, controlling the translation of DNA to mRNA. Let x_1 be the cellular concentration of mRNA, let x_2 be the concentration of the first enzyme, and so on, finally let x_n be the concentration of their substrate. Then this biochemical control circuit is described by the system of equations

$${x_1}' = g(x_n) - \alpha_1 x_1, \ \ {x_i}' = x_{i-1} - \alpha_i x_i, \ \ 2 \le i \le n, \tag{3.34}$$

where $\alpha_i > 0$ and the feedback function $g(u)$ is a bounded continuously differentiable function satisfying

$$0 < g(u) < M, \ g'(u) > 0, \ u > 0. \tag{3.35}$$

Hence it models a positive feedback. For the Griffith model (Griffith (1968)) we have

$$g(x_n) = \frac{x_n^p}{1 + x_n^p} \tag{3.36}$$

where p is a positive integer (the Hill coefficient). For the Tyson-Othmer model (Tyson and Othmer (1978)) we have

$$g(x_n) = \frac{1 + x_n^p}{K + x_n^p} \tag{3.37}$$

where p is a positive integer and $K > 1$. The solution flow for (3.34) is strongly monotone (see Smith (1995) for detail). The steady states for (3.34) are in one-to-one correspondence with solutions of

$$g(u) = \alpha u \tag{3.38}$$

where $\alpha = \prod \alpha_i$. Suppose that the line $v = \alpha u$ intersects the curve $v = g(u)$ ($u \ge 0$) transversally. Then every non-negative steady state for (3.34) is hyperbolic, which implies that the number of steady states for (3.34) is odd for either the Griffith or Tyson-Othmer model. For most of biological parameters in the Griffith or Tyson-Othmer model, there are exactly three steady states (Selgrade (1979, 1980, 1982) and Jiang (1992, 1994)). In this case, the least steady state and the greatest steady state are asymptotically stable and intermediate one is a saddle point through which there is an invariant threshold manifold whose norm is positive. In the multistable case, there are $\left[\dfrac{n-1}{2}\right]$ invariant threshold manifolds which separate the attracting domains for stable steady states (see Jiang et.al. (2004)). From a general result of Mallet-Paret and Smith (1990), we know that on each invariant threshold manifold every orbit either converges to the saddle point or is asymptotic to a nontrivial unstable periodic orbit. For $n \le 3$, all orbits tend to the corresponding saddle point on threshold manifolds, which was proved by using topological arguments in Selgrade (1979,1980), the Dulac criterion for 3-dimensional cooperative system in Hirsch (1989) and a Lyapunov function in Jiang (1992); for $n \geq 5$, in the bistable case for the Griffith or Tyson-Othmer model, there may exist Hopf bifurcation on the unique threshold manifold (see Selgrade (1982)). But for $n = 4$, whether there is a nontrivial periodic orbit or not on threshold manifold is an open problem. In Jiang (1994), it was proved that for 4-dimensional Griffith or Tyson-Othmer model all orbits are convergent to a steady state via Lyapunov method for parameters with biological significance.

Hetzer and Shen (2005) added a third equation to the classical Lotka-Volterra equations for two competing species, which describes explicitly the evolution of toxin, called an inhibitor. The equations in rescaled form are

$$\begin{cases} \dot{u} = u(1 - u - d_1 v - d_2 w), \\ \dot{v} = \rho v(1 - fu - v), \\ \dot{w} = v - (g_1 u + g_2)w, \end{cases} \tag{3.39}$$

where $d_1, d_2, \rho, f, g_1, g_2 > 0$. Note that $O(0,0,0)$, $E_x(1,0,0)$, and $E_y(0,1,g_2^{-1})$ are non-negative steady states of (3.39). Observing that O is a saddle, not a repeller, Hetzer and Shen (2005) studied the long-time behavior for (3.39) and the existence of threshold manifold in the bistable case, where they called a "thin separatrix" following Hsu, Smith and Waltman (1996), Smith and Thieme (2001). Jiang and Tang (2008) gave a complete classification for dynamical behavior for (3.39) and proved that the bistability occurs if and only if

$$a^* > 0,\ b^* < 0,\ c^* > 0,\ \Delta^* = (b^*)^2 - 4a^*c^* > 0, 2a^* + b^* > 0,\ a^* + b^* + c^* > 0, \tag{3.40}$$

where a^*, b^*, c^* are given by

$$a^* = g_1(1 - d_1 f),\ \ c^* = g_2(d_1 + \frac{d_2}{g_2} - 1), \tag{3.41}$$

and

$$a^* + b^* + c^* = (1 - f)(d_1 g_1 + d_1 g_2 + d_2). \tag{3.42}$$

In this case the system (3.39) has exactly two hyperbolic positive steady states, one of which is stable, denoted by E^*, while the other is a saddle point, denoted by E_*. (3.39) has exactly two stable steady states E_y and E^*. The stable manifold for the saddle point E_*, which is a 2-dimensional smooth surface, separates the basins of attraction for E_y and E^*. Hence this smooth surface is a threshold manifold.

The production of the various proteins in the biochemical control circuit model (3.34) is, of course, not instantaneous and it is reasonable to introduce time delays into these terms. If one does so, (3.34) becomes a delay differential equation:

$$x_1{}' = g(x_n(t - r_n)) - \alpha_1 x_1,\ \ x_i{}' = x_{i-1}(t - r_{j-1}) - \alpha_i x_i,\ \ 2 \leq i \leq n, \tag{3.43}$$

with all delays r_i positive. It is easy to see that all steady states for (3.43) are the same as (3.34) and if a steady state for (3.34) is linearly stable (unstable) then it is also linearly stable (unstable) for (3.43) (Smith (1995) p.111). Thus in the bistable case for

(3.43), there is a codimension-one threshold manifold through a saddle point separating the attracting domains for the two steady states. The only difference is that such a threshold manifold in the space of continuous functions is infinite dimensional and less information is known for the dynamics on the threshold manifold. The results are similar for the multistable case (see Jiang et.al. (2004)). Of course another way to have an infinite dimensional threshold manifold is to add diffusion to bistable (multistable) monotone ODEs or FDEs with no-flux boundary condition on a smooth and convex domain, so that codimension-one threshold manifolds still exist (see Jiang et.al. (2004)).

3.4 Concluding Remarks

Sharp regime shifts occur in some large-scale ecosystems such as lakes, coral reefs, grazed grasslands and forests. Mathematical models have been set up to explain the sudden changes and hysteresis cycles in these systems. In this article, we review some of these models with a focus on the impact of spatial dispersal and habitat fragmentation. The rich dynamics of these problems share some common mathematical features such as multiple steady states, threshold manifold (separatrix), and non-monotone bifurcation diagrams. Mathematical tools from partial differential equations, bifurcation theory, and monotone dynamical systems have been applied and further developed in studying these important problems rooted from various applied areas.

Establishing the basic structure of multiple steady states and threshold manifold is the first step in a complete understanding of the bistable dynamics, regime shifts and ecosystems resilience. The dynamics on the separatrix could be very complicated, and there is also evidence that bistability in a reaction-diffusion predator-prey system could imply existence of more complex patterns (see Morozov, Petrovskii and Li (2004,2006), Petrovskii, Morozov and Li (2005)). Another important question is how to make early warning of the regime shifts. The bifurcation diagrams suggest that the regime shifts occur at saddle-node bifurcation points, at which the largest eigenvalue (principal eigenvalue) of the linearized system is zero. Near bifurcation points, the principal eigenvalue is small. It has been recognized that the principal eigenvalue at a steady state is related to the return time, which is another definition of resilience of the system (see Pimm (1991)). The return time is how fast a variable that has been displaced from equilibrium returns to it. For the dynamical models described here, such return time to the equilibrium is characterized by $\exp(\lambda_1 t)$, where λ_1 is the principal eigenvalue at the equilibrium. Hence early warning for regime shifts in large scale could be triggered by a change in return time, provided that information on the return time is obtained from small scale experiments.

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