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Bifurcation analysis in a host-generalist parasitoid model with Holling II functional response

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Abstract

In this paper we study a host-generalist parasitoid model with Holling II functional response where the generalist parasitoids are introduced to control the invasion of the hosts. It is shown that the model can undergo a sequence of bifurcations including cusp, focus and elliptic types degenerate Bogdanov-Takens bifurcations of codimension three, and a degenerate Hopf bifurcation of codimension at most two as the parameters vary, and the model exhibits rich dynamics such as the existence of multiple coexistent steady states, multiple coexistent periodic orbits, homoclinic orbits, etc. Moreover, there exists a critical value for the carrying capacity of generalist parasitoids such that: (i) when the carrying capacity of the generalist parasitoids is smaller than the critical value, the invading hosts can always persist despite of the predation by the generalist parasitoids, i.e., the generalist parasitoids cannot control the invasion of hosts; (ii) when the carrying capacity of the generalist parasitoids is larger than the critical value, the invading hosts either tend to extinction or persist in the form of multiple coexistent steady states or multiple coexistent periodic orbits depending on the initial populations, i.e., whether the invasion can be stopped and reversed by the generalist parasitoids depends on the initial populations; (iii) in both cases, the generalist parasitoids always persist. Numerical simulations are presented to illustrate the theoretical results.

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1. Introduction

Biological invasions have been an interesting and important issue since the pioneering work of Fisher [8], and many mathematical models have been proposed to identify factors that humans should concentrate on to stop invasions and even sometimes to reverse them (Hastings [11]). Owen and Lewis [18] firstly proposed a series of reaction-diffusion predator-prey models to derive conditions under which specialist predators can slow, stall or reverse a spatial invasion of the prey. They examined the types of functional response which give such solutions and the circumstances under which the models are appropriate, and found that a slowdown of invasion can be obtained if the functional response is linear (Type I) and if the preys show a weak Allee effect in their growth. Later, Fagan et al. [7] confirmed the importance of Type I functional response and the Allee effect in stopping or reversing the process for specialist predators. However, the control capacity of a generalist predator depends on many factors, such as its preference, spatial and temporal scales, etc. (Walde [24]).

Motivated by the invasion of leaf-mining microlepidopteron attacking horse chestnut trees in Europe (in particular in France) and the need for a biological control and followed Owen and Lewis [18], Magal et al. [17] investigated the following host-parasitoid model with Holling Type II functional response

$$
\begin{aligned}
\dot{u} &= r_1 u\left(1-\tfrac{u}{K_1}\right)-\tfrac{\xi u v}{1+\xi h u},\\
\dot{v} &= r_2 v\left(1-\tfrac{v}{K_2}\right)+\tfrac{\gamma \xi u v}{1+\xi h u},
\end{aligned}
\tag{1.1}
$$

where $u(t)$ and $v(t)$ denote densities of the hosts (leafminers *Cameraria orhidella*) and generalist parasitoids (*Minotetrastichus frontalis*) at time t, respectively. r_1 represents the intrinsic growth rate of the hosts in absence of parasitoids, r_2 represents the intrinsic growth rate of the parasitoids in absence of hosts, K_1 denotes the carrying capacity of the host population, K_2 denotes the carrying capacity of the parasitoid population. ξ is the encounter rate of hosts and parasitoids, γ is the conversion rate of parasitoids, h describes the harvesting time. r_i, $K_i (i = 1, 2)$, γ, ξ, h are all positive constants.

Magal et al. [17] analyzed the number and stability of equilibria in system (1.1) and showed that the model always predicts persistence of the parasitoids. Special cases in which small carrying capacity leads to complex dynamical behaviors were studied by numerical simulations. Depending on the parameter values, the model may predict that the hosts persist and go extinct or there is something like an Allee effect where the outcome depends on the initial host density. Most recently, Seo and Wolkowicz [22] revisited system (1.1), gave a more detailed analysis of the model, and revised the criteria for control strategies of the leaf miner population proposed by Magal et al. [17]. They obtained analytical conditions that divide the K_1K_2-plane into regions in which there are zero, one, two, or three coexistence equilibria and considered the local and global stability of these equilibria. They then showed that the model displays interesting dynamical behavior using a bifurcation theory approach and provided analytical expressions for fold and Hopf bifurcations and for the criticality of the Hopf bifurcations. Moreover, their numerical results show very interesting dynamics resulting from codimension one bifurcations including Hopf, fold, transcritical, cyclic-fold, and homoclinic bifurcations as well as codimension two bifurcations including Bautin and Bogdanov-Takens bifurcations, and a codimension three Bogdanov-Takens bifurcation. Although plentiful results have been shown for system (1.1), the complete nonlinear dynamics and bifurcations still remain unknown and merit further investigation. This is the objective of this paper.

For simplicity, we first nondimensionalize system (1.1) with the following scaling

$$x = \frac{u}{K_1}, \quad y = \frac{r_2 v}{r_1 K_2}, \quad \bar{t} = r_1 t.$$

Dropping the bar of $\bar{t}$, model (1.1) becomes

$$\begin{aligned} \dot{x} &= x(1 - x - \tfrac{by}{a+x}), \\ \dot{y} &= y(\delta - y + \tfrac{cx}{a+x}), \end{aligned} \tag{1.2}$$

in which

$$a = \frac{1}{K_1 \xi h}, \quad b = \frac{K_2}{K_1 r_2 h}, \quad c = \frac{\gamma}{r_1 h}, \quad \delta = \frac{r_2}{r_1},$$

where a, b, c, δ are all positive constants. For system (1.2) (i.e., system (1.1)), we will show that there are cusp, focus and elliptic types of nilpotent singularities of codimension three and a weak focus of multiplicity at most two for various parameter values, and the model undergoes a sequence of bifurcations including cusp, focus and elliptic types degenerate Bogdanov-Takens bifurcations of codimension three, a Hopf bifurcation, and a degenerate Hopf bifurcation of codimension at most two as the parameters vary.

The paper is organized as follows: In section 2, we analyze the existence and type of equilibria in model (1.2). In section 3, we discuss various possible bifurcations of model (1.2), and show that the model exhibits cusp, focus and elliptic types degenerate Bogdanov-Takens bifurcations of codimension three, a Hopf bifurcation, and a degenerate Hopf bifurcation of codimension at most two as the parameters vary. The paper ends with a brief discussion in section 4.

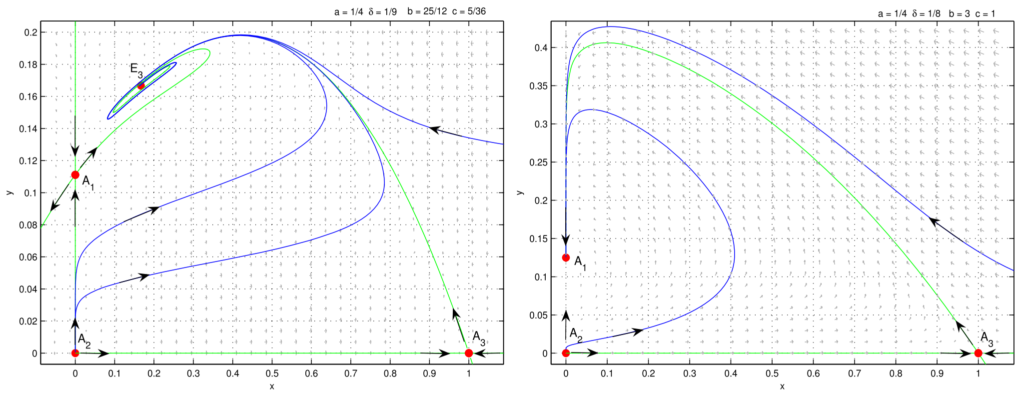
2. Equilibria and their types

By the biological implications, we only consider system (1.2) in $\mathbb{R}^2_+ = \{(x, y) | x \geqslant 0, y \geqslant 0\}$. It is easy to see that the positive invariant and bounded region of system (1.2) is

$$\Omega = \{(x, y) | 0 \leq x \leq 1, 0 \leq y \leq \delta + \frac{c}{a+1}\}.$$

Notice that system (1.2) always has three boundary equilibria $(0, 0)$, $(1, 0)$ and $(0, \delta)$ for all permissible parameters. The Jacobian matrix of system (1.2) at any equilibrium $E(x, y)$ of system (1.2) takes the form

$$J(E) = \begin{pmatrix} 1 - 2x - \frac{aby}{(a+x)^2} & -\frac{bx}{a+x} \\ \frac{acy}{(a+x)^2} & \delta - 2y + \frac{cx}{a+x} \end{pmatrix},$$



(a) (b)

Fig. 2.1. Three boundary equilibria: A_2 is an unstable hyperbolic node, A_3 is a hyperbolic saddle, and (a) A_1 is a hyperbolic saddle if $\delta < \frac{a}{b}$; (b) A_1 is a stable hyperbolic node if $\delta > \frac{a}{b}$.

and

$$\mathrm{Det}(J(E)) = (1-2x-\frac{aby}{(a+x)^2})(\delta-2y+\frac{cx}{a+x})+\frac{abcxy}{(a+x)^3},$$

$$\mathrm{Tr}(J(E)) = 1+\delta-2(x+y)+\frac{cx}{a+x}-\frac{aby}{(a+x)^2}.$$

It implies that $E(x,y)$ is an elementary equilibrium if $\mathrm{Det}(J(E)) \neq 0$, a hyperbolic saddle if $\mathrm{Det}(J(E)) < 0$, or a degenerate equilibrium if $\mathrm{Det}(J(E)) = 0$, respectively.

Considering the Jacobian matrix of system (1.2) at these boundary equilibria, we can easily get the following lemma.

Lemma 2.1. *System (1.2) always has three boundary equilibria $A_1(0,\delta)$, $A_2(0,0)$ and $A_3(1,0)$. A_2 is always a hyperbolic unstable node, A_3 is always a hyperbolic saddle, and A_1 is a hyperbolic saddle if $\delta < \frac{a}{b}$, a hyperbolic stable node if $\delta > \frac{a}{b}$ and a degenerate equilibrium if $\delta = \frac{a}{b}$. The phase portraits are given in Fig. 2.1.*

Remark 2.2. When $\delta < \frac{a}{b}$, i.e., $K_2 < \frac{r_1}{\xi}$, from Lemma 2.1 and Fig. 2.1(a), we can see that the invading hosts can always persist in spite of the predation of hosts by generalist parasitoids if the carrying capacity for generalist parasitoids is smaller than a critical value $\frac{r_1}{\xi}$, i.e., the generalist parasitoids cannot control the invasion of hosts; When $\delta \geq \frac{a}{b}$, i.e., $K_2 \geq \frac{r_1}{\xi}$, from Lemma 2.1 and Fig. 2.1(b), we can see that the invading hosts can go extinct because of the predation of the hosts by generalist parasitoids if the carrying capacity for generalist parasitoids is larger than the critical value $\frac{r_1}{\xi}$, i.e., the generalist parasitoids can stop or reverse the invasion of hosts. In both cases, the generalist parasitoids always persist.

Lemma 2.3. *If $\delta = \frac{a}{b}$, then $A_1(0,\delta)$ is a degenerate equilibrium. Moreover,*

(I) *if $c \neq \frac{a-a^2}{b}$, then $(0,\delta)$ is a saddle-node, which includes a stable parabolic sector;*

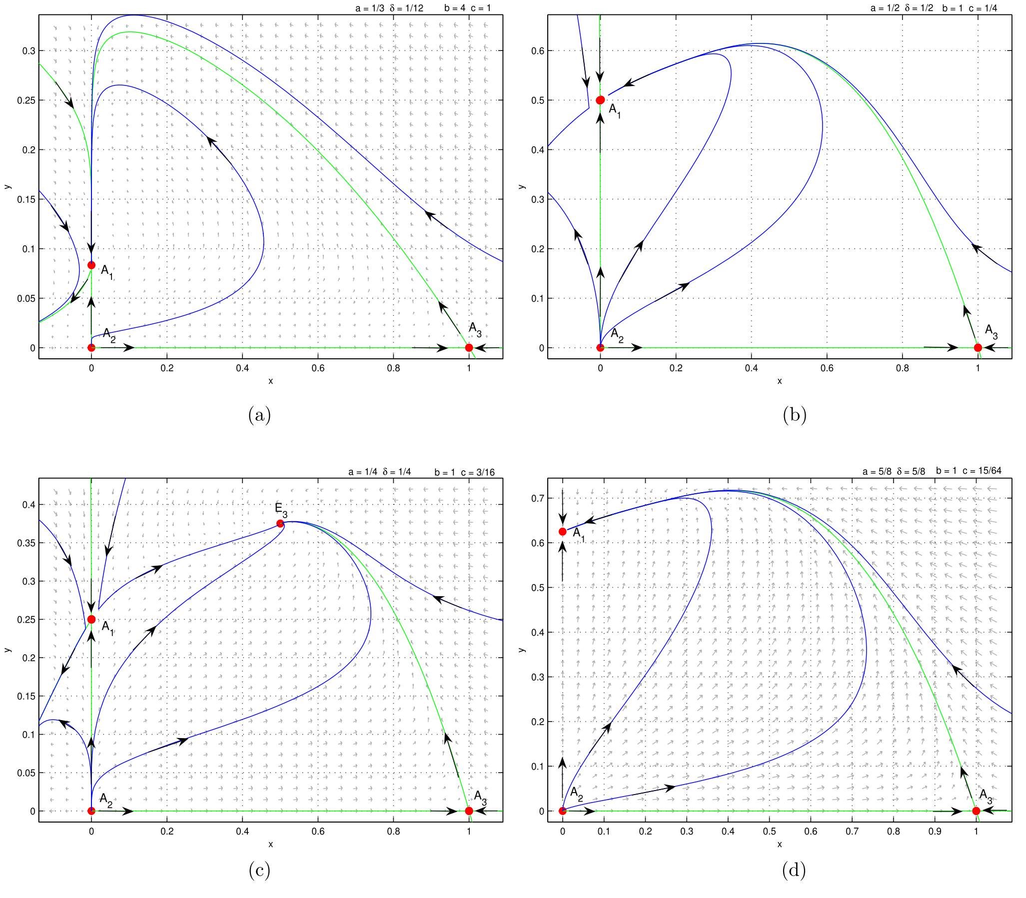


Fig. 2.2. Three boundary equilibria when $\delta = \frac{a}{b}$, where A_2 is an unstable hyperbolic node, A_3 is a hyperbolic saddle, and (a) A_1 is a saddle-node which includes a stable parabolic sector if $c \neq \frac{a-a^2}{b}$; (b) A_1 is a saddle-node which includes a stable parabolic sector if $c = \frac{a-a^2}{b}$ and $a = \frac{1}{2}$; (c) A_1 is a degenerate saddle if $c = \frac{a-a^2}{b}$ and $0 < a < \frac{1}{2}$; (d) A_1 is a stable degenerate node if $c = \frac{a-a^2}{b}$ and $\frac{1}{2} < a < 1$.

(II) *if* $c = \frac{a-a^2}{b}$, $0 < a < 1$ *and*

(i) *if* $a = \frac{1}{2}$, *then* $(0, \delta)$ *is a saddle-node, which includes a stable parabolic sector;*

(ii) *if* $0 < a < \frac{1}{2}$, *then* $(0, \delta)$ *is a degenerate saddle;*

(iii) *if* $\frac{1}{2} < a < 1$, *then* $(0, \delta)$ *is a stable degenerate node.*

The phase portraits are given in Fig. 2.2.

Proof. When $\delta = \frac{a}{b}$, we have $\mathrm{Det}(J(0,\delta)) = 0$ and $\mathrm{Tr}(J(0,\delta)) = -\delta$. Firstly, letting $(u, v) = (x, y - \delta)$ to translate $(0, \delta)$ to the origin, system (1.2) becomes

$$\begin{aligned} \dot{u} &= u\left(1 - u - \frac{b(v+\frac{a}{b})}{a+u}\right), \\ \dot{v} &= \left(v + \frac{a}{b}\right)\left(-v + \frac{cu}{a+u}\right). \end{aligned} \tag{2.1}$$

Secondly, making the following transformations

$$u=\frac{a}{c}X,\;\; v=X+Y,\;\; t=-\frac{a}{b}\tau,$$

and still denoting τ by t, we obtain the Taylor expansions of system (2.1) around the origin as follows

$$\begin{aligned}\dot{X}&=\widehat{a_{20}}X^2+\widehat{a_{11}}XY+\widehat{a_{30}}X^3+\widehat{a_{21}}X^2Y+\widehat{a_{40}}X^4+\widehat{a_{31}}X^3Y+f(X,Y),\\ \dot{Y}&=Y+\widehat{b_{20}}X^2+\widehat{b_{11}}XY+\widehat{b_{02}}Y^2+\widehat{b_{30}}X^3+\widehat{b_{21}}X^2Y+\widehat{b_{40}}X^4+\widehat{b_{31}}X^3Y+g(X,Y),\end{aligned}\tag{2.2}$$

where f, g are smooth functions in at least order five of (X, Y), and

$$\begin{aligned}&\widehat{a_{20}}=\frac{b(-a+a^2+bc)}{a^2c},\;\widehat{a_{11}}=\frac{b^2}{a^2},\;\widehat{a_{30}}=\frac{b(a-bc)}{a^2c^2},\;\widehat{a_{21}}=-\frac{b^2}{a^2c},\;\widehat{a_{40}}=\frac{b(-a+bc)}{a^2c^3},\\ &\widehat{a_{31}}=\frac{b^2}{a^2c^2},\;\widehat{b_{20}}=\frac{a^2+ab-a^2b-b^2c}{a^2c},\;\widehat{b_{11}}=\frac{(a-b)b}{a^2},\;\widehat{b_{02}}=\frac{b}{a},\\ &\widehat{b_{30}}=-\frac{(a+b)(a-bc)}{a^2c^2},\;\widehat{b_{21}}=\frac{b(a+b)}{a^2c},\;\widehat{b_{40}}=\frac{(a+b)(a-bc)}{a^2c^3},\;\widehat{b_{31}}=-\frac{b(a+b)}{a^2c^2}.\end{aligned}$$

By Theorem 7.1 in Zhang et al. [27], we know that $(0,\delta)$ is a saddle-node, which includes a stable parabolic sector if $c\neq\frac{a-a^2}{b}$.

If $c=\frac{a-a^2}{b}$, then $\widehat{a_{20}}=0$, by the center manifold theorem we suppose $Y=m_1X^2+m_2X^3+o(|X|^3)$ and substitute it to the second equation of system (2.2). By using the first equation of system (2.2), we have

$$m_1=\frac{b}{a^2-a},\;\; m_2=\frac{(a-b+2ab)b^2}{(a-1)^2a^3}.$$

Substituting $Y=m_1X^2+m_2X^3+o(|X|^3)$ into the first equation of system (2.2), then the reduced equation restricted to the center manifold takes the following form

$$\dot{X}=-\frac{b^3(1-2a)}{a^3(1-a)^2}X^3+o(|X|^3).$$

Noticing that when $a=\frac{1}{2}$, $\dot{X}=O(|X|^4)$, we substitute $a=\frac{1}{2}$ to the first equation of system (2.2) and obtain

$$\dot{X}=64b^4X^4+o(|X|^4).$$

Again by Theorem 7.1 in Chapter 2 of [27], and notice that we have made a time transformation $\tau=-\frac{b}{a}t$, then $(0,\delta)$ is a stable degenerate node if $\frac{1}{2}<a<1$; $(0,\delta)$ is a degenerate saddle if $0<a<\frac{1}{2}$; and $(0,\delta)$ is a saddle-node, which includes a stable parabolic sector if $a=\frac{1}{2}$. $\square$

Remark 2.4. When $\delta = \frac{a}{b}$, we have $K_2 = \frac{r_1}{\xi}$, i.e., the carrying capacity of generalist parasitoids is equal to a critical value $\frac{r_1}{\xi}$, from Lemma 2.3 and Fig. 2.2, we can see that whether the invading hosts persist or go extinct depends on other factors including the carrying capacity K_1 for the hosts and the conversion rate γ for generalist parasitoids.

We next consider the positive equilibria of system (1.2). If $E(x, y)$ is a positive equilibrium of system (1.2), then x is a root of the following equation

$$x^3 + (2a-1)x^2 + (a^2 - 2a + bc + b\delta)x + ab\delta - a^2 = 0 \tag{2.3}$$

in the interval (0, 1). Note that the third-order algebraic equation (2.3) can have one, two, or three positive roots in the interval (0, 1), correspondingly, so system (1.2) can have one, two, or three positive equilibria, respectively. In order to investigate the types of positive equilibria, we firstly let

$$\begin{aligned} f(x) &= x^3 + (2a-1)x^2 + (a^2 - 2a + bc + b\delta)x + ab\delta - a^2, \\ f'(x) &= 3x^2 + 2(2a-1)x + (a^2 - 2a + bc + b\delta). \end{aligned} \tag{2.4}$$

From $f(x) = 0$, we have

$$c = -\tfrac{(a+x)(a(x-1)-x+x^2+b\delta)}{bx}. \tag{2.5}$$

The Jacobian matrix of system (1.2) at $E(x, y)$ can be simplified as follows

$$\mathrm{J}(E) = \begin{pmatrix} x(\frac{1-x}{a+x} - 1) & -\frac{bx}{a+x} \\ \frac{acy}{(a+x)^2} & -\delta - \frac{cx}{a+x} \end{pmatrix},$$

and

$$\mathrm{Det}(J(E)) = \frac{x}{(a+x)^2}(2(c+\delta)x^2 + (3a\delta - c - \delta)x + a\delta(a-1) + ac),$$

$$\mathrm{Tr}(J(E)) = -\frac{1}{a+x}(2x^2 + (a+c+\delta-1)x + a\delta).$$

Substituting (2.5) into $\mathrm{Det}(J(E))$, we can rewrite $\mathrm{Det}(J(E))$ as

$$\begin{aligned} \mathrm{Det}(J(E)) &= \tfrac{x(x-1)(a+x)(-a^2+x^2-2ax^2-2x^3+ab\delta)}{bx(a+x)^2} \\ &= \tfrac{x(1-x)(a+x)}{bx(a+x)^2}(xf'(x) - f(x)) \\ &= \tfrac{x(1-x)}{b(a+x)} f'(x). \end{aligned} \tag{2.6}$$

According to the root formula of the third-order algebraic equation, we let

$$\begin{aligned} \widetilde{A} &= (2a-1)^2 - 3(a^2 - 2a + bc + b\delta), \\ \Delta &= -4\widetilde{A}^3 + \big(-3(1-2a)\widetilde{A} + (1-2a)^3 + 27(ab\delta - a^2)\big)^2. \end{aligned} \tag{2.7}$$

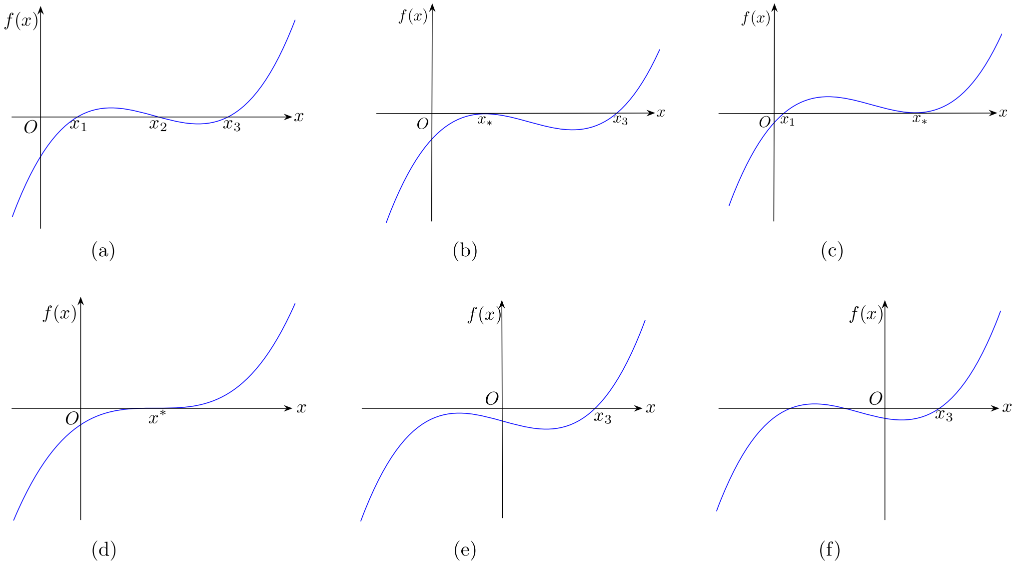


Fig. 2.3. The positive roots of $f(x) = 0$ when $\delta < \frac{a}{b}$. (a) Three single positive roots x_1, x_2 and x_3; (b)(c) Two positive roots: a double root x_* and a single root x_1 (or x_3); (d) A unique triple positive root x^*; (e)(f) A unique single positive root x_3.

Since the maximum number of positive roots of (2.3) is determined by the constant term of equation (2.3), we classify the number and type of positive equilibria of system (1.2) into the following two cases: $\delta < \frac{a}{b}$ (i.e., $K_2 < \frac{r_1}{\xi}$) and $\delta \geq \frac{a}{b}$ (i.e., $K_2 \geq \frac{r_1}{\xi}$).

2.1. The case $\delta < \frac{a}{b}$ (i.e., $K_2 < \frac{r_1}{\xi}$)

In this case, system (1.2) has three boundary equilibria: a hyperbolic unstable node $(0, 0)$, two hyperbolic saddles $(1, 0)$ and $(0, \delta)$, and at most three positive equilibria. According to Fig. 2.3 about the curve $f(x)$, we have the following lemma.

Lemma 2.5. *When $\delta < \frac{a}{b}$ (i.e., $K_2 < \frac{r_1}{\xi}$), system (1.2) has at least one positive equilibrium and at most three positive equilibria. Moreover,*

(I) *if $\Delta < 0$, then system (1.2) has three different positive equilibria: E_2 is a hyperbolic saddle, and $E_i(x_i, y_i)(i = 1, 3)$ is a hyperbolic stable node or focus if $\mathrm{Tr}(J(E_i)) < 0$, a hyperbolic unstable node or focus if $\mathrm{Tr}(J(E_i)) > 0$, and a weak focus or center if $\mathrm{Tr}(J(E_i)) = 0$, where $0 < x_1 < x_2 < x_3 < 1$;*

(II) *if $\Delta = 0$ and*

  (a) *$\widetilde{A} > 0$, then system (1.2) has two different positive equilibria: a degenerate equilibrium $E_*(x_*, y_*)$, and an elementary equilibrium $E_1(x_1, y_1)$ (or $E_3(x_3, y_3)$) which is a hyperbolic stable node or focus if $\mathrm{Tr}(J(E_i)) < 0$, a hyperbolic unstable node or focus if $\mathrm{Tr}(J(E_i)) > 0$, and a weak focus or center if $\mathrm{Tr}(J(E_i)) = 0$, where $x_1 < x_* < x_3$;*

  (b) *$\widetilde{A} = 0$, then system (1.2) has a unique positive equilibrium $E^*(\frac{1-2a}{3}, \frac{2(1+a)^2}{9b})$, which is a degenerate equilibrium, where $0 < a < \frac{1}{2}$;*

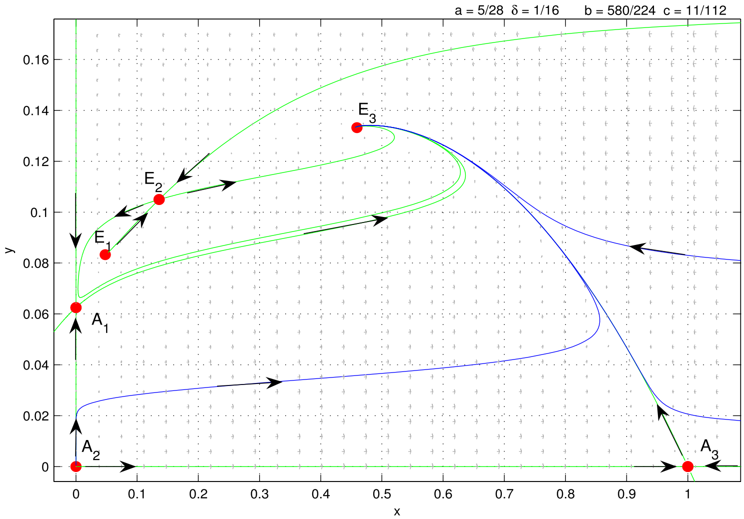


Fig. 2.4. The coexistence of three positive equilibria and three boundary equilibria when $\delta < \frac{a}{b}$: an unstable focus E_1, three saddles E_2, A_1 and A_3, a stable focus E_3, and an unstable node A_2.

(III) *if* $\Delta > 0$, *then system (1.2) has a unique positive equilibrium* $E_3(x_3, y_3)$, *which is a hyperbolic stable node or focus if* $\mathrm{Tr}(J(E_3)) < 0$, *a hyperbolic unstable node or focus if* $\mathrm{Tr}(J(E_3)) > 0$, *and a weak focus or center if* $\mathrm{Tr}(J(E_3)) = 0$, *where* $0 < x_3 < 1$.

Proof. From equation (2.6) and the derivative property of $f(x)$, it is easy to see that $\mathrm{Det}(J(E_i)) > 0$ $(i = 1, 3)$, $\mathrm{Det}(J(E_2)) < 0$, $\mathrm{Det}(J(E_*)) = 0$, $\mathrm{Det}(J(E^*)) = 0$, so E_1, E_2 and E_3 are all elementary equilibria and only E_2 is a hyperbolic saddle, E_* and E^* are all degenerate equilibria. □

Remark 2.6. When $\delta < \frac{a}{b}$, i.e., $K_2 < \frac{r_1}{\xi}$, from Lemma 2.5 and Fig. 2.4, we can see that there exist multiple positive steady states in system (1.2), and the boundary equilibria are all unstable, i.e., the invading hosts can always coexist with the generalist parasitoids if the carrying capacity for the generalist parasitoids is smaller than the critical value $\frac{r_1}{\xi}$.

Next we consider the case $(II)(a)$ in Lemma 2.5 and look for some parameter values (conditions) such that $E_1(x_1, y_1)$ is a nonhyperbolic equilibrium satisfying $\mathrm{Det}(J(E_1)) > 0$ and $\mathrm{Tr}(J(E_1)) = 0$, and the degenerate equilibrium $E_*(x_*, y_*)$ satisfying $\mathrm{Tr}(J(E_*)) = 0$. From $f(x_*) = f'(x_*) = 0$ and $\mathrm{Tr}(J(E_*)) = 0$, we can express b, c and δ by x_* and a as follows:

$$b = \frac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)}, \quad c = \frac{x_*(1-a-2x_*)^2}{a(1-x_*)}, \quad \delta = \frac{x_*(1-a-2x_*)(a-x_*+2x_*^2)}{a(a+x_*)(1-x_*)}. \tag{2.8}$$

Moreover, since $x_1 + 2x_* = 1 - 2a$, from $\mathrm{Tr}(J(E_1)) = 0$ and (2.8), we can get

$$a = a_1 \triangleq \frac{10x_*^2-9x_*+1+(1-x_*)\sqrt{-28x_*^2+20x_*+1}}{6-8x_*}, \tag{2.9}$$

where $0 < x_* < \frac{1}{2}$ and $x_* \neq \frac{1}{8}$. In fact, from $\mathrm{Tr}(J(E_1)) = 0$ and (2.8), we also can get $a = \frac{1-3x_*}{2}$ or $a = \frac{10x_*^2-9x_*+1-(1-x_*)\sqrt{-28x_*^2+20x_*+1}}{6-8x_*}$, while from $a = \frac{1-3x_*}{2}$ and $x_1 + 2x_* =$

$1-2a$, we have $x_1 = x_*$, i.e., x_1 is a triple root of $f(x) = 0$, which contradicts with the case $(II)(a)$. From $0 < x_* < \frac{1}{2}$, we have $10x_*^2 - 9x_* + 1 < (1-x_*)\sqrt{-28x_*^2 + 20x_* + 1}$, then $\frac{10x_*^2-9x_*+1-(1-x_*)\sqrt{-28x_*^2+20x_*+1}}{6-8x_*} < 0$. Thus, $a \neq \frac{1-3x_*}{2}$ and $a \neq \frac{10x_*^2-9x_*+1-(1-x_*)\sqrt{-28x_*^2+20x_*+1}}{6-8x_*}$ for case $(II)(a)$.

When b, c and δ satisfy equation (2.8), system (1.2) can be reduced as follows

$$\begin{aligned} \dot{x} &= x\left(1 - x - \tfrac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)(a+x)} y\right), \\ \dot{y} &= y\left(\tfrac{x_*(1-a-2x_*)(a-x_*+2x_*^2)}{a(a+x_*)(1-x_*)} - y + \tfrac{x_*(1-a-2x_*)^2}{a(1-x_*)(a+x)} x\right), \end{aligned} \tag{2.10}$$

it is easy to calculate that system (2.10) has two positive equilibria

$$E_1(x_1, y_1) = \left(1 - 2a - 2x_*, \frac{2x_*(1-a-2x_*)^2}{(a+x_*)(1-x_*)}\right), \quad E_*(x_*, y_*) = \left(x_*, \frac{x_*(1-a-2x_*)}{a+x_*}\right).$$

Next, we define

$$a_2 = \tfrac{1-3x_*-(1-x_*)\sqrt{1-8x_*}}{2}, \quad a_3 = \tfrac{1-3x_*+(1-x_*)\sqrt{1-8x_*}}{2}, \tag{2.11}$$

and have the following results.

Theorem 2.7. *If $\delta < \frac{a}{b}$, $x_*(1-2x_*) < a < \frac{1-2x_*}{2}$, $0 < x_* < \frac{1}{2}$ $(x_* \neq \frac{1}{8})$, and the conditions in (2.8) are satisfied, then system (1.2) has two positive equilibria $E_*(x_*, y_*)$ and $E_1(x_1, y_1)$ (or $E_3(x_3, y_3)$). Moreover,*

(I) *if $a = a_1$, then*
  (i) *E_1 (or E_3) is a weak focus with multiplicity at most two;*
  (ii) *E_* is a cusp of codimension two;*

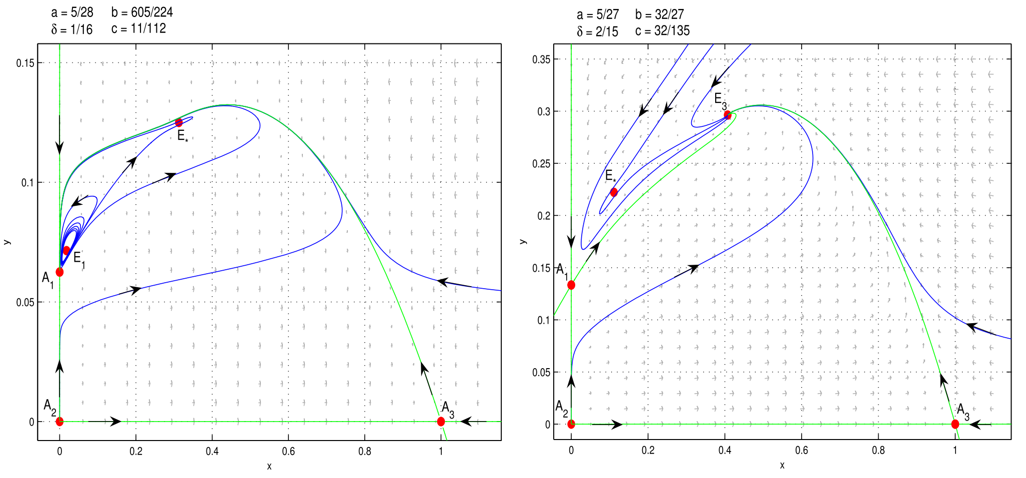
(II) *if $a = a_3$ and $\frac{8-\sqrt[3]{100+12\sqrt{69}}-\sqrt[3]{100-12\sqrt{69}}}{12} < x_* < \frac{1}{8}$ (or $a = a_2$ and $0 < x_* < \frac{1}{8}$), then*
  (i) *E_1 (or E_3) is a stable hyperbolic focus (or node);*
  (ii) *E_* is a cusp of codimension three.*

The phase portraits are given in Fig. 2.5.

Proof. (I)(i) We first verify that E_1 is an unstable weak focus with multiplicity at most two. Translate E_1 to the origin by letting $u = x - (1 - 2a - 2x_*)$, $v = y - \frac{2x_*(1-a-2x_*)^2}{(a+x_*)(1-x_*)}$ and $t = (a + u + x_1)\tau$, the Taylor expansion of system (2.10) around the origin takes the form (still denote τ by t)

$$\begin{aligned} \dot{u} &= \bar{a_{10}}u + \bar{a_{01}}v + \bar{a_{20}}u^2 + \bar{a_{11}}uv + \bar{a_{30}}u^3 + \bar{a_{21}}u^2v + o(|u, v|^3), \\ \dot{v} &= \bar{b_{10}}u + \bar{b_{01}}v + \bar{b_{20}}u^2 + \bar{b_{11}}uv + \bar{b_{02}}v^2 + \bar{b_{30}}u^3 + \bar{b_{21}}u^2v + o(|u, v|^3), \end{aligned} \tag{2.12}$$

where



(a) (b)

Fig. 2.5. Two positive equilibria when $\delta < \frac{a}{b}$. (a) An unstable weak focus E_1 with multiplicity one and a cusp E_* of codimension two. (b) A hyperbolic stable focus E_3 and a cusp E_* of codimension three.

$$
\begin{aligned}
&\bar{a}_{10} = -(1-2a-2x_*)(1-3a-4x_*),\ \ \bar{a}_{01} = -\frac{(1-x_*)(1-2a-2x_*)(a+x_*)^2}{x_*(1-a-2x_*)},\\
&\bar{a}_{20} = -(2-5a-6x_*),\ \ \bar{a}_{11} = -\frac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)},\ \ \bar{a}_{02} = 0,\ \ \bar{a}_{30} = -1,\\
&\bar{a}_{21} = 0,\ \ \bar{a}_{12} = 0,\ \ \bar{a}_{03} = 0,\ \ \bar{b}_{10} = \frac{2x_*^2(1-a-2x_*)^3}{(1-x_*)^2(a+x_*)},\ \ \bar{b}_{01} = \frac{2x_*(1-a-2x_*)^3}{(1-x_*)(a+x_*)},\\
&\bar{b}_{20} = 0,\ \ \bar{b}_{11} = -\frac{x_*(10x_*^2+(11a-9)x_*+3a^2-5a+2)}{(1-x_*)(a+x_*)},\ \ \bar{b}_{02} = -(1-a-2x_*),\\
&\bar{b}_{30} = 0,\ \ \bar{b}_{21} = 0,\ \ \bar{b}_{12} = -1,\ \ \bar{b}_{03} = 0.
\end{aligned}
$$

Make a change of variables as follows

$$
\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -\frac{\bar{a}_{01}\sqrt{\bar{D}}}{\bar{a}_{10}^{\,2}+\bar{D}} & -\frac{\bar{a}_{10}\bar{a}_{01}}{\bar{a}_{10}^{\,2}+\bar{D}} \\ 0 & 1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix},
$$

where $\bar{D} = \bar{a}_{10}\bar{b}_{01} - \bar{a}_{01}\bar{b}_{10}$, then system (2.12) can be written as

$$
\begin{aligned}
\dot{x} &= -\sqrt{\bar{D}}y + f(x, y),\\
\dot{y} &= \sqrt{\bar{D}}x + g(x, y),
\end{aligned} \tag{2.13}
$$

where

$$
\begin{aligned}
f(x, y) &= \bar{c}_{20}x^2 + \bar{c}_{11}xy + \bar{c}_{02}y^2 + \bar{c}_{30}x^3 + \bar{c}_{21}x^2y + \bar{c}_{12}xy^2 + \bar{c}_{03}y^3 + o(|x, y|^3),\\
g(x, y) &= \bar{d}_{20}x^2 + \bar{d}_{11}xy + \bar{d}_{02}y^2 + \bar{d}_{30}x^3 + \bar{d}_{21}x^2y + \bar{d}_{12}xy^2 + \bar{d}_{03}y^3 + o(|x, y|^3),
\end{aligned}
$$

$\bar{c_{ij}}$ and $\bar{d_{ij}}$ can be expressed by $\bar{a_{ij}}$ and $\bar{b_{ij}}$, we omit their expressions here for the sake of brevity, and the first-order Liapunov number (Perko [19]) can be expressed as

$$\begin{aligned}\sigma_1 &= \frac{1}{16}(f_{xxx} + f_{xyy} + g_{xxy} + g_{yyy} \\ &\quad + \frac{f_{xy}(f_{xx} + f_{yy}) - g_{xy}(g_{xx} + g_{yy}) - f_{xx}g_{xx} + f_{yy}g_{yy}}{\sqrt{\bar{D}}})|_{x=y=0} \\ &= \frac{1}{16}(6\bar{c_{30}} + 2\bar{c_{12}} + 2\bar{d_{21}} + 6\bar{d_{03}} + \frac{2\bar{c_{11}}(\bar{c_{20}} + \bar{c_{02}}) - 2\bar{d_{11}}(\bar{d_{20}} + \bar{d_{02}}) - 4\bar{c_{20}}\bar{d_{20}} + 4\bar{c_{02}}\bar{d_{02}}}{\sqrt{\bar{D}}}) \\ &= -\frac{2(1-x_*)^2 R_1}{x_*^3(5 - 6x_* - w)^4 R_2},\end{aligned}$$

where

$$\begin{aligned}R_1 &= 5120x_*^{10} + 128r_1x_*^9 - 320r_2x_*^8 + 32r_3x_*^7 - 80r_4x_*^6 + 8r_5x_*^5 - 64r_6x_*^4 + 480r_7x_*^3 \\ &\quad -24r_8x_*^2 - 10r_9x_* + w + 1, \\ R_2 &= 352x_*^5 - 4(227 - 4w)x_*^4 + (788 + 6w)x_*^3 - (243 + 41w)x_*^2 + (12 + 22w)x_* - 1 - w,\end{aligned}$$

and

$$\begin{aligned}&w = \sqrt{-28x_*^2 + 20x_* + 1}, \\ &r_1 = 195 - 68w,\ \ r_2 = 490 - 121w,\ \ r_3 = 9200 - 2127w,\ \ r_4 = 3354 - 743w, \\ &r_5 = 15997 - 3277w,\ \ r_6 = 470 - 81w,\ \ r_7 = 6 - w,\ \ r_8 = 95 - 6w,\ \ r_9 = 1 + 2w.\end{aligned}$$

Since σ_1 is an irrational function with respect to only one variable x_* in the interval $0 < x_* < \frac{1}{2}$ ($x_* \neq \frac{1}{8}$), we will see, in the section 3.3, that E_1 is a weak focus with multiplicity at most two.

(I)(ii) Next we show that the degenerate equilibrium E_* is a cusp of codimension two if $a = a_1$. Translate E_* to the origin by letting $u = x - x_*$, $v = y - \frac{x_*(1-a-2x_*)}{a+x_*}$, and the Taylor expansion of system (1.2) around the origin takes the form

$$\begin{aligned}\dot{u} &= \tfrac{x_*(1-a-2x_*)}{a+x_*}u - \tfrac{(1-x_*)(a+x_*)}{1-a-2x_*}v - \tfrac{a(a-1)+3ax_*+x_*^2}{(a+x_*)^2}u^2 - \tfrac{a(1-x_*)}{x_*(1-a-2x_*)}uv + o(|u,v|^2), \\ \dot{v} &= \tfrac{x_*^2(1-a-2x_*)^3}{(1-x_*)(a+x_*)^3}u - \tfrac{x_*(1-a-2x_*)}{(a+x_*)}v - \tfrac{x_*^2(1-a-2x_*)^3}{(1-x_*)(a+x_*)^4}u^2 + \tfrac{x_*(1-a-2x_*)^2}{(1-x_*)(a+x_*)^2}uv - v^2 + o(|u,v|^2).\end{aligned} \tag{2.14}$$

Next we transform the linear part of system (2.14) to the Jordan canonical form. To do so, let

$$u = X + \frac{(a + x_*)}{x_*(1 - a - 2x_*)}Y, \quad v = \frac{x_*(1 - a - 2x_*)^2}{(1 - x_*)(a + x_*)^2}X,$$

then system (2.14) can be rewritten as

$$\begin{aligned}\dot{X} &= Y - \tfrac{x_*(1-a-2x_*)}{(a+x_*)^2}X^2 - \tfrac{(1+a)}{(1-x_*)(a+x_*)}XY - \tfrac{1}{x_*(1-a-2x_*)}Y^2 + o(|X,Y|^2),\\ \dot{Y} &= \tfrac{x_*^2(1-a-2x_*)(1-2a-3x_*)}{(a+x_*)^3}X^2 + \tfrac{2x_*^2-4x_*-a+1}{(1-x_*)(a+x_*)}XY + \tfrac{(1-a-3x_*)}{x_*(1-a-2x_*)}Y^2 + o(|X,Y|^2).\end{aligned} \tag{2.15}$$

By Remark 1 of section 2.13 in Perko [19] (see also Lemma 3.1 in Huang et al. [12]), we obtain an equivalent system of (2.15) in the small neighborhood of (0,0) as follows:

$$\begin{aligned}\dot{x} &= y + o(|x,y|^2),\\ \dot{y} &= Dx^2 + Exy + o(|x,y|^2),\end{aligned} \tag{2.16}$$

where

$$D = \frac{x_*^2(1-a-2x_*)(1-2a-3x_*)}{(a+x_*)^3}, \quad E = -\frac{2x_*^3 - 2x_*^2 + (1+3a)x_* + a(a-1)}{(a+x_*)^2(1-x_*)}.$$

Since $0 < x_* < \frac{1}{2}$, $x_*(1-2x_*) < a < \frac{1-2x_*}{2}$ and $a \neq \frac{1-3x_*}{2}$, then $1-a-2x_* > 0$, and $1-2a-3x_* \neq 0$, it follows that $D \neq 0$. On the other hand, substituting $a = a_1$ into E, we have

$$E = \frac{4(32x_*^2 - 26x_* + 1 + \sqrt{1+20x_* - 28x_*^2})}{(1 - 2x_* + \sqrt{1+20x_* - 28x_*^2})^2},$$

it is not difficult to show that $E \neq 0$ if $0 < x_* < \frac{1}{2}$ and $x_* \neq \frac{1}{8}$. Hence the positive equilibrium E_* is a cusp of codimension two by the result in Perko [19].

(II)(i) By case **(I)**, we know that if $a(a-1) + (1+3a)x_* - 2x_*^2 + 2x_*^3 = 0$, i.e., $a = a_2$ or $a = a_3$, then $E = 0$, hence the degenerate positive equilibrium E_* is a cusp of codimension at least three. Substituting $a = a_2$ or $a = a_3$ into $\mathrm{Tr}(J(E_1))$, we have

$$\mathrm{Tr}(J(E_1)) = -\frac{4(1-x_*)(1-8x_*)}{1 \pm \sqrt{1-8x_*}} < 0,$$

since $0 < x_* < \frac{1}{8}$, the positive equilibrium E_1 is a stable hyperbolic focus or node.

(II)(ii) Next we discuss the exact codimension of cusp E_* when $a = a_2$ or $a = a_3$. We first transform E_* into the origin by letting $u = x - x_*,\ v = y - \frac{x_*(1-a-2x_*)}{a+x_*}$, then the Taylor expansion of system (2.10) around the origin takes the form

$$\begin{aligned}\dot{u} &= \tfrac{x_*(1-a-2x_*)}{a+x_*}u - \tfrac{(1-x_*)(a+x_*)}{1-a-2x_*}v - \tfrac{(a-1)a+3ax_*+x_*^2}{(a+x_*)^2}u^2 - \tfrac{a(1-x_*)}{x_*(1-a-2x_*)}uv - \tfrac{a(1-x_*)}{(a+x_*)^3}u^3\\ &\quad + \tfrac{a(1-x_*)}{x_*(a+x_*)(1-a-2x_*)}u^2v + \tfrac{a(1-x_*)}{(a+x_*)^4}u^4 + \tfrac{a(1-x_*)}{x_*(a+x_*)^2(-1+a+2x_*)}u^3v + o(|u,v|^4),\\ \dot{v} &= \tfrac{x_*^2(1-a-2x_*)^3}{(1-x_*)(a+x_*)^3}u - \tfrac{x_*(1-a-2x_*)}{a+x_*}v - \tfrac{x_*^2(1-a-2x_*)^3}{(1-x_*)(a+x_*)^4}u^2 + \tfrac{x_*(1-a-2x_*)^2}{(1-x_*)(a+x_*)^2}uv - v^2\\ &\quad + \tfrac{x_*^2(1-a-2x_*)}{(1-x_*)(a+x_*)^5}u^3 - \tfrac{x_*(1-a-2x_*)^2}{(1-x_*)(a+x_*)^3}u^2v - \tfrac{x_*^2(1-a-2x_*)^3}{(1-x_*)(a+x_*)^6}u^4 + \tfrac{x_*(1-a-2x_*)^2}{(1-x_*)(a+x_*)^4}u^3v + o(|u,v|^4).\end{aligned} \tag{2.17}$$

Note that the coefficient of the term v in the first equation of (2.17) is nonzero, we can make transformations $X = u$ and $Y = du/dt$ such that (2.17) is changed to the following system

$$\begin{aligned}\dot{X} &= Y,\\ \dot{Y} &= \alpha_1 X^2 + \alpha_2 Y^2 + \alpha_3 X^3 + \alpha_4 X^2 Y + \alpha_5 X Y^2 + \alpha_6 X^4 + \alpha_7 X^3 Y + \alpha_8 X^2 Y^2 + o(|X, Y|^4),\end{aligned} \tag{2.18}$$

where

$$\begin{aligned}
\alpha_1 &= \frac{x_*^2(1-2a-3x_*)(1-a-2x_*)}{(a+x_*)^3}, \quad \alpha_2 = \frac{1-2x_*}{x_*(1-x_*)},\\
\alpha_3 &= \frac{x_*(1-a-2x_*)(4x_*^3+(9a-2)x_*^2+2a(2a-3)x_*+a-2a^2)}{(1-x_*)(a+x_*)^4},\\
\alpha_4 &= -\frac{1+a+2(a-3)x_*+8x_*^2}{(1-x_*)(a+x_*)^2}, \quad \alpha_5 = \frac{a(4x_*^2+(2a-3)x_*-a)}{x_*^2(1-x_*)(a+x_*)^2},\\
\alpha_6 &= \frac{x_*(1-a-2x_*)(x_*^3+3ax_*^2+a(2+5a)x_*+a(2a^2-1))}{(1-x_*)(a+x_*)^5},\\
\alpha_7 &= \frac{1+a-4x_*+4x_*^2}{(1+x_*)(a+x_*)^3}, \quad \alpha_8 = -\frac{a(5{x_*}^3+(6a-4)x_*^2+2(a^2-2)x_*-a^2)}{{x_*}^3(1-x_*)(a+x_*)^3}.
\end{aligned}$$

Introducing a new time variable τ by $dt = (1-\alpha_2 X)d\tau$ and rewriting τ as t, we obtain

$$\begin{aligned}\dot{X} &= Y(1-\alpha_2 X),\\ \dot{Y} &= (1-\alpha_2 X)(\alpha_1 X^2 + \alpha_2 Y^2 + \alpha_3 X^3 + \alpha_4 X^2 Y + \alpha_5 X Y^2 + \alpha_6 X^4 + \alpha_7 X^3 Y\\ &\quad + \alpha_8 X^2 Y^2 + o(|X, Y|^4)).\end{aligned} \tag{2.19}$$

The transformation $x = X,\ y = Y(1-\alpha_2 X)$ brings (2.19) into

$$\begin{aligned}\dot{x} &= y,\\ \dot{y} &= \alpha_1 x^2 + (\alpha_3 - 2\alpha_1\alpha_2)x^3 + (\alpha_1{\alpha_2}^2 - 2\alpha_2\alpha_3 + \alpha_6)x^4 + \alpha_4 x^2 y + (\alpha_7 - \alpha_2\alpha_4)x^3 y\\ &\quad + (\alpha_5 - {\alpha_2}^2)xy^2 + (\alpha_8 - {\alpha_2}^3)x^2y^2 + o(|x, y|^4).\end{aligned} \tag{2.20}$$

Next we let $\omega = \sqrt{1-8x_*}$, i.e., $x_* = \frac{1-\omega^2}{8}$, then we have $a_2 = \frac{1-3x_*-(1-x_*)\sqrt{1-8x_*}}{2} = \frac{(1-\omega)(\omega^2-2\omega+5)}{16}$, $a_3 = \frac{1-3x_*+(1-x_*)\sqrt{1-8x_*}}{2} = \frac{(1+\omega)(\omega^2+2\omega+5)}{16}$. Moreover, when $a = a_2$, we have $0 < \omega < 1$ since $0 < x_* < \frac{1}{8}$; when $a = a_3$, we have $0 < \omega < \sqrt{\frac{2\sqrt[3]{100+12\sqrt{69}}+2\sqrt[3]{100-12\sqrt{69}}-13}{3}} \approx 0.139681$ since $\frac{8-(100+12\sqrt{69})^{\frac{1}{3}}-(100-12\sqrt{69})^{\frac{1}{3}}}{12} < x_* < \frac{1}{8}$, which comes from $x_*(1-2x_*) < a < \frac{1-2x_*}{2}$.

If $a = a_2 = \frac{(1-\omega)(5-2\omega+\omega^2)}{16}$ and $0 < x_* < \frac{1}{8}$, then $\alpha_1 = \frac{\omega(1+\omega)^3}{2(1-\omega)(7+\omega^2)} > 0$ since $0 < \omega < 1$. So we make the following changes of variables and time $X = x,\ Y = \frac{y}{\sqrt{\alpha_1}}$ and $\tau = \sqrt{\alpha_1}t$, system (2.20) becomes (still use t to denote τ)

$$\begin{aligned}\dot{X} &= Y,\\ \dot{Y} &= X^2 + \frac{(\alpha_3-2\alpha_1\alpha_2)}{\alpha_1}X^3 + \frac{(\alpha_1{\alpha_2}^2-2\alpha_2\alpha_3+\alpha_6)}{\alpha_1}X^4 + \frac{\alpha_4}{\sqrt{\alpha_1}}X^2Y + \frac{(\alpha_7-\alpha_2\alpha_4)}{\sqrt{\alpha_1}}X^3Y\\ &\quad + (\alpha_5 - {\alpha_2}^2)XY^2 + (\alpha_8 - {\alpha_2}^3)X^2Y^2 + o(|X, Y|^4).\end{aligned} \tag{2.21}$$

By Proposition 5.3 in Lamontage et al. [16] (see also Lemma 3.2 in Huang et al. [12]), we know that system (2.21) is equivalent to

$$\begin{aligned}\dot{X} &= Y,\\ \dot{Y} &= X^2 + MX^3Y + o(|X, Y|^4)),\end{aligned} \tag{2.22}$$

where

$$M = -\frac{256\sqrt{2}}{\sqrt{(1-\omega)\omega^3(1+\omega)^3(7+\omega^2)^3}} < 0$$

for $0 < \omega < 1$, then the equilibrium E_* is a cusp of codimension three (Dumortier et al. [5]).

If $a = a_3 = \frac{(1+\omega)(5+2\omega+\omega^2)}{16}$ and $0.122561 \approx \frac{8-\sqrt[3]{100+12\sqrt{69}}-\sqrt[3]{100-12\sqrt{69}}}{12} < x_* < \frac{1}{8}$, then $\alpha_1 = -\frac{\omega(1-\omega)^3}{2(1+\omega)(7+\omega^2)} < 0$ since $0 < \omega < \sqrt{\frac{2\sqrt[3]{100+12\sqrt{69}}+2\sqrt[3]{100-12\sqrt{69}}-13}{3}} \approx 0.139681$. We make the following changes of variables and time $X = -x$, $Y = -\frac{y}{\sqrt{-\alpha_1}}$ and $\tau = \sqrt{-\alpha_1}t$, system (2.20) can be rewritten as (still use t to denote τ)

$$\begin{aligned}\dot{X} &= Y,\\ \dot{Y} &= X^2 - \frac{(\alpha_3-2\alpha_1\alpha_2)}{\alpha_1}X^3 + \frac{(\alpha_1\alpha_2^2-2\alpha_2\alpha_3+\alpha_6)}{\alpha_1}X^4 + \frac{\alpha_4}{\sqrt{-\alpha_1}}X^2Y - \frac{(\alpha_7-\alpha_2\alpha_4)}{\sqrt{-\alpha_1}}X^3Y\\ &\quad +(\alpha_5-\alpha_2^2)XY^2 - (\alpha_8-\alpha_2^3)X^2Y^2 + o(|X, Y|^4).\end{aligned} \tag{2.23}$$

Similar as above, we have

$$M = -\frac{256\sqrt{2}}{\sqrt{(1+\omega)\omega^3(1-\omega)^3(7+\omega^2)^3}} < 0$$

for $0 < \omega < \sqrt{\frac{2\sqrt[3]{100+12\sqrt{69}}+2\sqrt[3]{100-12\sqrt{69}}-13}{3}} \approx 0.139681$, then the equilibrium E_* is a cusp of codimension three ([5]). $\square$

Next we consider the case **(II)(b)** of Lemma 2.5, where system (1.2) has a unique degenerate positive equilibrium $E^*(\frac{1-2a}{3}, \frac{2(1+a)^2}{9b})$. From $f(\frac{1-2a}{3}) = f'(\frac{1-2a}{3}) = 0$, we can express c and δ by a and b as follows

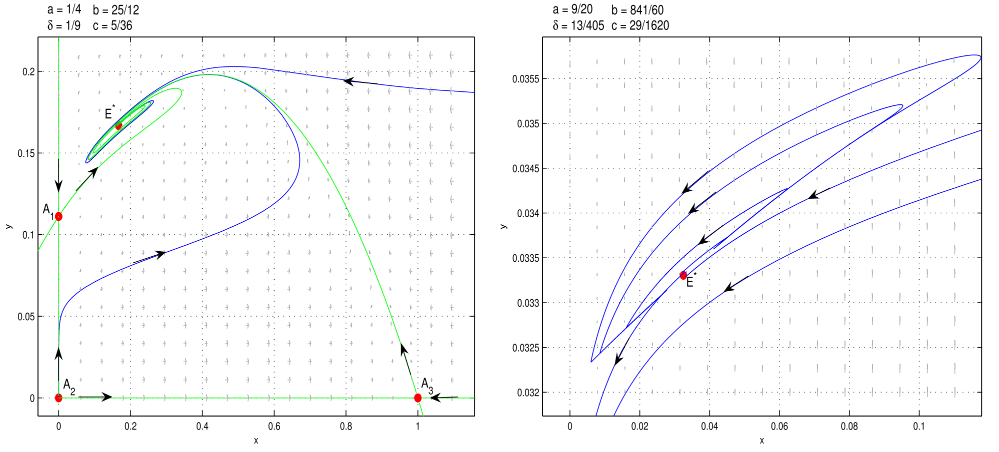
$$c = \frac{(1+a)^3}{27ab}, \quad \delta = \frac{(1+a)^2(8a-1)}{27ab}. \tag{2.24}$$

Moreover, from $\mathrm{Tr}(J(E^*)) = 0$ and (2.24), we have

$$b = \frac{2(1+a)^2}{3(1-2a)} \tag{2.25}$$

and get the following results.

Theorem 2.8. *If $\delta < \frac{a}{b}$, $\frac{1}{8} < a < \frac{1}{2}$, and the conditions in (2.24) are satisfied, then system (1.2) has a unique degenerate positive equilibrium $E^*(\frac{1-2a}{3}, \frac{2(1+a)^2}{9b})$. Moreover,*



(a) (b)

Fig. 2.6. A unique positive equilibrium when $\delta < \frac{a}{b}$. (a) A degenerate nilpotent focus E^* of codimension three. (b) A degenerate nilpotent elliptic equilibrium E^* of codimension three.

(I) *if* $b \neq \frac{2(1+a)^2}{3(1-2a)}$, *then* $E^*(\frac{1-2a}{3}, \frac{2(1+a)^2}{9b})$ *is a stable (or an unstable) degenerate node if* $0 < b < \frac{2(1+a)^2}{3(1-2a)}$ *(or if* $b > \frac{2(1+a)^2}{3(1-2a)}$*, respectively);*

(II) *if* $b = \frac{2(1+a)^2}{3(1-2a)}$, *then* $E^*(\frac{1-2a}{3}, \frac{1-2a}{3})$ *is a degenerate nilpotent focus of codimension three if* $\frac{1}{8} < a < \frac{5}{16}$ *or* $\frac{5}{16} < a < \frac{2+3\sqrt{2}}{16}$*; a degenerate nilpotent elliptic equilibrium of codimension three if* $\frac{2+3\sqrt{2}}{16} \leq a < \frac{1}{2}$*; and a nilpotent symmetric cusp of codimension two if* $a = \frac{5}{16}$.

The phase portraits are given in Fig. 2.6.

Proof. When $c = \frac{(1+a)^3}{27ab}$ and $\delta = \frac{(1+a)^2(8a-1)}{27ab}$, we have $\Delta = 0$ and $A = 0$. Moreover,

$$\mathrm{Det}(J(E^*)) = 0, \ \ \mathrm{Tr}(J(E^*)) = \frac{3(1-2a)b - 2(1+a)^2}{9b}.$$

(I) When $b \neq \frac{2(1+a)^2}{3(1-2a)}$, we have $\mathrm{Tr}(J(E^*)) \neq 0$, i.e., there is only one zero eigenvalue for the Jacobian matrix $J(E^*)$. Substituting (2.24) into system (1.2), we have

$$\begin{aligned} \dot{x} &= x(1 - x - \tfrac{by}{a+x}), \\ \dot{y} &= y(\tfrac{(1+a)^2(8a-1)}{27ab} - y + \tfrac{(1+a)^3}{27ab(a+x)}x). \end{aligned} \tag{2.26}$$

Firstly, we transform the linear part of (2.26) to the Jordan canonical form. To do so, let

$$u = x - \frac{1-2a}{3}, \ \ v = y - \frac{2(1+a)^2}{9b},$$

then system (2.26) becomes

$$\begin{aligned}\dot{u} &= \tfrac{1-2a}{3}u - \tfrac{(1-2a)b}{1+a}v - \tfrac{1-5a}{1+a}u^2 - \tfrac{9ab}{(1+a)^2}uv - \tfrac{18a}{(1+a)^2}u^3 + \tfrac{27ab}{(1+a)^3}u^2v + \tfrac{54a}{(1+a)^3}u^4 \\ &\quad - \tfrac{81ab}{(1+a)^4}u^3v + o(|u,v|^4), \\ \dot{v} &= \tfrac{2(1+a)^3}{27b^2}u - \tfrac{2(1+a)^2}{9b}v - \tfrac{2(1+a)^2}{9b^2}u^2 + \tfrac{1+a}{3b}uv - v^2 + \tfrac{2(1+a)}{3b^2}u^3 - \tfrac{1}{b}u^2v - \tfrac{2}{b^2}u^4 \\ &\quad + \tfrac{3}{(1+a)b}u^3v + o(|u,v|^4).\end{aligned} \tag{2.27}$$

Secondly, to eliminate the v^2 terms in system (2.27), we let

$$u = \frac{3b}{1+a}x + \frac{9(1-2a)b^2}{2(1+a)^3}y,\ \ v = x + y,\ \ \tau = -\frac{2(1+a)^2 - 3(1-2a)b}{9b}t,$$

and still denote τ by t, then system (2.27) can be rewritten as

$$\begin{aligned}\dot{x} &= \tilde{a_{20}}x^2 + \tilde{a_{11}}xy + \tilde{a_{02}}y^2 + \tilde{a_{30}}x^3 + \tilde{a_{21}}x^2y + \tilde{a_{12}}xy^2 + \tilde{a_{03}}y^3 + \tilde{a_{40}}x^4 \\ &\quad + \tilde{a_{31}}x^3y + \tilde{a_{22}}x^2y^2 + \tilde{a_{13}}xy^3 + \tilde{a_{04}}y^4 + o(|x,y|^4), \\ \dot{y} &= y + \tilde{b_{20}}x^2 + \tilde{b_{11}}xy + \tilde{b_{02}}y^2 + \tilde{b_{30}}x^3 + \tilde{b_{21}}x^2y + \tilde{b_{12}}xy^2 + \tilde{b_{03}}y^3 + \tilde{b_{40}}x^4 \\ &\quad + \tilde{b_{31}}x^3y + \tilde{b_{22}}x^2y^2 + \tilde{b_{13}}xy^3 + \tilde{b_{04}}y^4 + o(|x,y|^4),\end{aligned} \tag{2.28}$$

where the coefficients are given in Appendix A.

By center manifold method, we suppose $y = mx^2 + nx^3 + o(|x|^4)$, substitute it to the second equation of system (2.28), and obtain that $m = -\frac{18b}{2(1+a)^2-3(1-2a)b}$, $n = \frac{324b^2((1+a)^2+3(1-2a)b)}{(1+a)^2(2+2a^2-3b+a(4+6b))^2}$. Then the reduced equation restricted to the center manifold is as follows

$$\dot{x} = \frac{486(1-2a)b^3}{(1+a)^2(2(1+a)^2 - 3(1-2a)b)^2}x^3 + o(|x|^4).$$

By Theorem 7.1 of Chapter 2 in Zhang et al. [27], E^* is a degenerate stable node if $0 < b < \frac{2(1+a)^2}{3(1-2a)}$ and a degenerate unstable node if $b > \frac{2(1+a)^2}{3(1-2a)}$.

(II) When $b = \frac{2(1+a)^2}{3(1-2a)}$, we have $\mathrm{Tr}(J(E^*)) = 0$. It follows that $E^*(\frac{1-2a}{3}, \frac{1-2a}{3})$ is a nilpotent singularity with double-zero eigenvalue. To determine the exact type of E^*, we provide a series of explicitly smooth transformations to derive a normal form with terms up to the fourth order.

Firstly, we translate the unique positive equilibrium $E^*(\frac{1-2a}{3}, \frac{1-2a}{3})$ to the origin and expand system (1.2) in power series up to the fourth order around the origin. Let

$$(I): u = x - \frac{1-2a}{3},\ \ v = y - \frac{1-2a}{3},$$

then system (1.2) becomes

$$\begin{aligned}\dot{u}&=\tfrac{1-2a}{3}u-\tfrac{2(1+a)}{3}v-\tfrac{1-5a}{1+a}u^2-\tfrac{6a}{(1-2a)^2}uv-\tfrac{18a}{(1+a)^2}u^3+\tfrac{18a}{1-a-2a^2}u^2v+\tfrac{54a}{(1+a)^3}u^4\\&\quad-\tfrac{54a}{(1+a)^2(1-2a)}u^3v+o(|u,v|^4),\\\dot{v}&=\tfrac{(1-2a)^2}{6(1+a)}u-\tfrac{1-2a}{3}v-\tfrac{(1-2a)^2}{2(1+a)^2}u^2+\tfrac{1-2a}{2(1+a)}uv-v^2+\tfrac{3(1-2a)^2}{2(1+a)^3}u^3-\tfrac{3(1-2a)}{2(1+a)^2}u^2v\\&\quad-\tfrac{9(1-2a)^2}{2(1+a)^4}u^4+\tfrac{9(1-2a)}{2(1+a)^3}u^3v+o(|u,v|^4).\end{aligned}\tag{2.29}$$

Secondly, we transform the linear part of system (2.29) to the Jordan canonical form. Let

$$(II): u=\frac{2(1+a)}{1-2a}X+\frac{6(1+a)}{(1-2a)^2}Y,\ \ v=X,$$

then system (2.29) can be rewritten as

$$\begin{aligned}\dot{X}&=Y-2X^2-\tfrac{9}{1-2a}XY-\tfrac{18}{(1-2a)^2}Y^2+\tfrac{6}{1-2a}X^3+\tfrac{72}{(1-2a)^2}X^2Y+\tfrac{270}{(1-2a)^3}XY^2+\tfrac{324}{(1-2a)^4}Y^3\\&\quad-\tfrac{36}{(1-2a)^2}X^4-\tfrac{540}{(1-2a)^3}X^3Y-\tfrac{2916}{(1-2a)^4}X^2Y^2-\tfrac{6804}{(1-2a)^5}XY^3-\tfrac{5832}{(1-2a)^6}Y^4+o(|X,Y|^4),\\\dot{Y}&=\tfrac{8a-1}{1-2a}XY+\tfrac{18a}{(1-2a)^2}Y^2-\tfrac{2+8a}{1-2a}X^3-\tfrac{24(1+4a)}{(1-2a)^2}X^2Y-\tfrac{90(1+4a)}{(1-2a)^3}XY^2-\tfrac{108(1+4a)}{(1-2a)^4}Y^3\\&\quad+\tfrac{12(1+4a)}{(1-2a)^2}X^4+\tfrac{180(1+4a)}{(1-2a)^3}X^3Y+\tfrac{972(1+4a)}{(1-2a)^4}X^2Y^2+\tfrac{2268(1+4a)}{(1-2a)^5}XY^3+\tfrac{1944(1+4a)}{(1-2a)^6}Y^4\\&\quad+o(|X,Y|^4).\end{aligned}\tag{2.30}$$

Thirdly, to eliminate the X^2 and Y^2 terms in system (2.30), we make a near-identity transformation

$$(III):\ X=x-\frac{9(1-4a)}{2(1-2a)^2}x^2,\ \ Y=y+2x^2+\frac{18a}{(1-2a)^2}xy+\frac{18}{(1-2a)^2}y^2,$$

then it brings system (2.30) into

$$\begin{aligned}\dot{x}&=y+\tilde{c_{30}}x^3+\tilde{c_{21}}x^2y+\tilde{c_{12}}xy^2+\tilde{c_{03}}y^3+\tilde{c_{40}}x^4+\tilde{c_{31}}x^3y+\tilde{c_{22}}x^2y^2\\&\quad+\tilde{c_{13}}xy^3+\tilde{c_{04}}y^4+o(|x,y|^4),\\\dot{y}&=\tilde{d_{11}}xy+\tilde{d_{30}}x^3+\tilde{d_{21}}x^2y+\tilde{d_{12}}xy^2+\tilde{d_{03}}y^3+\tilde{d_{40}}x^4+\tilde{d_{31}}x^3y+\tilde{d_{22}}x^2y^2\\&\quad+\tilde{d_{13}}xy^3+\tilde{d_{04}}y^4+o(|x,y|^4),\end{aligned}\tag{2.31}$$

where the coefficients are given in Appendix A.

Notice that

$$\tilde{d_{11}}\tilde{d_{30}}=\frac{4(5-16a)}{1-2a},$$

then $\tilde{d_{11}}\tilde{d_{30}}\neq 0$ if $a\neq\frac{5}{16}$, by Lemma 3.1 in Cai et al. [1], in a small neighborhood of $(0,0)$ system (2.31) is locally topologically equivalent to the following system

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= \tilde{d_{11}}xy + \tilde{d_{30}}x^3 + (\tilde{d_{21}} + 3\tilde{c_{30}})x^2y + (\tilde{d_{04}} - \tilde{d_{11}}\tilde{c_{11}})x^4 \\ &\quad + (4\tilde{c_{40}} + \tilde{d_{31}} + \tfrac{\tilde{d_{11}}\tilde{c_{21}}}{3} + \tfrac{\tilde{d_{11}}\tilde{d_{12}}}{6})x^3y + Q(x, y), \end{aligned} \tag{2.32}$$

where $Q(x, y)$ is a smooth function of order at least five in (x, y). Moreover, since $\frac{1}{8} < a < \frac{1}{2}$, we have

$$5\tilde{d_{30}}(\tilde{d_{21}} + 3\tilde{c_{30}}) - 3\tilde{d_{11}}(\tilde{d_{40}} - \tilde{d_{11}}\tilde{c_{30}}) = -\frac{24(40a^2 - 28a - 5)}{(1 - 2a)^3} \neq 0$$

and

$$\tilde{d_{30}} = -4 < 0, \quad \tilde{d_{11}}^2 + 8\tilde{d_{30}} = \frac{128a^2 - 32a - 7}{(1 - 2a)^2},$$

$\tilde{d_{11}}^2 + 8\tilde{d_{30}} = 0$ if $a = \frac{2+3\sqrt{2}}{16} \approx 0.390165$. By Lemma 3.1 in Cai et al. [1] we can obtain that $E^*(\frac{1-2a}{3}, \frac{1-2a}{3})$ is a degenerate focus of codimension three if $\frac{1}{8} < a < \frac{5}{16}$ or $\frac{5}{16} < a < \frac{2+3\sqrt{2}}{16}$; a degenerate elliptic of codimension three if $\frac{2+3\sqrt{2}}{16} \leq a < \frac{1}{2}$.

Finally, we prove that the unique positive equilibrium $E^*(\frac{1}{8}, \frac{1}{8})$ is a nilpotent symmetric cusp of codimension two if $(a, b, c, \delta) = (\frac{5}{16}, \frac{49}{16}, \frac{7}{80}, \frac{1}{10})$. Substituting $a = \frac{5}{16}$ to system (2.31), we get the following system

$$\begin{aligned} \dot{X} &= Y - 64X^3 - 1152X^2Y - 8192XY^2 - 16384Y^3 + o(|X, Y|^3), \\ \dot{Y} &= -4X^3 - 32X^2Y - 128XY^2 - 2048Y^3 + o(|X, Y|^3). \end{aligned} \tag{2.33}$$

Next we make another affine coordinate transformation

$$X = x - \frac{1216}{3}x^3 - 5120x^2y - 16384xy^2, \;\; Y = y + 64x^3 - 64x^2y - 2048xy^2,$$

then the third order terms in system (2.33) can be simplified and the equivalent system of system (2.33) is as follows

$$\begin{aligned} \dot{x} &= y + o(|X, Y|^3), \\ \dot{y} &= -4x^3 - 224x^2y + o(|X, Y|^3). \end{aligned} \tag{2.34}$$

According to the result on Page 259 of Chow et al. [2], $(\frac{1}{8}, \frac{1}{8})$ is a nilpotent symmetric cusp of codimension two. □

2.2. *The case $\delta \geq \frac{a}{b}$ (i.e., $K_2 \geq \frac{r_1}{\xi}$)*

In this case system (1.2) has three boundary equilibria: $(0, 0)$ is an unstable hyperbolic node, $(1, 0)$ is a hyperbolic saddle, $(0, \delta)$ is a stable hyperbolic node if $\delta > \frac{a}{b}$, and at most two positive equilibria.

According to the curve of $f(x)$ in Fig. 2.7 and the root formula for third-order algebraic equation, we have the following results for the existence and number of positive equilibria.

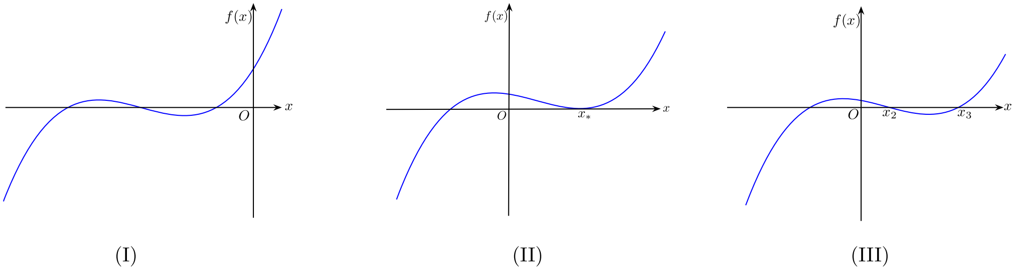


Fig. 2.7. The curve of $f(x)$ when $\delta \geq \frac{a}{b}$. (I) $f(x)=0$ has no positive root, (II) $f(x)=0$ has a positive double root x_*, (III) $f(x)=0$ has two different positive single roots x_2 and x_3.

Lemma 2.9. *When $\delta \geq \frac{a}{b}$ (i.e., $K_2 \geq \frac{r_1}{\xi}$), system (1.2) has at most two positive equilibria. Moreover,*

(I) *if $\Delta > 0$ or $\Delta = \widetilde{A} = 0$, then system (1.2) has no positive equilibrium;*
(II) *if $\Delta = 0$ and $\widetilde{A} > 0$, then system (1.2) has a unique positive equilibrium $E_*(x_*, y_*)$, which is a degenerate equilibrium;*
(III) *if $\Delta < 0$, then system (1.2) has two positive equilibria: $E_2(x_2, y_2)$ is a hyperbolic saddle, and $E_3(x_3, y_3)$ is a hyperbolic stable node or focus if $\mathrm{Tr}(J(E_3)) < 0$, a hyperbolic unstable node or focus if $\mathrm{Tr}(J(E_3)) > 0$, and a weak focus or center if $\mathrm{Tr}(J(E_3)) = 0$, where $0 < x_2 < x_3 < 1$.*

The phase portraits are given in Fig. 2.8.

Proof. From equation (2.6) and the derivative property of $f(x)$, it is easy to see that $\mathrm{Det}(J(E_2)) < 0$, $\mathrm{Det}(J(E_3)) > 0$, $\mathrm{Det}(J(E_*)) = 0$, then E_2 and E_3 are all elementary equilibria and only E_2 is a hyperbolic saddle, and E_* is a degenerate equilibrium. □

Remark 2.10. When $\delta \geq \frac{a}{b}$ (i.e., $K_2 \geq \frac{r_1}{\xi}$), system (1.2) can exhibit bistability phenomenon: $A_1(0, \delta)$ is a stable hyperbolic node and E_3 is a stable hyperbolic focus. From Lemma 2.9 and Fig. 2.8(a), we can see that the invading hosts will go extinct if the initial populations lie in the left of the two stable manifolds of the equilibrium E_2, and will persist if the initial populations lie in the right of the two stable manifolds of the equilibrium E_2.

We firstly consider case **(II)** of Lemma 2.9, where system (1.2) has a unique positive equilibrium $E_*(x_*, y_*)$, which is a degenerate equilibrium. From $f(x_*) = f'(x_*) = 0$, c and δ can be expressed by a, b and x_* as follows

$$c = \frac{(a+x_*)^2(1-a-2x_*)}{ab}, \quad \delta = \frac{(a+x_*)(a-x_*+2x_*^2)}{ab}. \tag{2.35}$$

Moreover, from $\mathrm{Tr}(J(E_*)) = 0$ and (2.35), b can be expressed by a and x_* as follows

$$b = \frac{(a+x_*)^2(1-x_*)}{x_*(1-a-2x_*)}. \tag{2.36}$$

We have the following results.

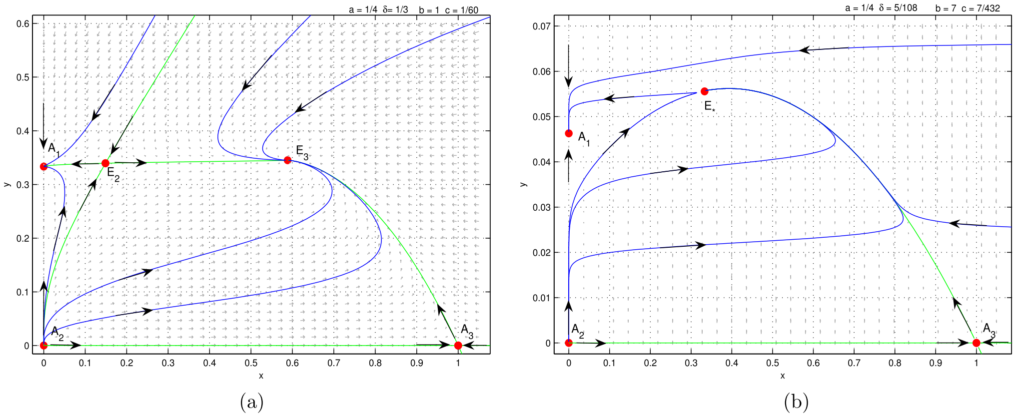


Fig. 2.8. (a) The coexistence of two positive equilibria and three boundary equilibria when $\delta \ge \frac{a}{b}$: A_1 is a stable hyperbolic node, A_2 is an unstable hyperbolic node, A_3 and E_2 are hyperbolic saddle, and E_3 is a stable hyperbolic focus. (b) A unique positive equilibrium E_* which is a saddle-node with a stable parabolic sector when $\delta \ge \frac{a}{b}$ and $0 < b < \frac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)}$.

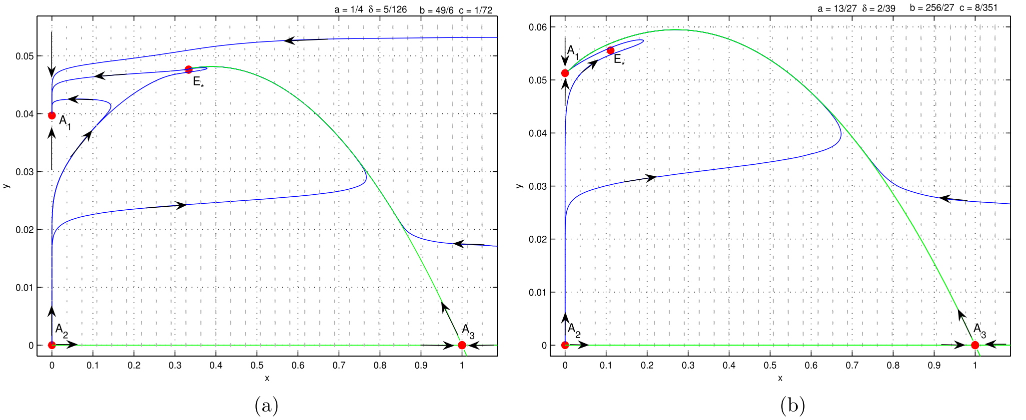


Fig. 2.9. A unique positive equilibrium E_* when $\delta \ge \frac{a}{b}$. (a) A cusp E_* of codimension two. (b) A cusp E_* of codimension three.

Theorem 2.11. *If $\delta \ge \frac{a}{b}$, $\frac{1-2x_*}{2} < a < 1 - 2x_*$, $0 < x_* < \frac{1}{2}$, and the conditions in (2.35) are satisfied, then system (1.2) has a unique positive equilibrium $E_*(x_*, y_*)$, which is a degenerate equilibrium. Moreover,*

(I) *when $b \neq \frac{(a+x_*)^2(1-x_*)}{x_*(1-a-2x_*)}$, then E_* is a saddle-node, which includes a stable parabolic sector (or an unstable parabolic sector) if $0 < b < \frac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)}$ (or $b > \frac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)}$);*

(II) *when $b = \frac{(a+x_*)^2(1-x_*)}{x_*(1-a-2x_*)}$, then E_* is a cusp of codimension two if $a \neq a_3$; a cusp of codimension three if $a = a_3$ and $0 < x_* < \frac{8-(100+12\sqrt{69})^{\frac{1}{3}}-(100-12\sqrt{69})^{\frac{1}{3}}}{12} \approx 0.122561$.*

The phase portraits are given in Figs. 2.8(b) and 2.9.

Proof. **(I)** If $b \neq \frac{(a+x_*)^2(1-x_*)}{x_*(1-a-2x_*)}$, then the Jacobian matrix of system (1.2) around E_* has only one zero eigenvalue. We first transform E_* into the origin by letting $u = x - x_*$, $v = y - \frac{(a+x_*)(1-x_*)}{b}$, then the Taylor expansion of system (1.2) around the origin takes the form

$$\begin{aligned} \dot{u} &= \tfrac{x_*(1-a-2x_*)}{a+x_*}u - \tfrac{bx_*}{a+x_*}v + \tfrac{a(1-a)+3ax_*+x_*{}^2}{(a+x_*)^2}u^2 - \tfrac{ab}{(a+x_*)^2}uv + o(|u,v|^2), \\ \dot{v} &= \tfrac{(1-x_*)(a+x_*)(1-a-2x_*)}{b^2}u - \tfrac{(1-x_*)(a+x_*)}{b}v - \tfrac{(1-x_*)(1-a-2x_*)}{b^2}u^2 \\ &\quad + \tfrac{1-a-2x_*}{b}uv - v^2 + o(|u,v|^2). \end{aligned} \tag{2.37}$$

Letting $u = \frac{b}{1-a-2x_*}X + \frac{b^2x_*}{(1-x_*)(a+x_*)^2}Y$, $v = X + Y$ and $dt = \frac{(x_*-1)(a+x_*)^2+bx_*(1-a-2x_*)}{b(a+x_*)}d\tau$, then system (2.37) can be rewritten as follows (still denote τ by t)

$$\begin{aligned} \dot{X} &= \hat{a_{20}}X^2 + \hat{a_{11}}XY + \hat{a_{02}}Y^2 + o(|X,Y|^2), \\ \dot{Y} &= Y + \hat{b_{20}}X^2 + \hat{b_{11}}XY + \hat{b_{02}}Y^2 + o(|X,Y|^2). \end{aligned} \tag{2.38}$$

where

$$\begin{aligned} \hat{a_{20}} &= -\frac{b^2x_*(1-x_*)(a+x_*)(1-2a-3x_*)}{(1-a-2x_*)((1-x_*)(a+x_*)^2-bx_*(1-a-2x_*))^2}, \\ \hat{a_{11}} &= \frac{b^2((1-x_*)(a+x_*)(a-x_*+2x_*^2)-bx_*(2x_*^2-4x_*-1-a))}{(1-x)((1-x_*)(a+x_*)^2-bx_*(1-a-2x_*))^2}, \\ \hat{a_{02}} &= \frac{b^2x_*(1-a-2x_*)(x_*^4+p_1x_*^3+p_2x_*^2+p_3x_*+p_4)}{(1-x_*)(a+x_*)^2((1-x_*)(a+x_*)^2-bx_*(1-a-2x_*))^2}, \\ \hat{b_{20}} &= \frac{(a+x_*)(1-x_*)(x_*^2-(1-a-b)x_*-a)}{(1-a-2x_*)((1-x_*)(a+x_*)^2-bx_*(1-a-2x_*))}, \\ \hat{b_{11}} &= -\frac{b(x_*^5+p_5x_*^4+p_6x_*^3+p_7x_*^2+p_8x_*+p_9)}{(a+x_*)((1-x_*)(a+x_*)^2-bx_*(1-a-2x_*))}, \\ \hat{b_{02}} &= \frac{b(1-x_*)(a+x_*)^3(1+p_{10}+p_{11}+p_{12})}{((1-x_*)(a+x_*)^2-bx_*(1-a-2x_*))^2}, \end{aligned}$$

and

$$\begin{aligned} & p_1 = 3a-2b-1, \quad p_2 = 3a^2+3b^2-4ab-3a+b, \\ & p_3 = a^3-2a^2b+ab^2-3a^2+2ab-b^2, \\ & p_4 = a^2(b-a), \quad p_5 = 4a-1, \quad p_6 = 6a^2+2b^2-2ab-4a-b, \\ & p_7 = a(4a^2+4b^2-4ab-6a-b), \quad p_8 = a(a^3-2a^2b+ab^2-4a^2+ab-b^2), \\ & p_9 = a^3(b-a), \quad p_{10} = \frac{b^2x_*^2(1-a-2x_*)}{(1-x_*)(a+x_*)^4}, \quad p_{11} = \frac{bx_*(a+2x_*-1)}{(1-x_*)(a+x_*)^2}, \\ & p_{12} = \frac{b^2x_*(a+2x_*-1)(a(1-x_*)(a+x_*)^2+bx_*(x_*^2+3ax_*+a^2-a))}{(1-x_*)^2(a+x_*)^6}. \end{aligned}$$

Notice that $\frac{1-2x_*}{2} < a < 1-2x_*$, then $\hat{a_{20}} \neq 0$ and, according to Theorem 7.1 in Zhang et al. [27], the equilibrium $E_*(x_*, \frac{(a+x_*)(1-x_*)}{b})$ is a saddle-node with a stable parabolic sector if $0 < b < \frac{(a+x_*)^2(1-x_*)}{x_*(1-a-2x_*)}$ and a saddle-node with an unstable parabolic sector if $\frac{(a+x_*)^2(1-x_*)}{x_*(1-a-2x_*)} < b$.

(II) The proofs are similar as those in cases **(I)(ii)** and **(II)(ii)** of Theorem 2.7, we omit the procedures for brevity. □

Remark 2.12. When $\delta \geq \frac{a}{b}$ (i.e., $K_2 \geq \frac{r_1}{\xi}$), we can see that the invading hosts will go extinct for some positive initial populations, and will persist for some other positive initial populations (see Theorem 2.11 and Fig. 2.8). On the other hand, from Fig. 2.9, we can see that the invading hosts will go extinct for almost all positive initial populations.

3. Bifurcations of system (1.2)

In this section, we are interested in studying various possible bifurcations in system (1.2). From Theorems 2.7 and 2.11, we know that system (1.2) may exhibit a cusp type degenerate Bogdanov-Takens bifurcation of codimension three around the equilibrium E_*, and a Hopf bifurcation around the equilibrium E_1 or E_3; From Theorem 2.8, we know that system (1.2) may exhibit a focus or elliptic type degenerate Bogdanov-Takens bifurcation of codimension three around the equilibrium E^*. Furthermore, from (2.3) we can see that the positive equilibrium depends on a polynomial equation of degree three, which makes the full bifurcation analysis very difficult and challenging.

3.1. Cusp type degenerate Bogdanov-Takens bifurcation of codimension three

From Theorems 2.7 and 2.11, we know that system (1.2) has a cusp $E_*(x_*, \frac{x_*(1-a-2x_*)}{a+x_*})$ of codimension three if the parameters satisfy

$$\delta < \frac{a}{b}, \;\; a = a_2, \;\; (b, c, \delta) = \left(\frac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)}, \frac{x_*(1-a-2x_*)^2}{a(1-x_*)}, \frac{x_*(1-a-2x_*)(a-x_*+2x_*^2)}{a(a+x_*)(1-x_*)}\right), \;\; 0 < x_* < \frac{1}{8}; \tag{3.1}$$

or

$$\begin{aligned} &\delta < \frac{a}{b}, \;\; a = a_3, \;\; (b, c, \delta) = \left(\frac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)}, \frac{x_*(1-a-2x_*)^2}{a(1-x_*)}, \frac{x_*(1-a-2x_*)(a-x_*+2x_*^2)}{a(a+x_*)(1-x_*)}\right), \\ &\textit{and} \;\; \frac{8-(100+12\sqrt{69})^{\frac{1}{3}}-(100-12\sqrt{69})^{\frac{1}{3}}}{12} < x_* < \frac{1}{8}; \end{aligned} \tag{3.2}$$

or

$$\begin{aligned} &\delta \geq \frac{a}{b}, \;\; a = a_3, \;\; (b, c, \delta) = \left(\frac{(1-x_*)(a+x_*)^2}{x_*(1-a-2x_*)}, \frac{x_*(1-a-2x_*)^2}{a(1-x_*)}, \frac{x_*(1-a-2x_*)(a-x_*+2x_*^2)}{a(a+x_*)(1-x_*)}\right), \\ &\textit{and} \;\; 0 < x_* < \frac{8-(100+12\sqrt{69})^{\frac{1}{3}}-(100-12\sqrt{69})^{\frac{1}{3}}}{12}. \end{aligned} \tag{3.3}$$

In the following we study if system (1.2) can undergo a cusp type degenerate Bogdanov-Takens bifurcation of codimension three in a small neighborhood of equilibrium $E_*(x_*, \frac{x_*(1-2a-2x_*)}{a+x_*})$ as parameters (a, b, c, δ) varies in a small neighborhood of $(a_0, b_0, c_0, \delta_0)$ which satisfies (3.1), (3.2) or (3.3). We firstly present the definition and a universal unfolding about a cusp type degenerate Bogdanov-Takens bifurcation of codimension three (see Dumortier et al. [5], Chow et al. [2] or Li et al. [15]).

Definition 3.1. The bifurcation that results from unfolding the following normal form of a cusp of codimension three

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= x^2 \pm x^3 y \end{aligned} \tag{3.4}$$

is called a *cusp type degenerate Bogdanov-Takens bifurcation of codimension three*.

Proposition 3.2. *A universal unfolding of the above normal form (3.4) is given by*

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= \mu_1 + \mu_2 y + \mu_3 xy + x^2 \pm x^3 y + R(x, y, \mu), \end{aligned} \tag{3.5}$$

where

$$R(x, y, \mu) = y^2 O(|x, y|^2) + O(|x, y|^5) + O(\mu)(O(|y|^2) + O(|x, y|^3)) + O(\mu^2)O(|x, y|). \tag{3.6}$$

We firstly consider the bifurcation around the cusp E_* of codimension three when (3.1) is satisfied. For simplicity, we let $\omega = \sqrt{1 - 8x_*}$, then $a_2 = \frac{1-3x_*-(1-x_*)\sqrt{1-8x_*}}{2} = \frac{(1-\omega)(5-2\omega+\omega^2)}{16}$. When $a = a_2$, from (3.1), we have

$$a = \tfrac{(1-\omega)(5-2\omega+\omega^2)}{16}, \;\; b = \tfrac{(1-\omega)(7+\omega^2)^2}{16(1+\omega)^2}, \;\; c = \tfrac{(1+\omega)^3(7+\omega^2)}{16(\omega^2-2\omega+5)}, \;\; \delta = \tfrac{(1-\omega)(1+\omega)^2}{2(\omega^2-2\omega+5)}, \tag{3.7}$$

if we choose a, c and δ as bifurcation parameters, then the unfolding system of (1.2) is as follows

$$\begin{aligned} \dot{x} &= x\Big(1 - x - \frac{\frac{(1-\omega)(7+\omega^2)^2}{16(1+\omega)^2} y}{\frac{(1-\omega)(5-2\omega+\omega^2)}{16} + \lambda_1 + x}\Big), \\ \dot{y} &= y\Big(\frac{(1-\omega)(1+\omega)^2}{2(5-2\omega+\omega^2)} + \lambda_2 - y + \frac{\big(\frac{(7+\omega^2)(1+\omega)^3}{16(5-2\omega+\omega^2)} + \lambda_3\big)x}{\frac{(1-\omega)(5-2\omega+\omega^2)}{16} + \lambda_1 + x}\Big), \end{aligned} \tag{3.8}$$

where $\lambda = (\lambda_1, \lambda_2, \lambda_3)$ is a parameter vector in a small neighborhood of $(0, 0, 0)$. If we can transform the unfolding system (3.8) into the versal unfolding (3.5) of Bogdanov-Takens singularity (cusp case) of codimension three by a series of near-identity transformations, and check the nondegenerate condition $\frac{D(\mu_1,\mu_2,\mu_3)}{D(\lambda_1,\lambda_2,\lambda_3)} \neq 0$ for small λ, then we can claim that system (3.8) (i.e., system (1.2)) undergoes a cusp type degenerate Bogdanov-Takens bifurcation of codimension three.

Theorem 3.3. *When $\delta < \frac{a}{b}$ and the conditions in (3.1) are satisfied, the degenerate equilibrium $E_*(x_*, \frac{x_*(1-a-2x_*)}{a+x_*})$ (i.e., $E_*(\frac{1-\omega^2}{8}, \frac{(1+\omega)^2}{8})$) of system (1.2) is a cusp of codimension three. System (1.2) undergoes a cusp type degenerate Bogdanov-Takens bifurcation of codimension three* *in a small neighborhood of E_* as (a, b, c, δ) varies in a small neighborhood of $(a_0, b_0, c_0, \delta_0)$, where $(a_0, b_0, c_0, \delta_0)$ satisfies (3.7). More precisely, system (1.2) can exhibit the coexistence of a stable homoclinic loop and an unstable limit cycle, coexistence of two limit cycles (the inner one unstable and the outer stable), and the existence of a semi-stable limit cycle for different sets of parameters.*

Proof. Firstly, we translate the equilibrium $E_*(\frac{(1-\omega^2)}{8}, \frac{(1+\omega)^2}{8})$ of system (3.8) when $\lambda = 0$ into the origin and expand system (3.8) in power series around the origin. Let

$$X = x - \frac{(1-\omega^2)}{8}, \;\; Y = y - \frac{(1+\omega)^2}{8},$$

then system (3.8) becomes

$$\begin{aligned}\dot{X} &= a_{00} + a_{10}X + a_{01}Y + a_{20}X^2 + a_{11}XY + a_{30}X^3 + a_{21}X^2Y + a_{40}X^4 + a_{31}X^3Y \\ &\quad + o(|X, Y|^4), \\ \dot{Y} &= b_{00} + b_{10}X + b_{01}Y + b_{20}X^2 + b_{11}XY + b_{02}Y^2 + b_{30}X^3 + b_{21}X^2Y + b_{40}X^4 \\ &\quad + b_{31}X^3Y + o(|X, Y|^4),\end{aligned} \tag{3.9}$$

where the coefficients are given in Appendix B, and all the coefficients depend on $\lambda_i (i = 1, 2, 3)$ which we omit for brevity.

Next, note that the coefficient a_{01} of the term Y in the first equation of (3.9) is nonzero, we make transformations $x_1 = X$ and $y_1 = \frac{dX}{dt}$ such that (3.9) is changed to the following equation

$$\begin{aligned}\dot{x}_1 &= y_1, \\ \dot{y}_1 &= c_{00} + c_{10}x_1 + c_{01}y_1 + c_{20}x_1^2 + c_{11}x_1y_1 + c_{02}y_1^2 + c_{30}x_1^3 + c_{21}x_1^2y_1 + c_{12}x_1y_1^2 \\ &\quad + c_{40}x_1^4 + c_{31}x_1^3y_1 + c_{22}x_1^2y_1^2 + o(|x_1, y_1|^4),\end{aligned} \tag{3.10}$$

where the coefficients are given in Appendix B.

Now following the procedure in Li et al. [15] (see also Huang et al. [14]), we use several steps to transform system (3.10) into the versal unfolding of a Bogdanov-Takens singularity (cusp case) of codimension three.

(I) Removing the y_1^2-term from $\dot{y_1}$ in system (3.10). We let $x_1 = x_2 + \frac{c_{02}}{2}x_2^2, \;\; y_1 = y_2 + c_{02}x_2y_2$, then system (3.10) is changed into

$$\begin{aligned}\dot{x}_2 &= y_2, \\ \dot{y}_2 &= d_{00} + d_{10}x_2 + d_{01}y_2 + d_{20}x_2^2 + d_{11}x_2y_2 + d_{30}x_2^3 + d_{21}x_2^2y_2 + d_{12}x_2y_2^2 + d_{40}x_2^4 \\ &\quad + d_{31}x_2^3y_2 + d_{22}x_2^2y_2^2 + o(|x_2, y_2|^4),\end{aligned} \tag{3.11}$$

where the coefficients are given in Appendix B.

(II) Removing the $x_2y_2^2$-term from $\dot{y_2}$ in system (3.11). Let $x_2 = x_3 + \frac{d12}{6}x_3^3, \; y_2 = y_3 + \frac{d12}{2}x_3^2y_3$, then we obtain the following system

$$\begin{aligned} \dot{x}_3 &= y_3, \\ \dot{y}_3 &= e_{00} + e_{10}x_3 + e_{01}y_3 + e_{20}x_3^2 + e_{11}x_3y_3 + e_{30}x_3^3 + e_{21}x_3^2y_3 + e_{40}x_3^4 \\ &\quad + e_{31}x_3^3y_3 + R_1(x_3, y_3, \lambda), \end{aligned} \tag{3.12}$$

where the coefficients are given in Appendix B, and $R_1(x_3, y_3, \lambda)$ has the property of (3.6).

(III) Removing the x_3^3 and x_3^4-terms from $\dot{y_3}$ in system (3.12). Note that $e_{20} = \frac{\omega(1+\omega)^3}{2(7+\omega^2)(1-\omega)} + O(\lambda) \neq 0$ for $0 < \omega < 1$ and small λ. We let

$$x_3 = x_4 - \frac{e_{30}}{4e_{20}}x_4^2 + \frac{15e_{30}^2 - 16e_{20}e_{40}}{80e_{20}^2}x_4^3, \quad y_3 = y_4,$$

$$d\tau = (1 + \frac{e_{30}}{2e_{20}}x_4 + \frac{48e_{20}e_{40} - 25e_{30}^2}{80e_{20}^2}x_4^2 + \frac{48e_{20}e_{30}e_{40} - 35e_{30}^3}{80e_{20}^3}x_4^3)dt,$$

and obtain the following system from system (3.12) (still denote τ by t):

$$\begin{aligned} \dot{x}_4 &= y_4, \\ \dot{y}_4 &= f_{00} + f_{10}x_4 + f_{01}y_4 + f_{20}x_4^2 + f_{11}x_4y_4 + f_{30}x_4^3 + f_{21}x_4^2y_4 + f_{40}x_4^4 \\ &\quad + f_{31}x_4^3y_4 + R_2(x_4, y_4, \lambda), \end{aligned} \tag{3.13}$$

where the coefficients are given in Appendix B, and $R_2(x_4, y_4, \lambda)$ has the property of (3.6).

(IV) Removing the $x_4^2y_4$-term from $\dot{y_4}$ in system (3.13). Note that $f_{20} = \frac{\omega(1+\omega)^3}{2(7+\omega^2)(1-\omega)} + O(\lambda) \neq 0$ for $0 < \omega < 1$ and small λ. Letting

$$x_4 = x_5, \quad y_4 = y_5 + \frac{f_{21}}{3f_{20}}y_5^2 + \frac{f_{21}^2}{36f_{20}^2}y_5^3,$$

and introducing a new time variable τ by $d\tau = (1 + \frac{f_{21}}{3f_{20}}y_5 + \frac{f_{21}^2}{36f_{20}^2}y_5^2)dt$, then system (3.13) can be rewritten as (still denote τ by t)

$$\begin{aligned} \dot{x}_5 &= y_5, \\ \dot{y}_5 &= g_{00} + g_{10}x_5 + g_{01}y_5 + g_{20}x_5^2 + g_{11}x_5y_5 + g_{31}x_5^3y_5 + R_3(x_5, y_5, \lambda)), \end{aligned} \tag{3.14}$$

where

$$g_{00} = f_{00}, \quad g_{10} = f_{10}, \quad g_{01} = f_{01} - \frac{f_{00}f_{21}}{f_{20}}, \quad g_{20} = f_{20}, \quad g_{11} = f_{11} - \frac{f_{10}f_{21}}{f_{20}},$$

$$g_{31} = f_{31} - \frac{f_{21}f_{30}}{f_{20}},$$

and $R_3(x_5, y_5, \lambda))$ has the property of (3.6).

(V) Changing g_{20} to 1 and g_{31} to -1 in $\dot{y_5}$ in system (3.14). We can see that $g_{20} = \frac{\omega(1+\omega)^3}{2(7+\omega^2)(1-\omega)} + O(\lambda) > 0$ and $g_{31} = -\frac{256}{\omega(1-\omega)(7+\omega^2)^2} + O(\lambda) < 0$ for $0 < \omega < 1$ and small λ. By making the following changes of variables and time:

$$x_5 = g_{20}^{\frac{1}{5}} g_{31}^{-\frac{2}{5}} x_6, \ \ y_5 = -g_{20}^{\frac{4}{5}} g_{31}^{-\frac{3}{5}} y_6, \ \ t = -g_{20}^{-\frac{3}{5}} g_{31}^{\frac{1}{3}} \tau,$$

system (3.14) becomes (still denote τ by t)

$$\begin{aligned} \dot{x}_6 &= y_6, \\ \dot{y}_6 &= h_{00} + h_{10}x_6 + h_{01}y_6 + h_{11}x_6y_6 + x_6^2 - x_6^3 y_6 + R_4(x_6, y_6, \lambda)), \end{aligned} \tag{3.15}$$

where

$$h_{00} = g_{00} g_{31}^{\frac{4}{5}} g_{20}^{-\frac{7}{5}}, \ \ h_{10} = g_{10} g_{31}^{\frac{2}{5}} g_{20}^{-\frac{6}{5}}, \ \ h_{01} = -g_{01} g_{31}^{\frac{1}{5}} g_{20}^{-\frac{3}{5}}, \ \ h_{11} = -g_{11} g_{20}^{-\frac{2}{5}} g_{31}^{-\frac{1}{5}},$$

and $R_4(x_6, y_6, \lambda)$ has the property of (3.6).

(VI) Removing the x_6-term from $\dot{y}_6$ in system (3.15). Let $x_6 = x_7 - \frac{h_{20}}{2}$, $y_6 = y_7$, then system (3.16) becomes

$$\begin{aligned} \dot{x}_7 &= y_7, \\ \dot{y}_7 &= \mu_1 + \mu_2 y_7 + \mu_3 x_7 y_7 + x_7^2 - x_7^3 y_7 + R_5(x_7, y_7, \lambda)), \end{aligned} \tag{3.16}$$

where $R_5(x_7, y_7, \lambda))$ has the property of (3.6), and

$$\begin{aligned} \mu_1 &= h_{00} - \frac{h_{10}^2}{4} = q_1\lambda_1 + q_2\lambda_2 + q_3\lambda_3 + o(\lambda), \\ \mu_2 &= h_{01} + \frac{1}{8}(h_{10}^3 - 4h_{10}h_{11}) = q_4\lambda_1 + q_5\lambda_2 + q_6\lambda_3 + o(\lambda), \\ \mu_3 &= h_{11} - \frac{3}{4}h_{10}^2 = q_7\lambda_1 + q_8\lambda_2 + q_9\lambda_3 + o(\lambda), \end{aligned}$$

the coefficients $q_i (i = 1, 2, 3, 4, 5, 6, 7, 8, 9)$ are given in Appendix B.

With the help of Mathematica software, we obtain that

$$\frac{D(\mu_1, \mu_2, \mu_3)}{D(\lambda_1, \lambda_2, \lambda_3)} = \frac{128\sqrt[5]{16}\sqrt[5]{(1-\omega)^3}(3+\omega)(\omega^2 - 2\omega + 5)(3\omega^2 - 6\omega + 7)}{\sqrt[5]{\omega^{21}(1+\omega)^{36}(7+\omega^2)^6}} + O(\lambda) \neq 0$$

for $0 < \omega < 1$ and small λ, it is obvious that system (3.16) is exactly in the form of system (3.5), by the results in Dumortier et al. [5] and Chow et al. [2], system (3.16) is the versal unfolding of the Bogdanov-Takens singularity (cusp case) of codimension three, the remainder term $R_5(x_7, y_7, \lambda)$ satisfying the property of (3.6) has no influence on the bifurcation phenomena, and the dynamics of system (1.2) in a small neighborhood of the positive equilibrium $(\frac{1-\omega^2}{8}, \frac{(1+\omega)^2}{8})$ as (a, c, δ) varying near (a_0, c_0, δ_0) are equivalent to system (3.16) in a small neighborhood of $(0, 0, 0)$ as (μ_1, μ_2, μ_3) varying near $(0, 0, 0)$.

Next we describe the bifurcation diagram of system (3.16) following Fig. 3 of Dumortier et al. [5] based on a time reversal transformation. The bifurcation diagram has the conical structure in $\mathbb{R}^3$ starting from $(\mu_1, \mu_2, \mu_3) = (0, 0, 0)$. It can be shown by drawing its intersection with the half sphere

$$S = \{(\mu_1, \mu_2, \mu_3) | \mu_1^2 + \mu_2^2 + \mu_3^2 = \epsilon^2, \mu_1 \leq 0, \epsilon > 0 \text{ sufficiently small}\}.$$

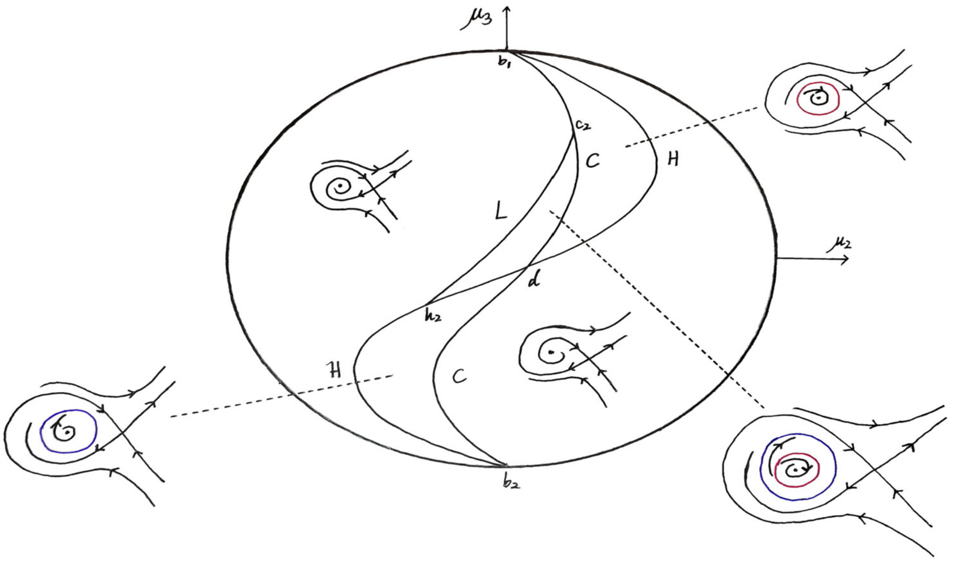


Fig. 3.1. Bifurcation diagram for system (3.16).

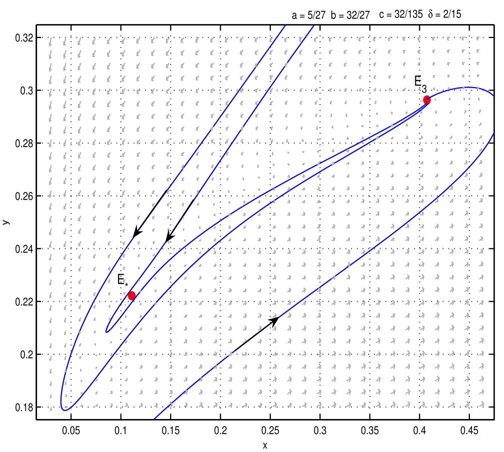
To see the trace of intersection clearly, we draw the projection of the trace onto the (μ_2, μ_3)-plane, see Fig. 3.1. The curves C, H, L denote the homoclinic bifurcation curve, Hopf bifurcation curve and saddle-node bifurcation curve of limit cycles, respectively. b_1 and b_2 are the Bogdanov-Takens bifurcation points. c_2 and h_2 correspond to a homoclinic bifurcation of codimension two and a Hopf bifurcation of codimension two, respectively. The point d represents a parameter value of simultaneous Hopf and homoclinic bifurcations, where an unstable limit cycle coexists with a stable homoclinic loop. For parameter values in the triangle dh_2c_2, there exist exactly two limit cycles: the inner one is unstable and the outer one is stable. The detailed bifurcation phenomena can be referred to Dumortier et al. [5] (see also Li et al. [15] or Huang et al. [14]). □

The typical phase portraits for a cusp type degenerate Bogdanov-Takens bifurcation of codimension three in system (1.2) are given in Fig. 3.2. The coexistence of a cusp E_* of codimension three and a hyperbolic focus E_3 is given in Fig. 3.2(a), the coexistence of an unstable limit cycle and a stable homoclinic loop is given in Fig. 3.2(b), and the existence of two limit cycles (the inner one is unstable and the outer one is stable) is given in Fig. 3.2(c).

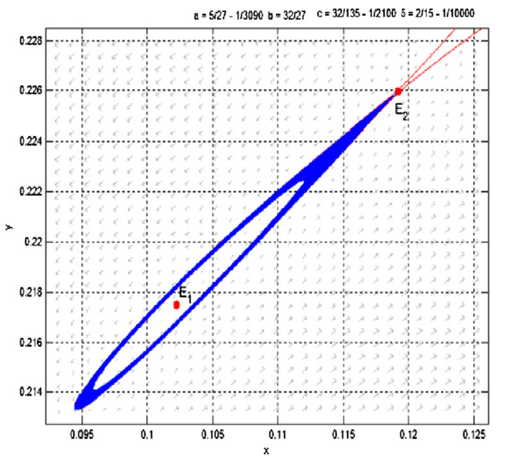
Next we consider the bifurcation around the cusp E_* of codimension three when the conditions in (3.2) or (3.3) are satisfied. For simplicity, we still let $\omega = \sqrt{1-8x_*}$, then $a_3 = \frac{1-3x_*+(1-x_*)\sqrt{1-8x_*}}{2} = \frac{(1+\omega)(5+2\omega+\omega^2)}{16}$. When $a = a_3$, from (3.2), we have

$$a = \frac{(1+\omega)(5+2\omega+\omega^2)}{16}, \quad b = \frac{(1+\omega)(7+\omega^2)^2}{16(1-\omega)^2}, \quad c = \frac{(1-\omega)^3(7+\omega^2)}{16(\omega^2+2\omega+5)}, \quad \delta = \frac{(1+\omega)(1-\omega)^2}{2(\omega^2+2\omega+5)}, \tag{3.17}$$

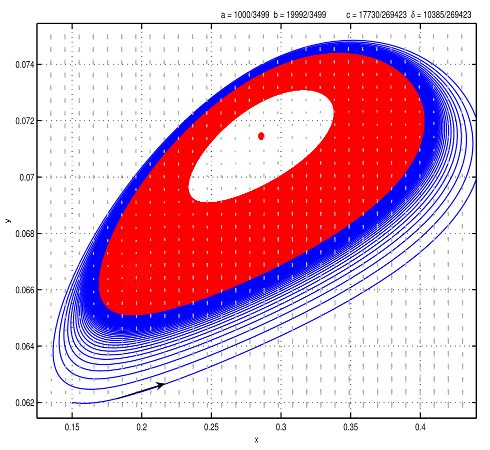
and $E_*(x_*, y_*) = E_*(\frac{1-\omega^2}{8}, \frac{(1-\omega)^2}{8})$, if we choose a, b and δ as bifurcation parameters, then the unfolding system of (1.2) is as follows



(a)



(b)



(c)

Fig. 3.2. Typical phase portraits of system (1.2) in a cusp type degenerate Bogdanov-Takens bifurcation of codimension three. (a) The coexistence of a cusp E_* of codimension three and a hyperbolic focus E_3; (b) The coexistence of an unstable limit cycle and a stable homoclinic loop; (c) The existence of two limit cycles.

$$\begin{aligned} \dot{x} &= x\Big(1 - x - \Big(\frac{\frac{(1+\omega)(7+\omega^2)^2}{16(1-\omega)^2} + \lambda_2)y}{\frac{(1+\omega)(5+2\omega+\omega^2)}{16} + \lambda_1 + x}\Big), \\ \dot{y} &= y\Big(\frac{(1+\omega)(1-\omega)^2}{2(5+2\omega+\omega^2)} + \lambda_3 - y + \frac{\frac{(7+\omega^2)(1-\omega)^3}{16(5+2\omega+\omega^2)}x}{\frac{(1+\omega)(5+2\omega+\omega^2)}{16} + \lambda_1 + x}\Big), \end{aligned} \tag{3.18}$$

where $\lambda = (\lambda_1, \lambda_2, \lambda_3)$ is a parameter vector in a small neighborhood of $(0, 0, 0)$.

Theorem 3.4. *When the conditions in (3.2) or (3.3) are satisfied, the degenerate equilibrium* $E_*(x_*, \frac{x_*(1-a-2x_*)}{a+x_*})$ *(i.e.,* $E_*(\frac{1-\omega^2}{8}, \frac{(1-\omega)^2}{8})$*) of system (1.2) is a cusp of codimension three. System (1.2) undergoes a cusp type Bogdanov-Takens bifurcation of codimension three in a small* *neighborhood of E_* as (a, b, c, δ) varies in a small neighborhood of $(a_0, b_0, c_0, \delta_0)$, where $(a_0, b_0, c_0, \delta_0)$ satisfies (3.17). More precisely, system (1.2) can exhibit the coexistence of a stable homoclinic loop and an unstable limit cycle, the coexistence of two limit cycles (the inner one unstable and the outer stable), and the existence of a semi-stable limit cycle for different sets of parameters.*

Proof. The proof is similar to that of Theorem 3.3. After making a sequence of transformations as those in the proof of Theorem 3.3, we obtain the following equivalent system of system (3.18)

$$\begin{aligned}\dot{x}_7 &= y_7,\\ \dot{y}_7 &= \mu_1 + \mu_2 y_7 + \mu_3 x_7 y_7 + x_7^2 - x_7^3 y_7 + \widetilde{R_5}(x_7, y_7, \lambda),\end{aligned} \tag{3.19}$$

where μ_1, μ_2 and μ_3 are the C^∞ function of $\lambda_1, \lambda_2, \lambda_3$ and ω, and $\widetilde{R_5}$ has the property of (3.6).

Under the help of Mathematica, when the conditions in (3.2) or (3.3) are satisfied, we obtain

$$\frac{D(\mu_1,\mu_2,\mu_3)}{D(\lambda_1,\lambda_2,\lambda_3)} = -\frac{128\sqrt[5]{16}\sqrt[5]{(1+\omega)^3}(3-\omega)(5+2\omega+\omega^2)(7+6\omega+3\omega^2)}{\sqrt[5]{\omega^{21}(1-\omega)^{36}(7+\omega^2)^6}} + O(\lambda) \neq 0$$

for $0 < \omega < 1$ and small λ, it is obvious that system (3.19) is exactly in the form of system (3.5), by the results in Dumortier et al. [5] and Chow et al. [2], system (3.19) is the versal unfolding of the Bogdanov-Takens singularity (cusp case) of codimension three, the remainder term $\widetilde{R_5}(x_7, y_7, \lambda)$ satisfies the property of (3.6) and has no influence on the bifurcation phenomena, and the dynamics of system (1.2) in a small neighborhood of the positive equilibrium $(\frac{1-\omega^2}{8}, \frac{(1-\omega)^2}{8})$ as (a, b, δ) varying near (a_0, b_0, δ_0) are equivalent to system (3.19) in a small neighborhood of $(0, 0, 0)$ as (μ_1, μ_2, μ_3) varying near $(0, 0, 0)$. □

3.2. Focus and elliptic types degenerate Bogdanov-Takens bifurcation of codimension three

Theorem 2.8(II) indicates that if

$$b = \frac{2(1+a)^2}{3(1-2a)}, \quad c = \frac{(1+a)(1-2a)}{18a}, \quad \delta = \frac{(1-2a)(8a-1)}{18a}, \tag{3.20}$$

then the unique triple positive equilibrium E^* of system (1.2) is a degenerate nilpotent focus or elliptic singularity of codimension three, system (1.2) may exhibit degenerate focus or elliptic type Bogdanov-Takens bifurcation of codimension three around E^*. If we choose b, c and δ as bifurcation parameters, then the unfolding system of system (1.2) is as follows

$$\begin{aligned}\dot{x} &= x\Big(1 - x - \frac{(\frac{2(1+a)^2}{3(1-2a)} + \lambda_1)y}{a+x}\Big),\\ \dot{y} &= y\Big(\frac{(1-2a)(8a-1)}{18a} + \lambda_2 - y + \frac{(\frac{(1+a)(1-2a)}{18a} + \lambda_3)x}{a+x}\Big),\end{aligned} \tag{3.21}$$

where $\lambda = (\lambda_1, \lambda_2, \lambda_3)$ is a parameter vector in a small neighborhood of $(0, 0, 0)$.

Theorem 3.5. *If $\delta < \frac{a}{b}$, $\frac{1}{8} < a < \frac{1}{2}$, $a \neq \frac{5}{16}$, and the conditions in (3.20) are satisfied, then the unique triple positive equilibrium E^* of system (1.2) is a degenerate nilpotent focus or elliptic singularity of codimension three. Moreover, if we choose b, c and δ as bifurcation parameters, then*

(i) *when* $\frac{5}{16} < a < \frac{2+3\sqrt{2}}{16}$, *system* (1.2) *undergoes a focus type degenerate Bogdanov-Takens bifurcation of codimension three around* E^* *in a small neighborhood of the point* $(a_0, b_0, c_0, \delta_0)$ *of the parameter space, where* $(a_0, b_0, c_0, \delta_0)$ *satisfies* (3.20)*. Thus, system* (1.2) *can exhibit a big limit cycle enclosing three hyperbolic positive equilibria, two big limit cycles enclosing three hyperbolic positive equilibria, and a big limit cycle enclosing three hyperbolic positive equilibria and a small limit cycle for different sets of parameters;*

(ii) *when* $\frac{2+3\sqrt{2}}{16} \le a < \frac{1}{2}$ *and* $a \ne \frac{23+3\sqrt{65}}{112}$, *system* (1.2) *undergoes an elliptic type degenerate Bogdanov-Takens bifurcation of codimension three around* E^* *in a small neighborhood of the point* $(a_0, b_0, c_0, \delta_0)$ *of the parameter space, where* $(a_0, b_0, c_0, \delta_0)$ *satisfies* (3.20)*. Thus, system* (1.2) *can exhibit the coexistence of three positive equilibria and a homoclinic loop, and one or two limit cycles enclosing only one positive equilibrium for different sets of parameters.*

Proof. Firstly, we make a sequence of smooth coordinate transformations (I), (II) and (III), which were used in the proof of Theorem 2.8, to get the following system from system (3.21)

$$\begin{aligned}
\dot{X} &= y + \tilde{c_{00}}(\lambda) + \tilde{c_{10}}(\lambda)X + \tilde{c_{01}}(\lambda)Y + \tilde{c_{20}}(\lambda)X^2 + \tilde{c_{11}}(\lambda)XY + \tilde{c_{02}}(\lambda)Y^2 \\
&\quad + \tilde{c_{30}}(\lambda)X^3 + \tilde{c_{21}}(\lambda)X^2Y + \tilde{c_{12}}(\lambda)XY^2 + \tilde{c_{03}}(\lambda)Y^3 + O(|X, Y|^4), \\
\dot{Y} &= \tilde{d_{00}}(\lambda) + \tilde{d_{10}}(\lambda)X + \tilde{d_{01}}(\lambda)Y + \tilde{d_{20}}(\lambda)X^2 + \tilde{d_{11}}(\lambda)XY + \tilde{d_{02}}(\lambda)Y^2 \\
&\quad + \tilde{d_{30}}(\lambda)X^3 + \tilde{d_{21}}(\lambda)X^2Y + \tilde{d_{12}}(\lambda)XY^2 + \tilde{d_{03}}(\lambda)Y^3 + O(|X, Y|^4),
\end{aligned} \tag{3.22}$$

where $\tilde{c_{ij}}(\lambda)$ and $\tilde{d_{ij}}(\lambda)$ are smooth functions whose long expressions are omitted here for the sake of brevity, $\tilde{c_{00}}(0) = \tilde{c_{10}}(0) = \tilde{c_{01}}(0) = \tilde{c_{20}}(0) = \tilde{c_{11}}(0) = \tilde{c_{02}}(0) = \tilde{d_{00}}(0) = \tilde{d_{10}}(0) = \tilde{d_{01}}(0) = \tilde{d_{20}}(0) = \tilde{d_{02}}(0) = 0$, $\tilde{c_{30}}(0) = \tilde{c_{30}}, \tilde{c_{21}}(0) = \tilde{c_{21}}, \tilde{c_{12}}(0) = \tilde{c_{12}}, \tilde{c_{03}}(0) = \tilde{c_{03}}, \tilde{d_{11}}(0) = \tilde{d_{11}}, \tilde{d_{30}}(0) = \tilde{d_{30}}, \tilde{d_{21}}(0) = \tilde{d_{21}}, \tilde{d_{12}}(0) = \tilde{d_{12}}, \tilde{d_{03}}(0) = \tilde{d_{03}}$, and $\tilde{c_{30}}, \tilde{c_{21}}, \tilde{c_{12}}, \tilde{c_{03}}, \tilde{d_{11}}, \tilde{d_{30}}, \tilde{d_{21}}, \tilde{d_{12}}, \tilde{d_{03}}$ are given in system (2.31).

Secondly, to simplify the third order terms when $\lambda = 0$, we make the following coordinate transformation

$$(IV): \quad X = x + \frac{2\tilde{c_{21}} + \tilde{d_{12}}}{6}x^3 + \frac{\tilde{c_{12}} + \tilde{d_{03}}}{2}x^2y + \tilde{c_{03}}xy^2, \;\; Y = y - \tilde{c_{30}}x^3 + \frac{\tilde{d_{12}}}{2}x^2y + \tilde{d_{03}}xy^2,$$

and rewrite system (3.22) as follows

$$\begin{aligned}
\dot{x} &= y + \tilde{e_{00}}(\lambda) + \tilde{e_{10}}(\lambda)x + \tilde{e_{01}}(\lambda)y + \tilde{e_{20}}(\lambda)x^2 + \tilde{e_{11}}(\lambda)xy + \tilde{e_{02}}(\lambda)y^2 + \tilde{e_{30}}(\lambda)x^3 \\
&\quad + \tilde{e_{21}}(\lambda)x^2y + \tilde{e_{12}}(\lambda)xy^2 + \tilde{e_{03}}(\lambda)y^3 + O(|x, y|^4), \\
\dot{v} &= \tilde{f_{00}}(\lambda) + \tilde{f_{10}}(\lambda)x + \tilde{f_{01}}(\lambda)y + \tilde{f_{20}}(\lambda)x^2 + \tilde{f_{11}}(\lambda)xy + \tilde{f_{02}}(\lambda)y^2 + \tilde{f_{30}}(\lambda)x^3 \\
&\quad + \tilde{f_{21}}(\lambda)x^2y + \tilde{f_{12}}(\lambda)xy^2 + \tilde{f_{03}}(\lambda)y^3 + O(|x, y|^4),
\end{aligned} \tag{3.23}$$

where $\tilde{e_{ij}}(\lambda)$ and $\tilde{f_{ij}}(\lambda)$ can be expressed by $\tilde{c_{i,j}}(\lambda), \tilde{d_{ij}}(\lambda)$, we also omit their expressions here to save spaces.

Thirdly, introduce the following transformation

$$\begin{aligned} X &= x, \\ Y &= x + \tilde{e_{00}}(\lambda) + \tilde{e_{10}}(\lambda)x + \tilde{e_{01}}(\lambda)y + \tilde{e_{20}}(\lambda)x^2 + \tilde{e_{11}}(\lambda)xy + \tilde{e_{02}}(\lambda)y^2 + \tilde{e_{30}}(\lambda)y^3 \\ &\quad + \tilde{e_{21}}(\lambda)x^2y + \tilde{e_{12}}(\lambda)xy^2 + \tilde{e_{03}}(\lambda)y^3 + O(|x,y|^4), \end{aligned}$$

and rewrite system (3.23) as

$$\begin{aligned} \dot{X} &= Y, \\ \dot{Y} &= \tilde{g_{00}}(\lambda) + \tilde{g_{10}}(\lambda)X + \tilde{g_{01}}(\lambda)Y + \tilde{g_{20}}(\lambda)X^2 + \tilde{g_{11}}(\lambda)XY + \tilde{g_{02}}(\lambda)Y^2 \\ &\quad + \tilde{g_{30}}(\lambda)X^3 + \tilde{g_{21}}(\lambda)X^2Y + \tilde{g_{12}}(\lambda)XY^2 + \tilde{g_{03}}(\lambda)Y^3 + O(|X,Y|^4), \end{aligned} \tag{3.24}$$

where $\tilde{g_{ij}}(\lambda)$ can be expressed by $\tilde{e_{ij}}(\lambda)$ and $\tilde{f_{ij}}(\lambda)$, we also omit their expressions here. With the help of Mathematica software we calculate that $\tilde{g_{30}}(0) = -4 < 0$ and $\tilde{g_{21}}(0) = \frac{3(224a^2-92a-1)}{2(1-2a)^3} \neq 0$ if $a \neq \frac{23+3\sqrt{65}}{112}$.

Fourthly, to remove the X^2-term in the second equation of system (3.24), we let $X = x - \frac{\tilde{g_{20}}(\lambda)}{3\tilde{g_{30}}(\lambda)}$, $Y = y$, then system (3.24) can be rewritten as

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= \tilde{h_{00}}(\lambda) + \tilde{h_{10}}(\lambda)x + \tilde{h_{01}}(\lambda)y + \tilde{h_{11}}(\lambda)xy + \tilde{h_{02}}(\lambda)y^2 \\ &\quad + \tilde{h_{30}}(\lambda)x^3 + \tilde{h_{21}}(\lambda)x^2y + \tilde{h_{12}}(\lambda)xy^2 + \tilde{h_{03}}(\lambda)y^3 + O(|x,y|^4), \end{aligned} \tag{3.25}$$

where

$$\begin{aligned} \tilde{h_{00}}(\lambda) &= \tilde{g_{00}}(\lambda) + \frac{2\tilde{g_{20}}^3(\lambda) - 9\tilde{g_{10}}(\lambda)\tilde{g_{20}}(\lambda)\tilde{g_{30}}(\lambda)}{27\tilde{g_{30}}^3(\lambda)}, \ \tilde{h_{10}}(\lambda) = \tilde{g_{10}}(\lambda) - \frac{\tilde{g_{20}}^2(\lambda)}{3\tilde{g_{30}}(\lambda)}, \\ \tilde{h_{03}}(\lambda) &= \tilde{g_{03}}(\lambda), \ \tilde{h_{01}}(\lambda) = \tilde{g_{01}}(\lambda) + \frac{\tilde{g_{20}}(\lambda)(\tilde{g_{20}}(\lambda)\tilde{g_{21}}(\lambda) - 3\tilde{g_{11}}(\lambda)\tilde{g_{30}}(\lambda))}{9\tilde{g_{30}}^2(\lambda)}, \\ \tilde{h_{11}}(\lambda) &= \tilde{g_{11}}(\lambda) - \frac{2\tilde{g_{20}}(\lambda)\tilde{g_{21}}(\lambda)}{3\tilde{g_{30}}(\lambda)}, \\ \tilde{h_{02}}(\lambda) &= \tilde{g_{02}}(\lambda) - \frac{\tilde{g_{12}}(\lambda)\tilde{g_{20}}(\lambda)}{3\tilde{g_{30}}(\lambda)}, \ \tilde{h_{30}}(\lambda) = \tilde{g_{30}}(\lambda), \ \tilde{h_{21}}(\lambda) = \tilde{g_{21}}(\lambda), \ \tilde{h_{12}}(\lambda) = \tilde{g_{12}}(\lambda). \end{aligned}$$

Fifthly, in order to change $\tilde{h_{30}}(\lambda)$ to -1 in the second equation of system (3.25), we let

$$x = \frac{X}{\sqrt[3]{-\tilde{h_{30}}(\lambda)}}, \quad y = Y,$$

then system (3.25) can be rewritten as

$$
\begin{aligned}
\dot{X} &= \sqrt[3]{-\tilde{h_{30}}(\lambda)}Y, \\
\dot{Y} &= j_{00}(\lambda) + j_{10}(\lambda)X + j_{01}(\lambda)Y + j_{11}(\lambda)XY + j_{02}(\lambda)Y^2 + j_{30}(\lambda)X^3 + j_{21}(\lambda)X^2Y \\
&\quad + j_{12}(\lambda)XY^2 + j_{03}(\lambda)Y^3 + O(|X, Y|^4),
\end{aligned} \tag{3.26}
$$

where

$$
j_{00}(\lambda) = \tilde{h_{00}}(\lambda), \quad j_{10} = \frac{\tilde{h_{10}}(\lambda)}{\sqrt[3]{-\tilde{h_{30}}(\lambda)}}, \quad j_{01}(\lambda) = \tilde{h_{01}}(\lambda), \quad j_{11}(\lambda) = \frac{\tilde{h_{11}}(\lambda)}{\sqrt[3]{-\tilde{h_{30}}(\lambda)}},
$$

$$
j_{02}(\lambda) = \tilde{h_{02}}(\lambda), \quad j_{30}(\lambda) = -1, \quad j_{21}(\lambda) = \frac{\tilde{h_{21}}(\lambda)}{\sqrt[3]{\tilde{h_{30}}^2(\lambda)}}, \quad j_{12} = \frac{\tilde{h_{12}}(\lambda)}{\sqrt[3]{-\tilde{h_{30}}(\lambda)}}, \quad j_{03}(\lambda) = \tilde{h_{30}}(\lambda).
$$

Finally, let

$$
X = \frac{(-j_{30}(\lambda))^{\frac{5}{6}}}{j_{21}(\lambda)}x, \quad Y = \frac{(-j_{30}(\lambda))^{\frac{3}{2}}}{j_{21}^2(\lambda)}y, \quad t = \frac{j_{21}(\lambda)}{-j_{30}(\lambda)}\tau,
$$

then we can get the versal unfolding of system (3.21) as follows (still denote τ by t)

$$
\begin{aligned}
\dot{x} &= y, \\
\dot{y} &= \eta_1(\lambda) + \eta_2(\lambda)x - x^3 + y[\eta_3(\lambda) + A(\lambda)x + x^2] + y^2 Q(x, y, \lambda) + O(|x, y|^4),
\end{aligned} \tag{3.27}
$$

where

$$
A(\lambda) = \frac{j_{11}(\lambda)}{\sqrt{-j_{30}(\lambda)}}, \; Q(x, y, \lambda) = \frac{j_{02}(\lambda)\sqrt{-j_{30}(\lambda)}}{j_{21}(\lambda)} - \frac{j_{12}(\lambda)j_{30}(\lambda)}{j_{21}^2(\lambda)}x + \frac{j_{30}^2(\lambda)j_{03}(\lambda)}{j_{21}^3(\lambda)}y,
$$

$$
\eta_1(\lambda) = \frac{j_{00}(\lambda)j_{21}^3(\lambda)}{(-j_{30}(\lambda))^{\frac{5}{2}}}, \; \eta_2(\lambda) = \frac{j_{10}(\lambda)j_{21}^2(\lambda)}{j_{30}^2(\lambda)}, \; \eta_3(\lambda) = -\frac{j_{10}(\lambda)j_{21}(\lambda)}{j_{30}(\lambda)}.
$$

Since $\frac{1}{8} < a < \frac{1}{2}$ and $a \neq \frac{5}{16}$, by lengthy calculation, we have

$$
\left|\frac{\partial(\eta_1(\lambda), \eta_2(\lambda), \eta_3(\lambda))}{\partial(\lambda_1, \lambda_2, \lambda_3)}\right|_{\lambda=0} = -\frac{81a(224a^2 - 92a - 1)^6}{131072(2a-1)^{13}(1+a)^3} \neq 0
$$

if $a \neq \frac{23+3\sqrt{65}}{112}$. Moreover, we have

$$
A(0) = \frac{16a - 5}{2(1-2a)},
$$

and it is easy to show that $0 < A(0) < 2\sqrt{2}$ if $\frac{5}{16} < a < \frac{3\sqrt{2}+2}{16}$, and $A(0) \geq 2\sqrt{2}$ if $\frac{2+3\sqrt{2}}{16} \leq a < \frac{23+3\sqrt{65}}{112}$ or $\frac{23+3\sqrt{65}}{112} < a < \frac{1}{2}$.

By the results in Dumortier et al. [4] or Xiao and Zhang [25], we know that system (3.27) is a generic 3-parameter family of nilpotent focus (or elliptic) singularity of codimension three if $\frac{1}{8} < a < \frac{2+3\sqrt{2}}{16}$ and $a \neq \frac{5}{16}$ (or $\frac{2+3\sqrt{2}}{16} \leq a < \frac{1}{2}$ and $a \neq \frac{23+3\sqrt{65}}{112}$), and system (1.2) undergoes a degenerate focus or elliptic type Bogdanov-Takens bifurcation of codimension three around E^* when (b, c, δ) vary in a small neighborhood of $(\frac{2(1+a)^2}{3(1-2a)}, \frac{(1+a)(1-2a)}{18a}, \frac{(1-2a)(8a-1)}{18a})$. □

3.3. Hopf bifurcation and degenerate Hopf bifurcation of codimension two

In this subsection, we discuss Hopf bifurcation around $E_1(x_1, y_1)$ or $E_3(x_3, y_3)$ in system (1.2). For simplicity, we use the same technique as in Dai et al. [3] and make the following scaling for system (1.2)

$$\bar{x} = \frac{x}{x_i}, \ \ \bar{y} = \frac{y}{y_i}, \ \ \tau = \sqrt{x_i y_i} t \ (i = 1, 3). \tag{3.28}$$

Dropping the bar and still denoting τ by t, then system (1.2) becomes

$$\begin{aligned} \dot{x} &= x(\alpha - \beta x - \tfrac{By}{A+x}), \\ \dot{y} &= y(\gamma - \tfrac{y}{\beta} + \tfrac{Cx}{A+x}), \end{aligned} \tag{3.29}$$

where

$$\alpha = \frac{1}{\sqrt{x_i y_i}}, \ \ \beta = \sqrt{\frac{x_i}{y_i}}, \ \ \gamma = \alpha\delta, \ \ A = \frac{a}{x_i}, \ \ B = \frac{b}{\beta x_i}, \ \ C = c\alpha,$$

and α, β, γ, A, B and C are all positive constants. Since $(1, 1)$ is an equilibrium of system (3.29), then we have

$$B = (\alpha - \beta)(1 + A), \ \ C = -(\gamma - \tfrac{1}{\beta})(1 + A), \tag{3.30}$$

and

$$\alpha > \beta, \ \ \gamma < \tfrac{1}{\beta}, \ \ \alpha > 0, \ \ \beta > 0, \ \ \gamma > 0, \ \ A > 0. \tag{3.31}$$

Make a time variation $\tau = \frac{t}{A+x}$, then system (3.29) becomes (still use t to denote τ)

$$\begin{aligned} \dot{x} &= x\big((\alpha - \beta x)(A + x) - (\alpha - \beta)(A + 1)y\big), \\ \dot{y} &= y\big((\gamma - \tfrac{y}{\beta})(A + x) - (\gamma - \tfrac{1}{\beta})(A + 1)x\big). \end{aligned} \tag{3.32}$$

Since the transformation (3.28) is a linear sign-reserving transformation, system (3.32) and system (1.2) have the same qualitative property. The Jacobian matrix of system (3.32) at a positive equilibrium $E(x, y)$ takes the form

$$J(E) = \begin{pmatrix} 2(\alpha - A\beta)x - 3\beta x^2 - (\alpha + A\alpha - \beta - A\beta)y + A\alpha & -(\alpha - \beta)(A + 1)x \\ -\frac{(A(1-\beta\gamma)+1-y)y}{\beta} & \frac{(1+A-A\beta\gamma)x-2Ay-2xy+A\beta\gamma}{\beta} \end{pmatrix},$$

and

$$\tilde{D} \triangleq \mathrm{Det}(J(1,1)) = \frac{(A+1)(\beta(2+A\beta\gamma)-\alpha(1+A\beta\gamma-A))}{\beta},$$

$$\mathrm{Tr}(J(1,1)) = \alpha-(A+2)\beta-\frac{A+1}{\beta}.$$

We let

$$\alpha_* = \frac{1+A+(2+A)\beta^2}{\beta}, \quad \gamma_* = \frac{2(A^2\beta^3+A^2\beta+A\beta^3-\beta^3)}{A(1+\beta^2+2A\beta^2+2\beta^4+2A\beta^4)},$$

and have the following results.

Lemma 3.6. *If $\gamma < \frac{2\beta+\alpha(A-1)}{A\beta(\alpha-\beta)}$ and the conditions in (3.31) are satisfied, then we have*

(I) *$E(1,1)$ is a stable hyperbolic focus or node if $0<\alpha<\alpha_*$, and an unstable hyperbolic focus or node if $\alpha>\alpha_*$;*
(II) *$E(1,1)$ is a weak focus or center if $\alpha=\alpha_*$.*

Proof. Since $0<\beta<\alpha$, from $\mathrm{Det}(J(1,1)) = \frac{(A+1)(\beta(2+A\beta\gamma)-\alpha(1+A\beta\gamma-A))}{\beta} > 0$, we have $\gamma < \frac{2\beta+\alpha(A-1)}{A\beta(\alpha-\beta)}$. From $\mathrm{Tr}(J(1,1)) = \alpha-(A+2)\beta-\frac{A+1}{\beta}=0$, we have $\alpha=\alpha_*$. The results follow. □

We next consider Case **(II)** in Lemma 3.6 and explore the exact multiplicity of the weak focus $E(1,1)$ when $\alpha=\alpha_*$. Firstly we check the transversality condition

$$\frac{d}{d\alpha}(\mathrm{Tr}(J(1,1)))|_{\alpha=\alpha_*} = 1 > 0.$$

We investigate the nondegenerate condition and stability of the bifurcating periodic orbit from the positive equilibrium $E(1,1)$ of system (3.32) by calculating the first Liapunov coefficient. When $\alpha=\alpha_*$, using the formula of the first Liapunov number σ in Perko [19], we have

$$\sigma_1 = \frac{(1+A)(1+\beta^2)Q}{8A(1-\beta\gamma)(A(1-\beta\gamma)(1+\beta^2)-1)},$$

where

$$Q = \gamma\{A(1+\beta^2+2A\beta^2+2\beta^4+2A\beta^4)\} - \{2(A^2\beta^3+A^2\beta+A\beta^3-\beta^3)\}.$$

From $\alpha=\alpha_*$ and $\mathrm{Det}(J(1,1))>0$, we have

$$\gamma < \frac{A(1+\beta^2)-1}{A\beta(1+\beta^2)},$$

i.e., $A(1-\beta\gamma)(1+\beta^2)-1>0$. Moreover, from $0<\beta\gamma<1$, we have $8A(1-\beta\gamma)(A(1-\beta\gamma)(1+\beta^2)-1)>0$. Thus, the sign of σ_1 is the same as Q. From $Q=0$, i.e., $\sigma_1=0$, we have

$$\gamma=\gamma_*=\frac{2(A^2\beta^3+A^2\beta+A\beta^3-\beta^3)}{A(1+\beta^2+2A\beta^2+2\beta^4+2A\beta^4)},$$

where

$$A^2\beta^3+A^2\beta+A\beta^3-\beta^3>0,\ \ \gamma_*<\min\{\tfrac{A(1+\beta^2)-1}{A\beta(1+\beta^2)},\tfrac{1}{\beta}\}. \tag{3.33}$$

Theorem 3.7. *When $\alpha=\alpha_*$, $\gamma<\frac{A(1+\beta^2)-1}{A\beta(1+\beta^2)}$, and the conditions in (3.31) are satisfied, the following statements hold.*

(I) *If $\gamma>\gamma_*$, then $E(1,1)$ is an unstable weak focus with multiplicity one, and system (3.32) exhibits a subcritical Hopf bifurcation;*
(II) *If $\gamma<\gamma_*$, then $E(1,1)$ is a stable weak focus with multiplicity one, and system (3.32) exhibits a supercritical Hopf bifurcation;*
(III) *If $\gamma=\gamma_*$, then $E(1,1)$ is a weak focus with multiplicity at least two, and system (3.32) exhibits a degenerate Hopf bifurcation.*

Next, using the formal series method in Zhang et al. [27] and MATLAB software, when $\alpha=\alpha_*$ and $\gamma=\gamma_*$, we obtain the second Liapunov coefficient as follows

$$\sigma_2=-\frac{\beta(1+A)^4(1+\beta^2)Q_1Q_2}{12(A+A\beta^2+2\beta^4)^2\tilde{D}^{\frac{3}{2}}},$$

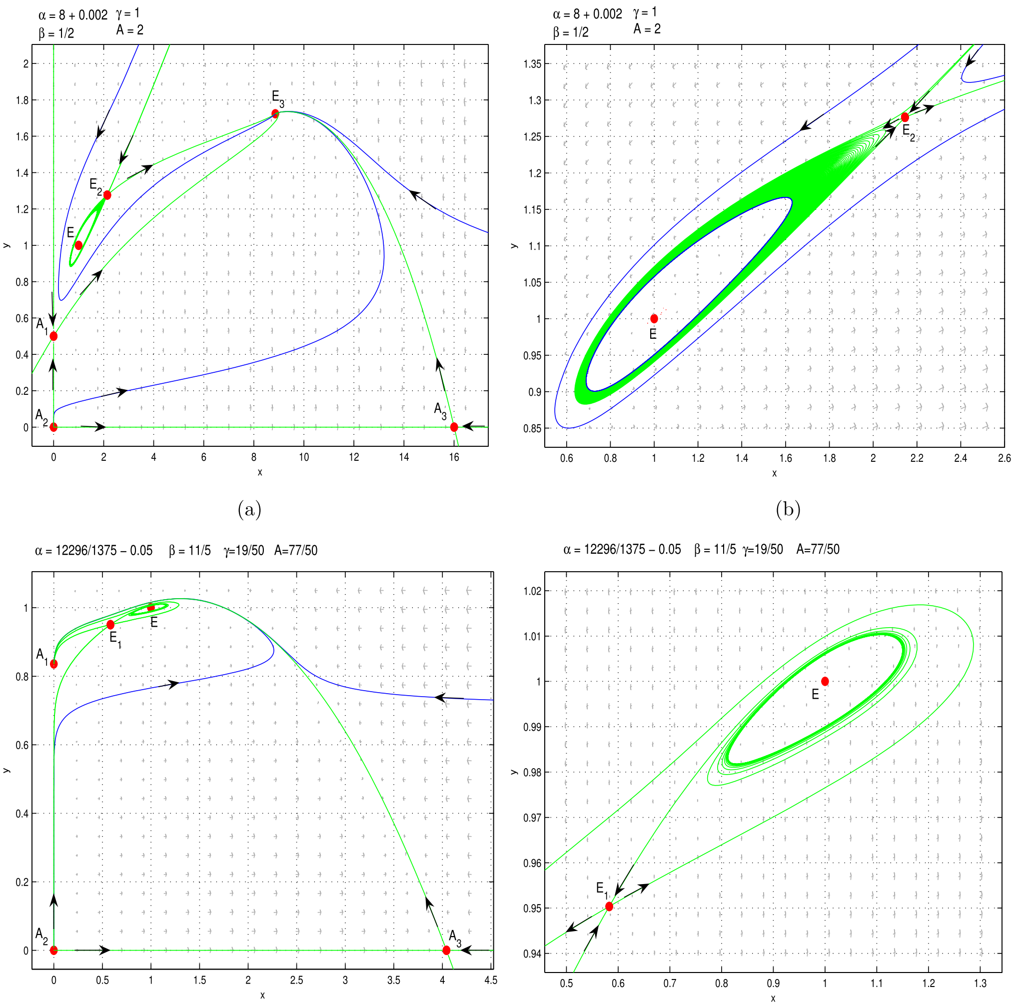
where

$$\tilde{D}=\mathrm{Det}(J(1,1))>0,\ \ Q_1=1+(1+2A)\beta^2+2(1+A)\beta^4,$$
$$Q_2=1+3\beta^4+6\beta^6+2A^2(1+\beta^2)^2+2A(1+\beta^2)^2(1+\beta^2).$$

Since $A>0$ and $\beta>0$, we have $Q_1>0$, $Q_2>0$, i.e., $\sigma_2<0$ when $\alpha=\alpha_*$, $\gamma=\gamma_*$ and the conditions in (3.31) and (3.33) are satisfied.

Theorem 3.8. *If $\alpha=\alpha_*$, $\gamma=\gamma_*$, and the conditions in (3.31) and (3.33) are satisfied, then the equilibrium $E(1,1)$ of system (3.32) (i.e., the equilibrium $E_1(x_1,y_1)$ or $E_3(x_3,y_3)$ of system (1.2)) is a stable weak focus with multiplicity exactly two. System (3.32) (or system (1.2)) can undergo a degenerate Hopf bifurcation of codimension two around $E(1,1)$ (or $E_1(x_1,y_1)$ or $E_3(x_3,y_3)$). Thus, system (3.32) (or system (1.2)) exhibits the coexistence of two limit cycles (the inner one unstable and the outer stable) for some parameters.*

Finally, we present some numerical simulations to show the existence of limit cycles. In Fig. 3.3(a), we show the existence of one stable limit cycle arising from a supercritical Hopf bifurcation around the equilibrium $E(1,1)$ of system (3.32), Fig. 3.3(b) is the local amplified



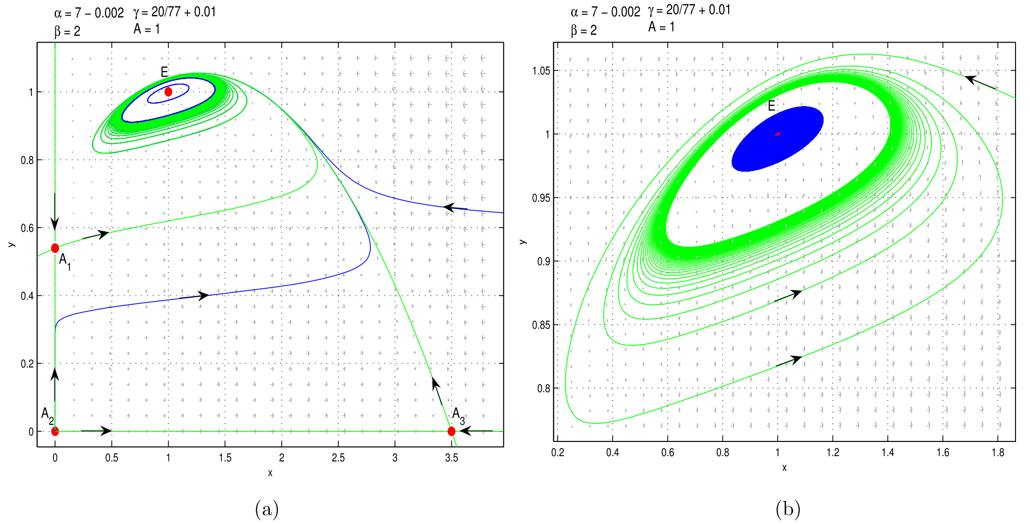
(a) (b)

(c) (d)

Fig. 3.3. (a) A stable limit cycle created by the supercritical Hopf bifurcation of system (3.32) with $\alpha = 8.002$, $\beta = \frac{1}{2}$, $\gamma = 1$ and $A = 2$; (b) Amplified phase portrait of (a) showing the existence of a stable limit cycle; (c) An unstable limit cycle created by the subcritical Hopf bifurcation of the system (3.32) with $\frac{12296}{1375} - 0.05$, $\beta = \frac{11}{5}$, $\gamma = \frac{19}{50}$ and $A = \frac{77}{50}$; (d) Amplified phase portrait of (c) showing the existence of an unstable limit cycle.

phase portrait of Fig. 3.3(a); In Fig. 3.3(c), we show the existence of one unstable limit cycle arising from a subcritical Hopf bifurcation around the equilibrium $E(1, 1)$ of system (3.32), Fig. 3.3(d) is the local amplified phase portrait of Fig. 3.3(c).

Next we give some numerical simulations in Fig. 3.4(a) to show the existence of two limit cycles based on Theorems 3.7 and 3.8, Fig. 3.4(b) is the local amplified phase portrait of Fig. 3.4(a). Firstly, we fix $A = 1$ and $\beta = 2$, then get $\alpha = 7$ and $\gamma = \frac{20}{77}$ from $\alpha = \alpha_*$ and $\gamma = \gamma_*$, respectively, i.e., $E(1, 1)$ is a stable weak focus with multiplicity two for those fixed parameters. Next we first perturb γ such that γ increases to $\frac{20}{77} + 0.01$, then $E(1, 1)$ becomes an unstable weak focus with multiplicity one, a stable limit cycle occurs around $E(1, 1)$ which is the outer limit



(a) (b)

Fig. 3.4. (a) The existence of two limit cycles (the inner one unstable and the outer stable) enclosing a stable hyperbolic focus $E(1,1)$ in system (3.32) with $\alpha = 7$, $\beta = 2$, $\gamma = \frac{20}{77} + 0.01$ and $\alpha = 7 - 0.002$; (b) The local amplified phase portrait of (a).

cycle in Fig. 3.4. Secondly, we perturb α such that α decreases to $7 - 0.002$, then $E(1,1)$ becomes a stable hyperbolic focus, another unstable limit cycle occurs around $E(1,1)$, which is the inner limit cycle in Fig. 3.4.

Remark 3.9. From Fig. 3.3(a) and Fig. 3.4, where $K_2 < \frac{r_1}{\xi}$, we can see that the boundary equilibria are all unstable, and there exist multiple positive equilibria or multiple limit cycles, i.e., the invading hosts and generalist parasitoids can always tend to coexistent steady states or coexistent periodic orbits, if the carrying capacity for the generalist parasitoids is smaller than a critical value $\frac{r_1}{\xi}$. From Fig. 3.3(c) and (d), when $K_2 \geq \frac{r_1}{\xi}$, we can see that the boundary equilibrium A_1 is a stable hyperbolic node, and there exist multiple positive equilibria and an unstable limit cycle, i.e., the invading hosts will die out for almost all positive initial populations outside the unstable periodic orbit, tend to periodic outbreaks for almost all positive initial populations on the unstable periodic orbit, and persist in the form of a positive steady state when the positive initial populations lie inside the unstable periodic orbit, if the carrying capacity for the generalist parasitoids is larger than a critical value $\frac{r_1}{\xi}$.

4. Conclusions

In this paper, we rivisited a host-generalist parasitoid model with Holling II functional response, which was proposed by Magal et al. [17]. After performing a complete qualitative and bifurcation analysis depending on all four parameters, our results revealed that model (1.2) exhibits complex dynamics and bifurcations, such as the existence of cusp, focus and elliptic types degenerate Bogdanov-Takens bifurcations of codimension three, Hopf bifurcation, and degenerate Hopf bifurcation of codimension at most two. Thus, there exist various parameter values such that model (1.2) exhibits one or two limit cycles enclosing only one positive equilibrium, or the coexistence of a limit cycle and a homoclinic loop, or a big limit cycle enclosing three hyperbolic positive equilibria, or two big limit cycles enclosing three hyperbolic positive equilibria, or a big limit cycle enclosing three hyperbolic positive equilibria and a small limit cycle, etc. We also presented numerical examples which have one and two limit cycles, and the coexistence of an unstable limit cycle and a stable homoclinic loop, respectively.

Complex bifurcation phenomena have been found in some models arising in applications, such as Bogdanov-Takens bifurcation of codimension two in Ruan and Xiao [20], cusp type degenerate Bogdanov-Takens bifurcation of codimension three in Zhu et al. [26] (see also Li et al. [15], Huang et al. [12], [14]), focus type degenerate Bogdanov-Takens bifurcation of codimension three in Xiao and Zhang [25] (see also Huang et al. [13]), saddle type degenerate Bogdanov-Takens bifurcation of codimension three in Etoua and Rousseau [6], elliptic type degenerate Bogdanov-Takens bifurcation of codimension three in Cai et al. [1]. Moreover, Shan et al. [23] observed the existence of nilpotent cusp, focus and elliptic singularities of codimension three in a SIR type of compartmental model with hospital resources. In this paper, we have established the existence of cusp, focus and elliptic types degenerate Bogdanov-Takens bifurcations of codimension three in model (1.2). To the best of our knowledge, we believe that this is the first time the existence of three topological types Bogdanov-Takens bifurcations of codimension three in a single model is rigorously proved.

We also found that there exists a critical value for the carrying capacity of the generalist parasitoids such that: (i) when the carrying capacity for the generalist parasitoids is smaller than the critical value, the invading hosts can always persist in spite of the predation of hosts by the generalist parasitoids, i.e., the generalist parasitoids cannot control the invasion of hosts; (ii) when the carrying capacity for the generalist parasitoids is larger than the critical value, the invading hosts can tend to extinction, or persist in the form of multiple coexistent steady states or multiple coexistent periodic orbits depending on the initial populations, i.e., whether the invading hosts can be stopped and reversed by the generalist parasitoids depends on the initial populations; (iii) in both cases, the generalist parasitoids always persist. These results may be useful for the control of invading species by introducing generalist predators.

The ODE model (1.1) and its PDE version

$$
\begin{aligned}
u_t &= Du_{xx} + r_1 u(1 - \tfrac{u}{K_1}) - \tfrac{\xi uv}{1+\xi hu}, \\
v_t &= Dv_{xx} + r_2 v(1 - \tfrac{v}{K_2}) + \tfrac{\gamma \xi uv}{1+\xi hu}
\end{aligned}
\tag{4.1}
$$

(under certain boundary conditions) were proposed in Magal et al. [17] to study the invasion problem of lepidopteron, *Cameraria orhidella* (Lep. Gracillariidae), in the east of Europe since 1985 and in France since 1998. This moth attacks horse chestnut trees by mining their leaves and infested chestnut trees turn completely yellow early summer and lose almost all leaves. There are three generations of *C. ohridella* per year from May to October and the spatial spread is estimated to be about 60 km per year (Sefrova and Lastuvka [21]). Moths disperse a few hundred meters per generation (Gilbertet al. [9]). In order to control the invasion of the leafminer, several parasitoids were introduced to attack the leafminer. The most common parasitoid is *Minotetrastichus frontalis* (Hym. Eulophidae). Parasitism rate varies from 0 to 33.4%, with an average low of 6.5% (Grabenweger et al. [10]). In this paper we have provided detailed bifurcation analysis of the ODE host-parasitoid model (1.1). Though some numerical simulations were carried out for the PDE model (4.1) in Magal et al. [17], detailed mathematical analysis on the spatial dynamics such as the existence of traveling waves of the PDE model (4.1) has not been done, which deserves further investigation.

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Appendix A. Coefficients in the proof of Theorem 2.8

In this appendix, we list the expressions of some coefficients that were used in the proof of Theorem 2.8.

$$\tilde{a_{20}} = 0,\ \tilde{a_{11}} = \frac{27(8a-1)b^2}{2(1+a)^2(2+2a^2-3b+a(4+6b))},$$

$$\tilde{a_{02}} = \frac{27(2a-1)(1+a^2+a(2-9b))b^2}{2(1+a)^4(2+2a^2-3b+a(4+6b))},$$

$$\tilde{a_{30}} = \frac{243(1+4a)b^3}{(1+a)^2(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{a_{21}} = -\frac{243b^3(1+4a)(1+a^2-6b+2a(1+6b))}{(1+a)^4(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{a_{12}} = \frac{729b^4(8a^2-2a-1)(4+4a^2-15b+a(8+30b))}{4(1+a)^6(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{a_{03}} = -\frac{2187b^5(1-2a)^2(1+4a)(1+a^2-3b+a(2+6b))}{4(1+a)^8(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{a_{40}} = -\frac{2187b^4(1+4a)}{(1+a)^4(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{a_{31}} = \frac{2187b^4(1+4a)(2+2a^2-15b+a(4+30a))}{2(1+a)^6(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{a_{22}} = -\frac{19683b^5(8a^2-2a-1)(2+2a^2-9b+2a(2+9b)))}{4(1+a)^8(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{a_{13}} = \frac{59049b^6(1-2a)^2(1+4a)(2+2a^2-7b+2a(2+7b))}{8(1+a)^{10}(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{a_{04}} = -\frac{59049b^7(2a-1)^3(1+4a)(1+a^2-3b+a(2+6b))}{8(1+a)^{12}(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{b_{20}} = \frac{18b}{2+4a+2a^2-3b+6ab},\ \tilde{b_{11}} = \frac{9b(1+a^2+a(2-2ab)+6b)}{(1+a)^2(2+2a^2-3b+a(4+6b))},$$

$$\tilde{b_{02}} = \frac{9b(2+8a^3+2a^4+9b^2+a(8-63b^2)+6a^2(2+15b^2))}{2(1+a)^4(2+2a^2-3b+a(4+6b))},$$

$$\tilde{b_{30}} = -\frac{162b^2(1+a^2+a(2+9b))}{(1+a)^2(2+2a^2-3b+a(4+6b))^2},\ \tilde{b_{40}} = \frac{1458b^3(1+a^2+a(2+9b))}{(1+a)^4(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{b_{21}} = \frac{162b^2(1+a^4-6b+a^3(4+21b)+a(4+9b-54b^2)+6a^2(1+6b+18b^2))}{(1+a)^4(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{b_{12}} = -\frac{243b^3(2a-1)(4+4a^4-15b+2a^3(8+33b)+a(16+36b-135b^2)+3a^2(8+39b+90b^2))}{2(1+a)^6(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{b_{03}} = \frac{729b^4(1-2a)^2(1+a^4-3b+a^3(4+15b)+a(4+9b-27b^2)+3a^2(2+9b+18b^2))}{2(1+a)^8(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{b_{31}} = -\frac{729b^3(2+2a^4-15b+8a^3(1+6b)+a(8+18b-135b^2)+3a^2(4+27b+90b^2))}{(1+a)^6(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{b_{22}} = \frac{6561b^4(2a-1)(2+2a^4-9b+4a^3(2+9b)+a(8+18b-81b^2)+3a^2(4+21b+54b^2))}{2(1+a)^8(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{b_{13}} = -\frac{19683b^5(1-2a)^2(2+2a^4-7b+8a^3(1+4b)+a(8+18b-63b^2)+3a^2(4+19b+42b^2))}{4(1+a)^{10}(2+2a^2-3b+a(4+6b))^2},$$

$$\tilde{b_{04}} = \frac{19683b^6(2a-1)^3(1+a^4-3b+a^3(4+15b)+a(4+9b-27b^2)+3a^2(2+9b+18b^2))}{4(1+a)^{12}(2+2a^2-3b+a(4+6b))^2}.$$

$$\tilde{c_{30}} = \frac{6-48a}{(1-2a)^2},\quad \tilde{c_{21}} = \frac{81(8a-1)}{2(1-2a)^3},\quad \tilde{c_{12}} = \frac{108(8a-1)}{(1-2a)^4},\quad \tilde{c_{03}} = -\frac{324}{(1-2a)^4},$$

$$\tilde{c_{40}} = \frac{9(272a^2-104a+11)}{2(1-2a)^4},\quad \tilde{c_{31}} = \frac{27(424a^2-142a+19)}{2(1-2a)^5},\quad \tilde{c_{22}} = -\frac{486(4a^2-10a+1)}{(1-2a)^6},$$

$$\tilde{c_{13}} = \frac{11664a}{(1-2a)^6},\quad \tilde{c_{04}} = \frac{5832}{(1-2a)^6},\quad \tilde{d_{11}} = \frac{16a-5}{1-2a},\quad \tilde{d_{30}} = -4,\quad \tilde{d_{21}} = \frac{3(32a^2+28a-13)}{2(1-2a)^3},$$

$$\tilde{d_{12}} = \frac{72(31a^2-13a+1)}{(1-2a)^4},\quad \tilde{d_{03}} = -\frac{108}{(1-2a)^3},\quad \tilde{d_{40}} = -\frac{12(44a^2-17a+2)}{(1-2a)^3},$$

$$\tilde{d_{04}} = -\frac{11664a}{(1-2a)^6},\quad \tilde{d_{31}} = \frac{-4464a^2+576a+18}{(1-2a)^4},\quad \tilde{d_{22}} = \frac{81(104a^3-30a^2-45a+8)}{(1-2a)^6},$$

$$\tilde{d_{13}} = -\frac{324(208a^2-64a+7)}{(1-2a)^6}.$$

Appendix B. Coefficients in the proof of Theorem 3.3

Here we provide the expressions of some coefficients that were used in the proof of Theorem 3.3.

$$a_{00} = \frac{(1-\omega^2)(7+\omega^2)\lambda_1}{4((1-\omega)(7+\omega^2)+16\lambda_1)},\quad a_{01} = -\frac{(1-\omega)^2(7+\omega^2)^2}{8(1+\omega)((1-\omega)(7+\omega^2)+16\lambda_1)},$$

$$a_{10} = \frac{(1-\omega^2)^2(7+\omega^2)^2+16(1-\omega)(7+\omega^2)(5+3\omega^2)\lambda_1+512(3+\omega^2)\lambda_1^2}{8((1-\omega)(7+\omega^2)+16\lambda_1)^2},$$

$$a_{20} = -\frac{4096\lambda_1^3+768m_3\lambda_1^2+16m_2\lambda_1-m_1}{((1-\omega)(7+\omega^2)+16\lambda_1)^3},$$

$$a_{11} = -\frac{(1-\omega)(7+\omega^2)^2((1-\omega)(\omega^2-2\omega+5)+16\lambda_1)}{(1+\omega)^2((1-\omega)(7+\omega^2)+16\lambda_1)^2},$$

$$a_{30} = -\frac{32(1-\omega)(7+\omega^2)^2((1-\omega)(\omega^2-2\omega+5)+16\lambda_1)}{((1-\omega)(7+\omega^2)+16\lambda_1)^4},$$

$$a_{21} = \frac{16(1-\omega)(7+\omega^2)^2((1-\omega)(\omega^2-2\omega+5)+16\lambda_1)}{(1+\omega)^2((1-\omega)(7+\omega^2)+16\lambda_1)^3},$$

$$a_{40} = \frac{512(1-\omega)(7+\omega^2)^2((1-\omega)(\omega^2-2\omega+5)+16\lambda_1)}{((1-\omega)(7+\omega^2)+16\lambda_1)^5},$$

$$a_{31} = -\frac{256(1-\omega)(7+\omega^2)^2((1-\omega)(\omega^2-2\omega+5)+16\lambda_1)}{(1+\omega)^2((1-\omega)(7+\omega^2)+16\lambda_1)^4},$$

$$b_{00} = \frac{(1+\omega)^2\big(2((1+\omega)^4-8(\omega^2-2\omega+5)\lambda_2)\lambda_1-(1-\omega)(5-2\omega+\omega^2)((7+\omega^2)\lambda_2+2(1+\omega)\lambda_3)\big)}{8(\omega^2-2\omega+5)((\omega-1)(7+\omega^2)-16\lambda_1)},$$

$$b_{10} = -\frac{(1+\omega)^2\big(\omega^3-3\omega^2+7\omega-5-16\lambda_1\big)\big((1+\omega)^3(7+\omega^2)+16(\omega^2-2\omega+5)\lambda_3\big)}{8(\omega^2-2\omega+5)(\omega^3-\omega^2+7\omega-7-16\lambda_1)^2},$$

$$b_{01} = \frac{1}{8}\Big(\frac{(\omega^2-1)((1+\omega)^3(7+\omega^2)+16(\omega^2-2\omega+5)\lambda_3)}{(\omega^2-2\omega+5)(\omega^3-\omega^2+7\omega-7-16\lambda_1)}+\frac{4(1-\omega)(1+\omega)^2}{\omega^2-2\omega+5}$$
$$-2(1+\omega)^2+8\lambda_2\Big),$$

$$b_{20} = -\frac{2(1+\omega)^2((1-\omega)(5-2\omega+\omega^2)+16\lambda_1)((1+\omega)^3(7+\omega^2)+16(\omega^2-2\omega+5)\lambda_3)}{(\omega^2-2\omega+5)((1-\omega)(7+\omega^2)+16\lambda_1)^3},$$

$$b_{11} = \frac{((1-\omega)(5-2\omega+\omega^2)+16\lambda_1)((1+\omega)^3(7+\omega^2)+16(\omega^2-2\omega+5)\lambda_3)}{(\omega^2-2\omega+5)((1-\omega)(7+\omega^2)+16\lambda_1)^2}, b_{02} = -1,$$

$$b_{30} = \frac{32(1+\omega)^2((1-\omega)(5-2\omega+\omega^2)+16\lambda_1)((1+\omega)^3(7+\omega^2)+16(\omega^2-2\omega+5)\lambda_3)}{(\omega^2-2\omega+5)((1-\omega)(7+\omega^2)+16\lambda_1)^4},$$

$$b_{21} = -\frac{16(((1-\omega)(5-2\omega+\omega^2)+16\lambda_1)((1+\omega)^3(7+\omega^2)+16(\omega^2-2\omega+5)\lambda_3)}{(\omega^2-2\omega+5)((1-\omega)(7+\omega^2)+16\lambda_1)^3},$$

$$b_{40} = -\frac{512((1+\omega)^2((1-\omega)(5-2\omega+\omega^2)+16\lambda_1)((1+\omega)^3(7+\omega^2)+16(\omega^2-2\omega+5)\lambda_3)}{(\omega^2-2\omega+5)((1-\omega)(7+\omega^2)+16\lambda_1)^5},$$

$$b_{31} = \frac{256((1-\omega)(5-2\omega+\omega^2)+16\lambda_1)((1+\omega)^3(7+\omega^2)+16(\omega^2-2\omega+5)\lambda_3)}{(\omega^2-2\omega+5)((1-\omega)(7+\omega^2)+16\lambda_1)^4},$$

$$m_1 = (1+\omega)(3+\omega^2)(1-\omega)^2(7+\omega^2)^2, \;\; m_2 = (1-\omega)(1-3\omega)(7+\omega^2)^2,$$

$$m_3 = (1-\omega)(7+\omega^2).$$

$$c_{00} = \frac{a_{01}^2 b_{00} - a_{00}a_{01}b_{01} + a_{00}^2 b_{02}}{a_{01}}, \; c_{01} = \frac{a_{01}a_{10} - a_{00}a_{11} + a_{01}b_{01} - 2a_{00}b_{02}}{a_{01}},$$

$$c_{10} = \frac{a_{01}^2 a_{11} b_{00} - a_{01}^2 a_{10} b_{01} + 2a_{00}a_{10}b_{02} - a_{00}^2 a_{11} b_{02} + a_{01}^3 b_{10} - a_{00}a_{01}^2 b_{11}}{a_{01}^2},$$

$$c_{20} = a_{21}b_{00} - a_{20}b_{01} + a_{11}b_{10} + a_{01}b_{20} - a_{10}b_{11} - a_{00}b_{21} + \frac{m_4}{a_{01}^3},$$

$$c_{11}=\frac{a_{00}a_{11}^2-a_{01}a_{10}a_{11}+2a_{01}^2a_{20}-2a_{00}a_{01}a_{21}-2a_{01}a_{10}b_{02}+2a_{00}a_{11}b_{02}+a_{01}^2b_{11}}{a_{01}^2},$$

$$c_{02}=\frac{a_{11}+b_{02}}{a_{01}},\ c_{12}=\frac{2a_{01}a_{21}-a_{11}b_{02}-a_{11}^2}{a_{01}^2},\ c_{31}=\frac{m_5+m_6+m_7}{a_{01}^4},$$

$$c_{30}=a_{31}b_{00}-a_{30}b_{01}+a_{21}b_{10}-a_{20}b_{11}+a_{11}b_{20}-a_{10}b_{21}+a_{01}b_{30}-a_{00}b_{31}+\frac{m_8}{a_{01}^4},$$

$$\begin{aligned}c_{21}=&\,3a_{30}+b_{21}\\&+\frac{a_{01}a_{10}a_{11}^2-a_{00}a_{11}^3-a_{01}^2a_{11}a_{20}-2a_{01}^2a_{10}a_{21}+3a_{00}a_{01}a_{11}a_{21}-3a_{00}a_{01}^2a_{31}+m_9}{a_{01}^3},\end{aligned}$$

$$\begin{aligned}c_{40}=&\,a_{31}b_{10}-a_{30}b_{11}+a_{21}b_{20}-a_{20}b_{21}+a_{11}b_{30}-a_{10}b_{31}+a_{01}b_{40}-a_{40}b_{01}\\&+\frac{m_{10}+m_{11}+m_{12}}{a_{01}^4},\end{aligned}$$

$$c_{22}=\frac{a_{11}^3-3a_{01}a_{11}a_{21}+3a_{01}^2a_{31}+a_{11}^2b_{02}-a_{01}a_{21}b_{02}}{a_{01}^3},$$

$$m_4=a_{01}^2a_{10}^2b_{02}-2a_{00}a_{01}a_{10}a_{11}b_{02}+a_{00}^2a_{11}^2b_{02}+2a_{00}a_{01}^2a_{20}b_{02}-a_{00}^2a_{01}a_{21}b_{02},$$

$$m_5=-a_{01}a_{10}a_{11}^3-a_{00}a_{11}^4+a_{01}^2a_{11}^2a_{20}+3a_{01}^2a_{10}a_{11}a_{21}+4a_{00}a_{01}a_{11}^2a_{21}-2a_{01}^3a_{20}a_{21},$$

$$m_6=-2a_{00}a_{01}^2a_{21}^2-a_{01}^3a_{11}a_{30}-3a_{01}^3a_{10}a_{31}-4a_{00}a_{01}^2a_{11}a_{31}+4a_{01}^4a_{40},$$

$$m_7=-2a_{01}a_{10}a_{11}^2b_{02}+2a_{01}^2a_{11}a_{20}b_{02}+2a_{01}^2a_{10}a_{21}b_{02}-2a_{01}^3a_{30}b_{02}+a_{01}^4b_{31}.$$

$$\begin{aligned}m_8=&\,a_{00}^2a_{11}^4-4a_{00}^2a_{01}a_{11}^2a_{21}+2a_{00}^2a_{01}^2a_{21}^2+4a_{00}^2a_{01}^2a_{11}a_{31}-a_{01}^2a_{10}^2a_{11}b_{02}\\&+2a_{00}a_{01}a_{10}a_{11}^2b_{02}+2a_{01}^3a_{10}a_{20}b_{02}-2a_{00}a_{01}^2a_{11}a_{20}b_{02}-2a_{00}a_{01}^2a_{10}a_{21}b_{02}\\&+2a_{00}a_{01}^3a_{30}b_{02},\end{aligned}$$

$$m_9=2a_{01}a_{10}a_{11}b_{02}-2a_{00}a_{11}^2b_{02}-2a_{01}^2a_{20}b_{02}+2a_{00}a_{01}a_{21}b_{02},$$

$$\begin{aligned}m_{10}=&\,a_{00}a_{10}a_{11}^4-a_{00}a_{01}a_{11}^3a_{20}-4a_{00}a_{01}a_{11}^2a_{21}+3a_{00}a_{01}^2a_{11}a_{20}a_{21}+2a_{00}a_{01}^2a_{10}a_{21}^2\\&+a_{00}a_{01}^2a_{11}^2a_{30},\end{aligned}$$

$$m_{11}=-2a_{00}a_{01}^3a_{21}a_{30}+4a_{00}a_{01}^2a_{10}a_{11}a_{31}-3a_{00}a_{01}^3a_{20}a_{31}-a_{00}a_{01}^3a_{11}a_{40}+a_{01}a_{10}^2a_{11}^2b_{02},$$

$$m_{12}=-2a_{01}^2a_{10}a_{11}a_{20}b_{02}+a_{01}^3a_{20}^2b_{02}-a_{01}^2a_{10}^2a_{21}b_{02}+2a_{01}^3a_{10}a_{30}b_{02}.$$

$$d_{00}=c_{00},d_{10}=c_{10}-c_{00}c_{02},d_{01}=c_{01},d_{20}=c_{20}+c_{00}c_{02}^2-\frac{c_{10}c_{02}^2}{2},$$

$$d_{11}=c_{11},d_{30}=c_{30}-c_{00}c_{02}^3+\frac{c_{10}c_{02}^2}{2},\ d_{21}=c_{21}+\frac{c_{11}c_{02}}{2},\ d_{12}=c_{12}+2c_{02}^2,$$

$$d_{31}=c_{31}+c_{02}c_{21},$$

$$d_{40}=\frac{4c_{00}c_{02}^4-2c_{10}c_{02}^3+c_{20}c_{02}^2+2c_{02}c_{30}+4c_{40}}{4},\ d_{22}=c_{22}+\frac{3c_{02}c_{12}}{2}-c_{02}^3.$$

$$e_{00}=d_{00},\ \ e_{10}=d_{10},e_{01}=d_{01},\ \ e_{20}=d_{20}-\frac{d_{00}d_{12}}{2},\ \ e_{11}=d_{11},\ \ e_{30}=d_{30}-\frac{d_{10}d_{12}}{3},$$

$$e_{21}=d_{21},\ \ e_{40}=d_{40}+\frac{d_{00}d_{12}^2}{4}-\frac{d_{12}d_{20}}{6},\ \ e_{31}=d_{31}+\frac{d_{11}d_{12}}{6}.$$

$$f_{00}=e_{00},\ \ f_{10}=e_{10}-\frac{e_{00}e_{30}}{2e_{20}},\ \ f_{01}=e_{01},$$

$$f_{20}=1+\frac{45e_{00}e_{30}^2-60e_{10}e_{20}e_{30}-48e_{00}e_{20}e_{40}}{80e_{20}^2},$$

$$f_{11}=e_{11}-\frac{e_{01}e_{30}}{2e_{20}},\ \ f_{30}=\frac{e_{10}(35e_{30}^2-32e_{20}e_{40})}{40e_{20}^2},$$

$$f_{21}=e_{21}-\frac{60e_{11}e_{20}e_{30}-45e_{01}e_{30}^2+48e_{01}e_{20}e_{40}}{80e_{20}^2},$$

$$f_{40}=\frac{100e_{10}e_{20}e_{30}(16e_{20}e_{40}-15e_{30}^2)+e_{00}(2304e_{20}^2e_{40}^2-275e_{30}^4-1440e_{20}e_{30}^2e_{40})}{6400e_{20}^4},$$

$$f_{31}=e_{31}+\frac{7e_{11}e_{30}^2}{8e_{20}^2}-\frac{5e_{30}e_{21}+4e_{11}e_{40}}{5e_{20}}.$$

$$q_1=\frac{8\sqrt[5]{16(1-\omega)^3}(3+\omega^2)}{(\omega^2-2\omega+5)\sqrt[5]{\omega^{11}(1+\omega)^6(7+\omega^2)}},\ q_2=-\frac{2\sqrt[5]{16(1-\omega)^8(7+\omega^2)^4}}{\sqrt[5]{\omega^{11}(1+\omega)^{16}}},$$

$$q_3=-\frac{4\sqrt[5]{16(1-\omega)^8}}{\sqrt[5]{\omega^{11}(1+\omega)^{11}(7+\omega^2)}},\ q_4=\frac{8\sqrt[5]{2(1-\omega)^2)(\omega^4-3\omega^3+9\omega^2-9\omega+42)}}{\sqrt[5]{\omega^9(1+\omega)^9(7+\omega^2)^4}(\omega^2-2\omega+5)},$$

$$q_5=-\frac{4\sqrt[5]{2(1-\omega)^2(7+\omega^2)}(3\omega^2-6\omega+7)}{\sqrt[5]{\omega^9(1+\omega)^{19}}},\ q_6=-\frac{8\sqrt[5]{2(1-\omega)^2}(3\omega^2-6\omega+7)}{\sqrt[5]{\omega^9(1+\omega)^{14}(7+\omega^2)^4}},$$

$$q_7=\frac{2\sqrt[5]{16}(5\omega^6-\omega^5+52\omega^4-98\omega^3+109\omega^2-205\omega+42)}{\sqrt[5]{\omega^{11}(1-\omega)^2(1+\omega)^{11}(7+\omega^2)^6}(\omega^2-2\omega+5)},$$

$$q_8=\frac{\sqrt[5]{16}(3\omega^2-6\omega+7)(2\omega^3-\omega^2+4\omega-1)}{\sqrt[5]{\omega^{11}(1-\omega)^2(1+\omega)^{21}(7+\omega^2)}},\ q_9=\frac{2\sqrt[5]{16}(3\omega^2-6\omega-1)(3\omega^2-6\omega+7)}{\sqrt[5]{\omega^{11}(1-\omega)^2(1+\omega)^{16}(7+\omega^2)^6}}.$$

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