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Generalized Beddington model with the host subject to the Allee Effect

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Abstract: We investigate the stability and invariant manifolds of generalized Beddington model with the host population subject to the Allee effect. We obtain the condition for the existence of the fixed points and investigate the stability of the system.

Keywords: host-parasitoid; predator-prey; beddington model; allee effect; discrete dynamical systems

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1 Introduction

Parasitoids have long been popular subjects for ecological study since they are important for biological pest control, which has stimulated much empirical and theoretical works on the attributes that make parasitoids effective pest control agents.

The host-parasitoid models can have simple structures when compared with the corresponding predator-prey models. Simple predator-prey and host-parasite models show unstable dynamics, causing extinction [10]. These findings prompted a search for mechanisms that prevent or promote coexistence. For instance, works in the literature have shown that spatio-temporal environmental heterogeneity, density-dependence, interference among parasitoids, spatial aggregation of predators in areas of high prey density, dispersal, and genetic variation may promote coexistence. Using the Nicholson-Bailey model as a starting point, theories have been sought for mechanisms that stabilize its dynamics; the rationale is that stability should ensure the persistence of the host and par-

asitoid. Many species of parasitoids and their hosts can readily be cultured in laboratory microcosms, and this has greatly increased the amount of empirical information on host-parasitoid interactions under controlled conditions [2].

Many stabilizing mechanisms have been identified, including mutual interference among parasitoid aggregations and patchy environments [9], several types of parasitoid aggregation, density-dependent parasitoid sex ratios [2–5], competition among parasitoid larvae, and Allee effects [7].

The general host-parasitoid model has the form:

$$\begin{aligned} N_{t+1} &= rN_t \exp(-aP_t), \\ P_{t+1} &= eN_t(1 - \exp(-aP_t)). \end{aligned} \quad (1)$$

Kapcak et. al. [8] studied a generalization of (1) which is given by [6] as an open problem.

S.R.-J. Jang and S.L. Diamond [7] investigated the following Beddington model 1 with the host subject to an Allee effect:

$$\begin{aligned} N_{t+1} &= N_t \exp \left[r \left(1 - \frac{N_t}{K} \right) - aP_t \right] \frac{N_t}{A + N_t}, \\ P_{t+1} &= eN_t[1 - \exp(-aP_t)], \end{aligned} \quad (2)$$

where the parameters r , K , a , A , and e are positive.

In this paper we analyze the following discrete-time model which is the generalization of the model (2):

$$\begin{aligned} N_{t+1} &= N_t \exp \left[r \left(1 - \frac{N_t}{K} \right) - aP_t \right] \frac{N_t}{A + N_t}, \\ P_{t+1} &= eN_t[1 - \exp(-bP_t)], \end{aligned} \quad (3)$$

where the parameters r , K , a , A , e and b are positive.

Now, we eliminate some of the parameters by changing the variables. Taking $x_t = \frac{N_t}{K}$, and $y_t = bP_t$, we obtain

$$\begin{aligned} x_{t+1} &= x_t \exp [r(1 - x_t) - qy_t] \frac{x_t}{B + x_t}, \\ y_{t+1} &= mx_t[1 - \exp(-y_t)], \end{aligned} \quad (4)$$

where $m = beK$, $q = \frac{a}{b}$ and $B = \frac{A}{K}$.

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2 Equilibrium Points

In this section we analyze the fixed points of the discrete system (4). Firstly, we have to focus on the following isocline equations:

$$\begin{aligned}x &= x \exp[r(1-x) - qy] \frac{x}{B+x}, \\ y &= mx[1 - \exp(-y)].\end{aligned}\quad (5)$$

2.1 Extinction and Exclusion Fixed Points

In the equation (5), if $x = 0$, we have the extinction fixed point $P_1^* = (x_1^*, y_1^*) = (0, 0)$.

In order to find the exclusion fixed points, we take $x \neq 0$ and $y = 0$ in system of equations (5). Hence, we obtain

$$B = x(e^{r(1-x)} - 1). \quad (6)$$

Let us denote $z = F(x) = x(e^{r(1-x)} - 1)$. When this curve intersects with the horizontal line $z = B$, some fixed points are obtained.

Notice that F is continuous, $F(0) = F(1) = 0$, $F'(0) > 0$, $\lim_{x \rightarrow \infty} F(x) = -\infty$ and there is a unique x such that $F'(x) = 0$, where $x \in (0, 1)$. See Figure 1.

Now, we have to determine in which condition the horizontal line $z = B$ intersects the function $z = F(x)$, which is the condition when B is less than the height of the maximum value of the curve $z = F(x)$. Let us denote the maximum point by $(\bar{x}, \bar{y})$. In order to find that point, we have

$$F'(\bar{x}) = e^{r(1-\bar{x})}(1 - r\bar{x}) - 1 = 0. \quad (7)$$

We focus on the case where the horizontal line $z = B$ is a tangent to the curve $z = F(x)$, which is $F(\bar{x}) = B$:

$$\bar{x}(e^{r(1-\bar{x})} - 1) = B. \quad (8)$$

Eliminating the term $e^{r(1-\bar{x})}$ in equations (7) and (8), we obtain

$$r\bar{x}^2 + Br\bar{x} - B = 0. \quad (9)$$

The positive solution of equation (9) for $\bar{x}$ is as follows:

$$\bar{x} = \frac{1}{2} \left[-B + \sqrt{B^2 + \frac{4B}{r}} \right]. \quad (10)$$

Hence, the condition for the existence of the exclusion fixed points is obtained. There exist no fixed points if $B >$

$F(\bar{x})$, there exist only one fixed point if $B = F(\bar{x})$, and there exist two exclusion fixed points if $B < F(\bar{x})$. Furthermore, since $B > 0$ and the function F is positive only on the interval $(0, 1)$, the intersections always occur on this interval; from which we conclude that for the exclusion fixed points, say $P_2^* = (x_2^*, y_2^*)$ and $P_3^* = (x_3^*, y_3^*)$, we have $0 < x_2^* < 1$ and $0 < x_3^* < 1$. See Figure 1

Hence, we obtain the following result:

Theorem 1. *Let*

$$F(x) = x(e^{r(1-x)} - 1)$$

and

$$\theta = \frac{1}{2} \left[-B + \sqrt{B^2 + \frac{4B}{r}} \right].$$

For the system given in (4),

- for any values of parameters, there exists an extinction fixed point $(0, 0)$.
- there exist no exclusion fixed points if $B > F(\theta)$.
- there exists one exclusion fixed point $(\theta, 0)$ if $B = F(\theta)$.
- there exist two exclusion fixed points if $B < F(\theta)$.

Notice that the exclusion fixed points are obtained by taking $y = 0$, which vanishes in the second equation of the system (5). We give the graphs of the isoclines in Figure 2 with some values of parameters which confirms our results in the theorem. In Figure 2, $B = .5$ and the values for $F(\theta)$ are as follows: (a) $F(\theta) = 0.372 < B$, (b) $F(\theta) = 0.499 \approx B$, (c) $F(\theta) = 0.773 > B$.

2.2 Coexistence Fixed Points

Since there are complex, non-algebraic, equations for the isoclines, it is not easy to obtain a simple condition for the positive fixed points. However, we investigate this points numerically and find that for particular values of parameters there may exist zero, one, or two positive fixed points. Figure 3 represents the possible numbers of coexistence fixed points.

Notice that, since

$$y'' = \frac{1}{q} \left[\frac{1}{(B+x)^2} - \frac{1}{x^2} \right] < 0$$

for the first equation in (5), the first isocline is concave downwards, thus the only interval where the curve is above the x axis is (x_2^*, x_3^*) . Hence, if a positive fixed point

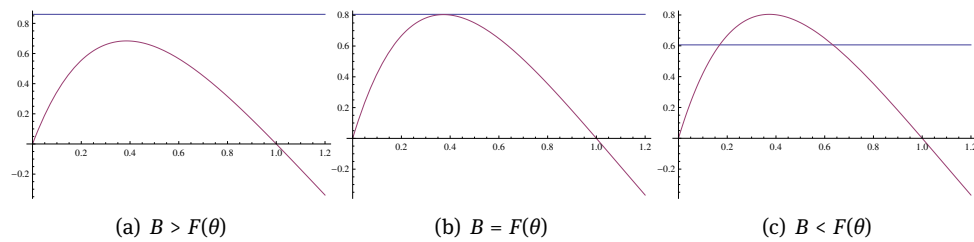


Figure 1: $z = F(x)$, $z = B$.

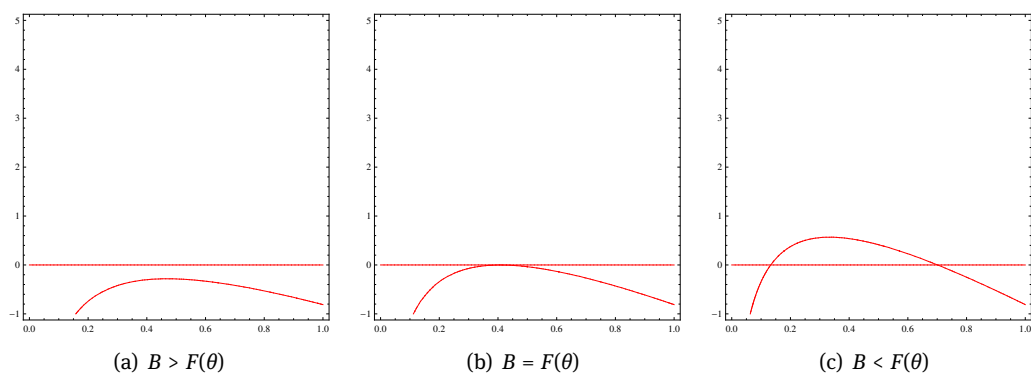


Figure 2: The graphs represent isoclines of the system. The horizontal line is the part of the isocline whose equation is the second equation of the system (5). The graph of the first equation is given by the curve.

(a) $m = .1$, $B = .5$, $q = .5$, $r = 1.1$; (b) $m = .1$, $B = .5$, $q = .5$, $r = 1.35$; (c) $m = .1$, $B = .5$, $q = .5$, $r = 1.8$.

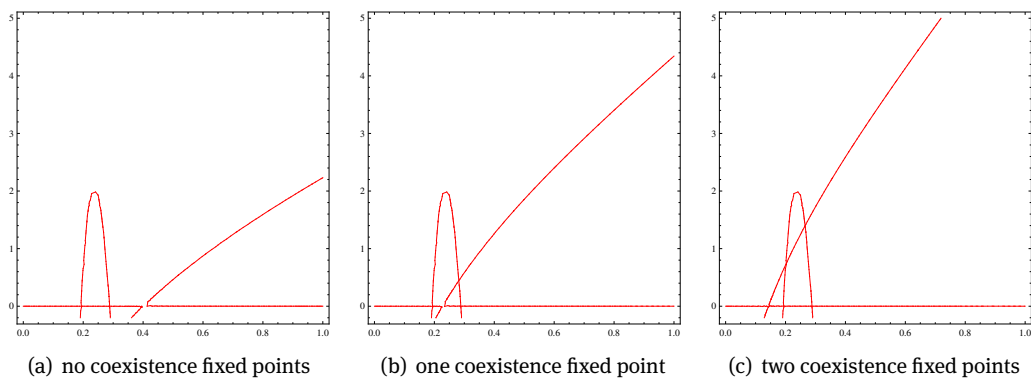


Figure 3: Isoclines of the system.

(a) $m = 2.5$, $B = 4.75$, $q = .01$, $r = 4.02$; (b) $m = 4.4$, $B = 4.75$, $q = .01$, $r = 4.02$; (c) $m = 7$, $B = 4.75$, $q = .01$, $r = 4.02$.

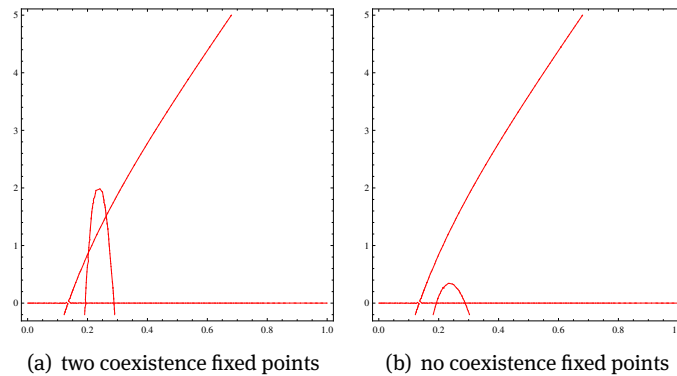


Figure 4: The parameter q affects the existence of the positive fixed points if m is large enough.

(a) $m = 7.4$, $B = 4.75$, $q = .01$, $r = 4.02$; (b) $m = 7.4$, $B = 4.75$, $q = .06$, $r = 4.02$.

(x_+^*, y_+^*) exists, then it satisfies the condition $x_2^* < x_+^* < x_3^*$.

Furthermore, since $\theta = \theta(B, r)$ and $F(x)$ in Theorem 1 doesn't depend on the parameters q and m , we can conclude that the existence of any kind of fixed point does not depend on the parameters m and q . Even these parameters do not change the position of the exclusion fixed points. However, the existence and the position of the coexistence fixed points are affected by each of the parameters. Figure 4 represents the effect of the parameter q . For large values of m , the parameter q affects the existence of the positive fixed points. However, for moderate values of m , where $x_2^* < \frac{1}{m} < x_3^*$, the parameter q does not affect the existence nor the number of positive fixed points, but the positions of them. This is shown in Figure 5.

Since, for some positive fixed points, $x_+^* < x_3^* < 1$ and the x -intercept of the second isocline is $\frac{1}{m}$, for $m < 1$ the isoclines do not intersect and hence there are no coexistence fixed points for this case. The inverse of this statement is not true (an example is shown in Figure 3 (a), for which $m = 2.5 > 1$ and there are no positive fixed points).

3 Stability of the System (4)

In this section, we analyze the stability of the system (4).

Let

$$F(x) = x (\exp[r(1-x)] - 1) \quad (11)$$

and

$$\theta = \frac{1}{2} \left[-B + \sqrt{B^2 + \frac{4B}{r}} \right]. \quad (12)$$

Case 1. $B > F(\theta)$

Theorem 2. For the system (4), when $B > F(\theta)$, the extinction fixed point $(0, 0)$ is globally asymptotically stable.

Proof. With the assumption that $B > F(\theta)$, the only fixed point is at $(0, 0)$. Furthermore, notice that if $B > F(\theta)$, then $B > F(x_n)$ for any x_n .

If we start with (x_n, y_n) , where $x_n = 0$ and $y_n \geq 0$, then $x_{n+1} = y_{n+1} = 0$.

Now, let us start with some point on the plane (x_n, y_n) , where $x_n > 0$ and $y_n \geq 0$, and show that $x_{n+1} < x_n$ and $y_{n+1} < y_n$. Hence, proving the inequalities, the sequences must converge to the only fixed point $(0, 0)$:

$$\begin{aligned} x_{n+1} &= x_n \exp[r(1-x_n) - qy_n] \frac{x_n}{B+x_n} \\ &< x_n \exp[r(1-x_n)] \frac{x_n}{B+x_n} \\ &< (B+x_n) \frac{x_n}{B+x_n} \\ &< x_n. \end{aligned}$$

Hence, $x_n \rightarrow 0$ as $n \rightarrow \infty$.

We also know that $y_{n+1} = mx_n(1 - e^{-y_n}) < mx_n$, from which we conclude that $y_n \rightarrow 0$ as $x_n \rightarrow 0$. $\square$

Case 2. $B = F(\theta)$

Now, for the system (4), we are going to analyze the fixed point $(\theta, 0)$ when $B = F(\theta)$.

The Jacobian matrix of the map

$$G(x, y) = \left(x e^{r(1-x)-qy} \frac{x}{B+x}, mx(1 - e^{-y}) \right)$$

is

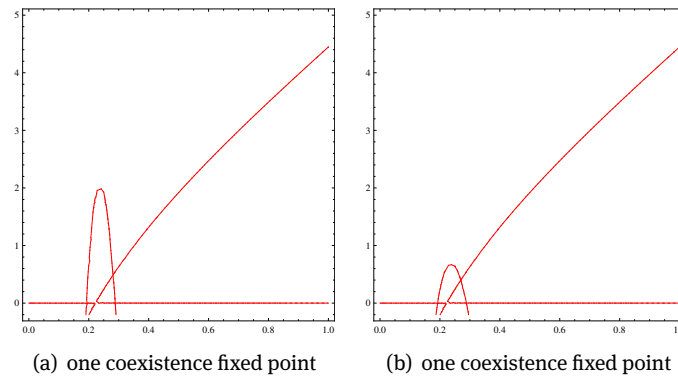


Figure 5: The parameter q does not affect the number of positive fixed points but the positions of them if $x_2^* < \frac{1}{m} < x_3^*$.
 (a) $m = 4.5$, $B = 4.75$, $q = .01$, $r = 4.02$; (b) $m = 4.5$, $B = 4.75$, $q = .03$, $r = 4.02$.

$$JG(x, y) = \begin{pmatrix} -\frac{e^{r-rx-xy} x(B(-2+rx)+x(-1+rx))}{m - e^{-y}m} & -\frac{e^{r-rx-xy} qx^2}{B+x} \\ 0 & e^{-y}mx \end{pmatrix}.$$

The Jacobian evaluated at the point $(\theta, 0)$ is

$$JG(\theta, 0) = \begin{pmatrix} -\frac{e^{r-r\theta} \theta(B(-2+r\theta)+\theta(-1+r\theta))}{(B+\theta)^2} & -\frac{e^{r-r\theta} q\theta^2}{B+\theta} \\ 0 & m\theta \end{pmatrix},$$

where θ is given in equation (12). By using equations (11) and (12), after some calculations, we obtain the following Jacobian matrix for the exclusion fixed point $(\theta, 0)$:

$$JG(\theta, 0) = \begin{pmatrix} 1 & -q\theta \\ 0 & m\theta \end{pmatrix},$$

which makes the fixed point non-hyperbolic.

The eigenvalues of $JG(\theta, 0)$ are $\lambda_1 = 1$ and $\lambda_2 = m\theta$. If $m\theta > 1$, then the fixed point $(\theta, 0)$ is unstable. If $m\theta < 1$, then in order to investigate the stability of this case, we have to apply the center manifold theory [1].

It is more convenient to make a change of variables in the system (4) so we can have a shift from the point $(\theta, 0)$ to $(0, 0)$. Let $u = x - \theta$ and $v = y$. Then the new system is given by

$$\begin{aligned} u_{t+1} &= \frac{e^{r-qv_t-r(u_t+\theta)}(u_t+\theta)^2}{B+u_t+\theta} - \theta, \\ v_{t+1} &= \mu(u_t+\theta)[1 - \exp(-v_t)]. \end{aligned} \quad (13)$$

At the point $(0, 0)$, the Jacobian of the planar map given in (13) is

$$\tilde{J}G(0, 0) = \begin{pmatrix} 1 & -q\theta \\ 0 & m\theta \end{pmatrix}.$$

Now we can write the equations in the system (13) as

$$\begin{aligned} u_{t+1} &= u_t - q\theta v_t + \tilde{f}(u_t, v_t), \\ v_{t+1} &= m\theta v_t + \tilde{g}(u_t, v_t), \end{aligned} \quad (14)$$

where

$$\tilde{f}(u_t, v_t) = -u_t - \theta + qv_t\theta + \frac{e^{-ru_t-qv_t}(B+\theta)(u_t+\theta)^2}{\theta(B+u_t+\theta)}$$

and

$$\tilde{g}(u_t, v_t) = -mv_t\theta + (1 - e^{-v_t})m(u_t+\theta).$$

Let us assume that the map h takes the form

$$h(u) = \alpha u^2 + \beta u^3 + O(u^4), \quad \alpha, \beta \in \mathbb{R}.$$

Now we have to compute the constants α and β . The function h must satisfy the center manifold equation

$$h(u - q\theta h(u) + \tilde{f}(u, h(u))) - m\theta h(u) - \tilde{g}(u, h(u)) = 0.$$

The Taylor series expansions, at the point $u = 0$, are evaluated for the equation above. Equating the coefficients of the series and using the equations (11) and (12), after some manipulations, we obtain $\alpha = \beta = 0$.

Thus on the center manifold $v = h(u)$ we find the following map

$$P(u) = -\theta + \frac{e^{-r(-1+u+\theta)}(u+\theta)^2}{B+u+\theta},$$

where θ is given in equation (12).

Calculations show that $P'(0) = 1$ and

$$P''(0) = -\frac{B^2 \left(4 + Br + r\sqrt{\frac{B(4+Br)}{r}} \right)}{r \left(-B + \sqrt{\frac{B(4+Br)}{r}} \right)} < 0.$$

Hence, for the map P , the origin is semi-stable from the right. See Figure 6.

Notice that this result is valid when $m\theta < 1$ which yields the condition $r > \frac{Bm^2}{1+Bm}$.

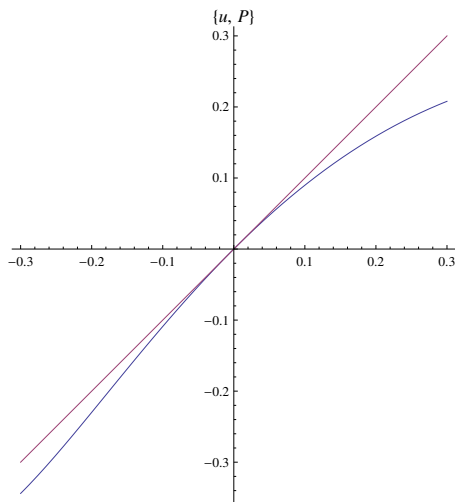


Figure 6: Map P on the center manifold $v = h(u)$. $(0, 0)$ is semi-stable from the right.

$$B = .500 \text{ and } r = 1.351.$$

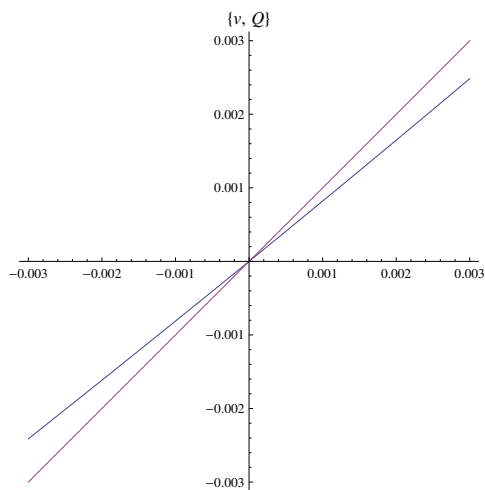


Figure 7: Map Q on the center manifold $u = h(v)$. $(0, 0)$ is asymptotically stable. Notice that $m\theta < 1$.

$$B = .5, q = 1.1, m = 2 \text{ and } r = 1.351.$$

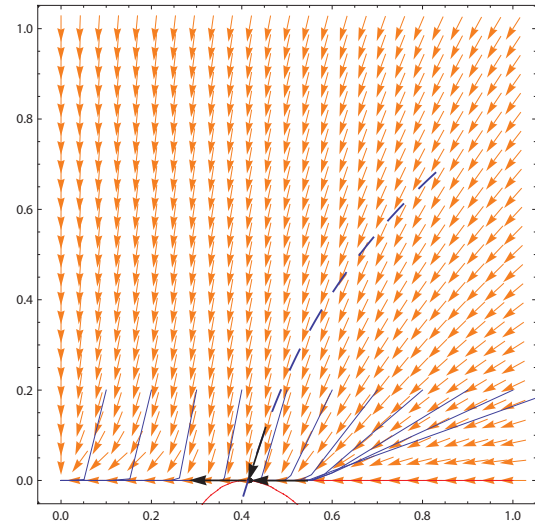


Figure 8: The phase diagram showing the stable and center manifolds when $B = F(\theta)$ and $m\theta < 1$. Semi-stability of map P on the center manifold $v = h(u) = 0$ can be also seen.

$$m = .1, B = .5, q = .5, \text{ and } r = 1.351.$$

Case 3. $B < F(\theta)$

The dynamics of this case, for which there may exist zero, one, or two positive fixed points, is much more complicated due to the non-algebraic equations of the isoclines.

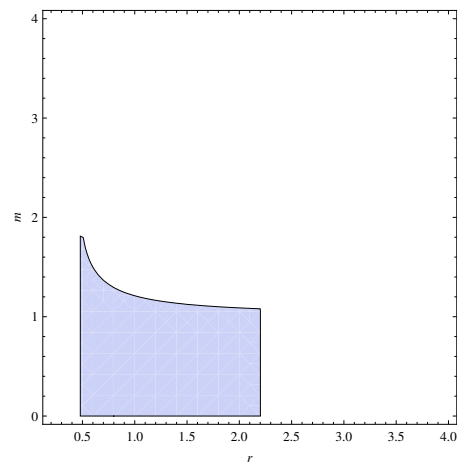


Figure 9: The estimated stability region of exclusion fixed point P_3^* .

$$B = 0.1, q = 0.6.$$

Now, we are going to find the stable manifold, which exists when $m\theta < 1$. Since the stable manifold is at a tangent to the eigenvector at the point, let us take

$$h(v) = \frac{q\theta}{m\theta - 1}v + \alpha v^2 + \beta v^3.$$

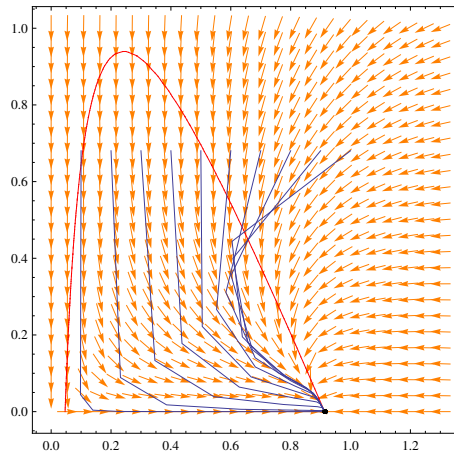


Figure 10: Phase diagram of the system when there is no positive fixed points.

$$m = .9, B = .1, q = .6 \text{ and } r = 1.2.$$

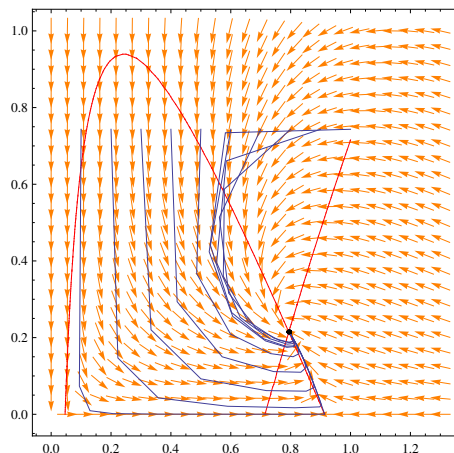


Figure 11: Phase diagram of the system when there exist a positive fixed points.

$$m = 1.4, B = .1, q = .6 \text{ and } r = 1.2.$$

This map must satisfy the center manifold equation

$$h(m\theta v + \tilde{g}(h(v), v)) - h(v) + q\theta v - \tilde{f}(h(v), v) = 0.$$

We calculate the map Q on the stable manifold and found that $Q'(0) = m\theta$, which is expected. Because of the long output of the computations we omit them here. Figure 7 shows the map Q .

Stable and center manifolds are given in Figure 8.

By symbolic/numeric computations we obtain the stability region of the exclusion fixed point when there are no coexistence fixed points. Figure 9 represents the stability region for the exclusion fixed point P_3^* on the r - m parameter space. In Figure 10, we give the phase diagram of the system when there exist no positive fixed point. In Figure 11, the phase diagram represents the dynamics of the system when there exists a positive fixed point and for

the given values of parameters, the positive fixed point is asymptotically stable.

4 Conclusions

In this paper, we generalized the model studied by S.R.-J. Jang and S.L. Diamond [7]. The condition for the existence of the fixed points are found. We also obtained the center manifold for the exclusion fixed point when $B = F(\theta)$.

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