

UNIQUENESS OF LIMIT CYCLES AND MULTIPLE  
ATTRACTORS IN A GAUSE-TYPE PREDATOR-PREY MODEL  
WITH NONMONOTONIC FUNCTIONAL RESPONSE AND  
ALLEE EFFECT ON PREY

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**ABSTRACT.** The main purpose of this work is to analyze a Gause type predator-prey model in which two ecological phenomena are considered: the Allee effect affecting the prey growth function and the formation of group defence by prey in order to avoid the predation.

We prove the existence of a separatrix curves in the phase plane, determined by the stable manifold of the equilibrium point associated to the Allee effect, implying that the solutions are highly sensitive to the initial conditions.

Trajectories starting at one side of this separatrix curve have the equilibrium point  $(0, 0)$  as their  $\omega$ -limit, while trajectories starting at the other side will approach to one of the following three attractors: a stable limit cycle, a stable coexistence point or the stable equilibrium point  $(K, 0)$  in which the predators disappear and prey attains their carrying capacity.

We obtain conditions on the parameter values for the existence of one or two positive hyperbolic equilibrium points and the existence of a limit cycle surrounding one of them. Both ecological processes under study, namely the nonmonotonic functional response and the Allee effect on prey, exert a strong influence on the system dynamics, resulting in multiple domains of attraction.

Using Liapunov quantities we demonstrate the uniqueness of limit cycle, which constitutes one of the main differences with the model where the Allee effect is not considered. Computer simulations are also given in support of the conclusions.

**1. Introduction.** Current theory of predator-prey dynamics rests necessarily on the study of non-linear mathematical models [36]. The model, as a unit of study, is assumed to be representative of the natural phenomena of interest and should capture the essence of that process. With the development of ecological knowledge due to theoretical, empirical, and observational research, more elements are recognized

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as essential to the phenomenon of predation and accordingly, modelers have added complexity to their abstractions in order to gain realism.

Allee effect affecting the prey population and formation of defence group are one of those, influencing qualitative stability and quantitative aspects of dynamics in predation models. The influences of this phenomena as a potential mechanism of population oscillations is an important objective of this present work. They are represented by inverse density-dependence of the prey growth rate [13] and a non-monotonic functional response [35], respectively.

We have focused in determining the stability of the system and particularly in establishing the quantity of limit cycles originated by multiple Hopf bifurcations [7, 18], surrounding a positive equilibrium point of the center-focus type [7]. Our analysis will have in mind a similar model without considering the Allee effect in the growth prey population, which has exactly two limit cycles around a unique positive equilibrium point [22].

This result is related with solving the well-known Hilbert 16th Problem (proposed by David Hilbert in 1900) on the maximum number and relative position of limit cycles [10, 18]. This question also yet remains unsolved in the case of a two-dimensional polynomial differential equation systems, whose degree must be less than or equal to  $n \in \mathbb{N}$  [18]. Particularly, for the Gause type predator-prey models, the problem is unanswered [10]; using the Lyapunov quantities method [7], we will try to answer this problem constituting one of our goals.

The studied system is defined in an open positive invariant region and the Poincaré–Bendixon theorem does not apply. Due to the existence of an heteroclinic curve determined by the equilibrium point associated to the strong Allee effect, a subregion in the phase plane is determined, where two positive equilibrium points can exist.

This paper is organized as follows: In the subsequent subsections, we present the main features of the Gause type predator models, the Allee effect and the non-monotonic functional response. In Section 2, a model topologically equivalent to the Gause type predator–prey model is obtained; in Section 3, the main properties of this model are presented. Ecological consequences of the mathematical results are given in Section 4.

**1.1. Gause-type predator-prey models.** The classical Gause-type predator-prey model [16] is continuous-time model represented by the second order differential equations system:

$$G : \begin{cases} \frac{dx}{dt} = x g(x) - h(x) y \\ \frac{dy}{dt} = (\psi(x) - c) y \end{cases} \quad (1)$$

where  $x(t)$  and  $y(t)$  denote the population size (number, density or biomass) of prey and predator, respectively; in order to establish a general theory of predation, the functions  $f(x)$ ,  $h(x)$  and  $\psi(x)$  are smooth as required for  $t \geq 0$  [26, 43] representing the natural per capita growth function, the functional response and the numerical response of predators, respectively.

Different forms for these functions have been proposed rendering a large variety of predator-prey models [36]. Usually,  $h(x)$  can be assumed to be a constant, or a function dependent on  $x$  [16] and  $g(x) = x f(x)$  the logistic growth function, meanwhile function  $\psi(x)$  is assumed linear respect to  $h(x)$ .

Some issues of interest in these types of models are: i) to determine properties of the functions  $g$ ,  $h$  and  $\psi$  for the existence or non-existence of limit cycles [26, 28, 43], ii) to establish the number of limit cycles that can bifurcate of the a positive equilibrium point of the center-focus type [7, 22, 31] and, iii) to derive results for ensure that local asymptotically stability, which in the Liapunov sense implies global stability of the unique positive equilibrium point [26].

**1.2. The Allee effect.** Any ecological mechanism leading to a positive relationship between a component of individual fitness and the abundance of conspecific is a mechanism of the *Allee effect* [13, 33]. In Population Dynamics it has been also called: *negative competition effect*, *allelocatalysis*, *undercrowding*, *negative density dependence*, *inverse density dependence*, *positive density dependence* or *automatic cooperation* [29], and *depensation* in fisheries sciences [8, 29].

The Allee effect dynamics may appear due to a wide range of biological phenomena, such as reduced antipredator vigilance, social thermoregulation, genetic drift, mating difficulty, reduced defense against the predator, and deficient feeding to low densities [13, 33, 34]. However, several other causes may generate these phenomena (see Table 1 in [5] or Table 2.1 in [14]).

Recent ecological research suggests that two or more Allee effects can lead to mechanisms acting simultaneously on a single population (see Table 2 in [5]); the combined influence of some of these phenomena is known as *multiple Allee effect* [5].

The simplest phenomenological form for growth rate in a population affected by the Allee effect, obtained modifying the logistic growth rate, is described by a cubic polynomial differential equation [4, 27]

$$\frac{dx}{dt} = r \left(1 - \frac{x}{K}\right) (x - m)x \quad (2)$$

where  $-K < m \ll K$  and  $r > 0$  is a constant related to how fast the population will grow at its maximum possible growth rate. We named *multiplicative Allee effect* to this form [2, 25, 31].

When  $m > 0$ , the population growth rate decreases if the population size is below the threshold level  $m$  and the population goes to extinction. In this case, equation (2) describes the *strong Allee effect* [37, 39].

If  $-K < m \leq 0$ , it is said that the population is affected by a *weak Allee effect* [8, 39]. In fisheries the same phenomena are called *critical* and *pure depensation*, respectively [8, 9, 29]. When  $m < 0$  the right side of equation (2) describes a compensatory curve and for  $m \geq 0$  the curve is depensatory [8, 9]. In this work, we consider that  $m \geq 0$ .

Many algebraic forms can be employed to describe the Allee effect [6, 12, 39, 45] but it is possible to prove that many of them are topologically equivalent [21]. Nonetheless, different forms may produce a change in the quantity of limit cycles surrounding a positive equilibrium point in predator-prey models [2, 23, 24, 25, 31].

**1.3. Non-monotonic functional response.** The predator *functional response* or *consumption rate function* expresses the consumption rate of prey per predator as a function of prey abundance. Here, we assume that this function is non-monotonic and described by the rational function  $h(x) = \frac{q x}{x^2 + a}$ , which tends to 0, as  $x \rightarrow \infty$ . This function corresponds to the dome-shaped Holling type-IV functional response [35] or simplified Monod-Haldane function [32] and can be regarded as a modification of the Holling type-II function.

A non-monotonic functional response can be used to describe a type of antipredator behavior (APB) called *group defence*; this term describes the phenomenon whereby predators decrease, or are even prevented altogether, due to the increased ability of the prey to better defend or disguise themselves when their number is large enough [17, 32, 41, 42], that is, it indicates a decreasing risk of being eaten by predators as prey number is large.

Another manifestation of an APB in which a non-monotonic functional response (or Holling-type IV or Monod-Haldane) can be used is the phenomenon of *aggregation*, a social behavior of prey in which prey congregate on a fine scale relative to the predator so that the predator's hunting is not spatially homogeneous [35], such as succeeds with mile-long schools of certain class of fishes. In this case, a primary advantage of schooling seems to be confusion of the predator when it attacks. The more important benefit of aggregation is an increasing in wariness. Moreover, aggregation can both decrease the vulnerability to be attacked and increase the time that group members can devote to activities other than surveillance [35].

Other related example of non-monotone consumption occurs at the microbial level where evidence indicates that when faced with overabundance of nutrients the effectiveness of the consumer can begin to decline. This is often seen when micro-organisms are used for waste treatment and water purification, a phenomenon which has been called *inhibition* [17, 32, 43].

Without consider the Allee effect, the model is analyzed in [32], and in [20] is proved that for a subset of the parameter space there exists a unique equilibrium point surrounded by two limit cycles, the innermost unstable and the outermost stable.

A function of the form  $h(x) = \frac{qx}{a+bx+x^2}$ , also satisfies the assumptions of the Holling type-IV functional response, and it is used by Collings [11] in a mite predator-prey model of Leslie type [36] with some temperature-dependency. Also in [44], for a Gause type model using this functional response it is shown that there exists a Bogdanov-Takens bifurcation of codimension 3, which acts as an organizing center for the system.

Furthermore, Gause type models with non-monotonic functional response have been partially analyzed when  $h(x) = \frac{qx^m}{a+x^n}$ , with  $m < n$  [1, 38] and it has been proved that the resulting dynamics are not topologically equivalent, in general.

We note that the phenomena of the Allee effect and aggregation described by a non-monotonic functional response are quite compatible and justify our assumptions in the model studied. Although it may seem that the two aspects considered in the model contradict each other since the prey population exhibits the Allee effect for low densities, while a non-monotonic functional response is suggested for the aggregation (group defense) when the prey population size is large, it is known that predation induces an Allee effect [19].

Strikingly, a wide range of predator-driven Allee effects have been reported [5]; in particular, there is the case of the Atlantic cod (*Gadus morhua*) that forms schools during the day, since commercial fishing (men as predator) provokes stock collapse because a higher proportion of this aggregated population is caught per unit effort when population declines [9].

Also, for obligatory cooperative breeders as the African wild dog (*Lycaon pictus*) and meerkat (*Suricata suricatta*), there is a similar situation, because juvenile survival is lower in small groups than large groups in areas with high predator densities

but lower in large groups than small groups in areas with low predator densities [14].

**2. The model.** The model considering Allee effect on prey and non-monotonic functional response is given by

$$X_\mu : \begin{cases} \frac{dx}{dt} = \left( r \left( 1 - \frac{x}{K} \right) (x - m) - \frac{q y}{x^2 + a} \right) x \\ \frac{dy}{dt} = \left( \frac{p x}{x^2 + a} - c \right) y \end{cases} \quad (3)$$

System (3) or vector field  $X_\mu$ , is a Kolmogorov type system [16] defined in

$\Omega = \{(x, y) \in \mathbb{R}^2 \mid x \geq 0, y \geq 0\} = \mathbb{R}_0^+ \times \mathbb{R}_0^+$ , where  $\mu = (r, K, q, a, p, c, m) \in \mathbb{R}_+^6 \times \mathbb{R}$  with  $0 < a < K$  and  $-K < m \ll K$ .

The parameters have the following ecological meanings:

$r$  is the intrinsic per capita growth rate or biotic potential of prey,

$K$  is the prey carrying capacity,

$m$  is the minimum viable population, i.e., the threshold below which the population goes to extinction,

$q$  is the per capita attack rate of predators,

$\sqrt{a}$  is the amount of prey at which predation rate is maximal,

$p$  is the conversion efficiency of consumed prey into new predators, and

$c$  is the per capita mortality rate of predators.

The equilibrium points of system (3) are  $O = (0, 0)$ ,  $Q_m = (m, 0)$ ,  $Q_K = (K, 0)$  and  $Q_1 = (x_1, y_1)$  and  $Q_2 = (x_2, y_2)$ , where  $Q_1, Q_2$  exist in  $\Omega$ , if and only if,  $p^2 - 4ac^2 \geq 0$  and  $y_1, y_2 > 0$ .

In order to simplify the calculus, we reduce the system (3) to a normal form [7], following the methodology used in [20, 22, 31], we make a change of variables and a time rescaling given by the function

$\varphi : \tilde{\Omega} \times \mathbb{R} \rightarrow \Omega \times \mathbb{R}$  with

$\tilde{\Omega} = \{(u, v) \in \mathbb{R}^2 \mid u \geq 0 \text{ and } v \geq 0\}$  such that

$\varphi(u, v, \tau) = \left( Ku, \frac{K^2 r}{q} v, \frac{(K^2 u^2 + a) \tau}{r K^2} \right) = (x, y, t)$ ; thus,

$\det D\varphi(u, v, \tau) = \frac{K(K^2 u^2 + a)}{q} > 0$ .

Then,  $\varphi$  is a diffeomorphism [7] that preserves the orientation of the time; hence, we obtain a qualitatively (topologically) equivalent vector field  $Y_\nu = \varphi \circ X_\mu$ , which has the form  $Y_\nu = P(u, v) \frac{\partial}{\partial u} + Q(u, v) \frac{\partial}{\partial v}$  [15].

The associated second order differential equations system is the following Kolmogorov type polynomial [16]:

$$Y_\nu : \begin{cases} \frac{du}{d\tau} = ((1-u)(u-M)(A+u^2) - v)u \\ \frac{dv}{d\tau} = B(u - C(A+u^2))v \end{cases} \quad (4)$$

where  $\nu = (A, B, C, M) \in (\mathbb{R}_+^3) \times ]-1, 1[$ , with

$A = \frac{a}{K^2} < 1$ ,  $B = \frac{p}{rK}$ ,  $C = \frac{cK}{p}$  and  $M = \frac{m}{K} \ll 1$ .

The singularities of the vector field  $Y_\nu$  or equilibrium points of system (4) on  $\tilde{\Omega}$  are:  $P_0 = (0, 0)$ ,  $P_1 = (1, 0)$ , which exists for all parameter values and  $P_M = (M, 0)$  exists in the first quadrant for  $M > 0$ . The equilibrium point  $P_M = (M, 0)$  collapses with  $P_0 = (0, 0)$  for  $M = 0$ , and it is out of the first quadrant when  $M < 0$ .

Moreover, the positive equilibrium points lie on the curve  $v = \frac{u}{C} (1-u)(u-M)$ , (or  $v = \frac{u^2}{C} (1-u)$  when  $M = 0$ ), determined by the intersection of isoclines

$$Cu^2 - u + AC = 0 \text{ and } v = (1 - u)(u - M)(A + u^2),$$

The quadratic equation  $Cu^2 - u + AC = 0$  has two positive roots  $u_4$  and  $u_5$ , if and only if  $1 - 4AC^2 > 0$ , independent of  $M$ .

Denoting  $W^2 = 1 - 4AC^2$ , the equilibrium points  $P_4 = (u_4, v_4)$  and  $P_5 = (u_5, v_5)$  have as coordinates:

$$u_4 = \frac{1-W}{2C} \text{ and } v_4 = \frac{(1-W)(2C-1+W)(1-W-2MC)}{8C^4} \text{ and}$$

$$u_5 = \frac{1+W}{2C} \text{ and } v_5 = \frac{(1+W)(2C-1+W)(1-W-2MC)}{8C^4}.$$

Clearly,  $0 < u_4 < u_5$ .

As  $0 < A = \frac{1-W^2}{4C^2} < 1$  then  $1 - W^2 > 0$  and  $1 - W^2 - 4C^2 < 0$ .

Furthermore:

1. Assuming  $1 - 4C^2A > 0$ , then:

$P_4 = (u_4, v_4)$  and  $P_5 = (u_5, v_5)$ , lie at the interior of the first quadrant, if and only if,  $0 \leq M < u_4 < u_5 < 1$ .

If  $u_4 = M$ , then  $v_4 = 0$  and  $1 - W - 2CM = 0$ , coinciding  $(u_4, v_4)$  with  $(M, 0)$ .

If  $u_4 < M$ , then  $v_4 < 0$ ,  $1 - W - 2CM = 0$  and  $(u_4, v_4)$  lies in the fourth quadrant.

If  $u_5 = 1$ , then  $v_5 = 0$  and  $1 + W - 2C = 0$ , (or  $A = \frac{1-C}{C}$ ), collapsing  $(u_5, v_5)$  with  $(1, 0)$ .

If  $u_5 > 1$ , then  $v_5 < 0$  and  $1 + W - 2C > 0$  (or  $A < \frac{1-C}{C}$ ) and  $P_4$  is the unique equilibrium point at the interior of  $\tilde{\Omega}$ .

2. If  $1 - 4C^2A = 0$ , there exists a unique equilibrium point at the interior of  $\tilde{\Omega}$ , then  $P_4$  collapses with  $P_5$ ; then,  $P_4 = \left(\frac{1}{2C}, \frac{(2C-1)(1-2CM)}{8C^4}\right)$  lies in the first quadrant, if and only if,  $C > \frac{1}{2}$  and  $C < \frac{1}{2M}$ , for  $M > 0$ .

3. If  $1 - 4C^2A < 0$ , there exist no equilibrium points at the interior of  $\tilde{\Omega}$ .

In Figure 1 we present the bifurcation diagram for the positive equilibrium points, depending of  $A$ ,  $C$  and  $M$  fixed.

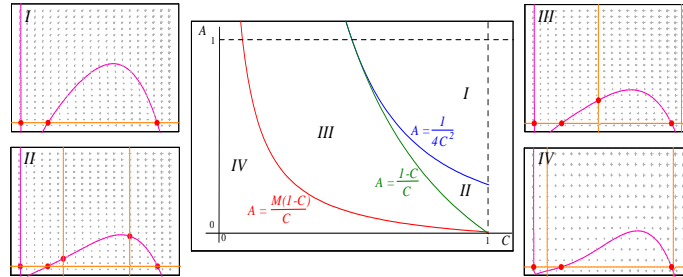


FIGURE 1. Bifurcation diagram of the positive equilibrium points, depending of the parameters  $A$  and  $C$ . In region  $I$  no positive equilibrium points exist; in region  $II$ , there exist two equilibrium points  $(u_4, v_4)$  and  $(u_5, v_5)$ , in region  $III$ , there exist a unique equilibrium  $(u_4, v_4)$ ; in region  $IV$ , no positive equilibrium points exist.

The Jacobian matrix associated to system (4) is given by:

$$DY_\eta(u, v) = \begin{pmatrix} Y_\eta 11(u, v) & -u \\ B(1 - 2Cu)v & B(u - Cu^2 - AC) \end{pmatrix} \text{ where}$$

$$Y_{\eta 11}(u, v) = -5u^4 + 4(1 + M)u^3 - 3(M + A)u^2 + 2A(1 + M)u - MA - v.$$

The Jacobian matrix evaluated at the points  $P_0$ ,  $P_M$  and  $P_1$  are:

$$\begin{aligned} DY_{\eta}(0, 0) &= \begin{pmatrix} -MA & 0 \\ 0 & -ABC \end{pmatrix} \\ DY_{\eta}(M, 0) &= \begin{pmatrix} M(1 - M)(M^2 + A) & -M \\ 0 & B(M - CM^2 - AC) \end{pmatrix} \\ DY_{\eta}(1, 0) &= \begin{pmatrix} -(1 + A)(1 - M) & -1 \\ 0 & B(1 - C - AC) \end{pmatrix} \end{aligned}$$

**3. Main results.** For system (4) we have

**Lemma 3.1.** a) The set  $\bar{\Gamma} = \{(u, v) \in \bar{\Omega} / 0 \leq u \leq 1, 0 \leq v\} \subset \mathbb{R}_0^+ \times \mathbb{R}_0^+$  is an invariance region.

b) The solutions are bounded.

c) The equilibrium points lie on the curve  $v = \frac{u}{C}(1 - u)(u - M)$ .

*Proof.* a) If  $u = 0$ , then  $\frac{du}{d\tau} = 0$  and  $\frac{dv}{d\tau} = -ABCv < 0$  and the trajectories remain over the  $v$ -axis.

If  $v = 0$ , then  $\frac{du}{d\tau} = (1 - u)(u - M)(u^2 + A)u < 0$ , if  $u < M$

and  $\frac{du}{d\tau} = (1 - u)(u - M)(u^2 + A)u > 0$  if  $u > M$ , then, the trajectories remain over the  $u$ -axis.

If  $u = 1$ , then  $\frac{du}{d\tau} = -vu < 0$  and  $\frac{dv}{d\tau} = B(1 - C - AC)v$ , which can be positive or negative, but the trajectories point inside  $\bar{\Gamma}$ .

b) By using the Poincaré compactification [30], through the change of variables  $X = \frac{u}{v}$  and  $Y = \frac{1}{v}$ , we have that  $\frac{dX}{d\tau} = \frac{1}{v^2}(v\frac{du}{d\tau} - u\frac{dv}{d\tau})$  and  $\frac{dY}{d\tau} = -\frac{1}{v^2}\frac{dv}{d\tau}$ , and it is shown that the point  $(0, \infty)$  is a saddle point.

c) As  $A + u^2 = \frac{u}{C}$  it is clearly obtained that  $v = \frac{u}{C}(1 - u)(u - M)$ .  $\square$

**3.1. The strong Allee effect.** Considering  $M > 0$  in system (4); we obtain the following properties:

**Lemma 3.2.** a) For all parameter values there exist at  $\bar{\Gamma}$  the singularities  $P_0 = (0, 0)$ ,  $P_M = (M, 0)$  and  $P_1 = (1, 0)$ .

b) If  $1 - 4C^2A > 0$ , then singularities  $P_4 = (u_4, v_4)$  and  $P_5 = (u_5, v_5)$  exist at  $\bar{\Gamma}$ .

c) If  $1 - 4C^2A = 0$ , there exists a unique equilibrium point at the interior of  $\bar{\Gamma}$ ,

$$P_4 = \left( \frac{1}{2C}, \frac{(2C-1)(1-2CM)}{8C^4} \right), \text{ if and only if, } C > \frac{1}{2} \text{ and } M < \frac{1}{2C}.$$

d) If  $1 - 4C^2A < 0$ , there exist no equilibrium points at the interior of  $\bar{\Gamma}$ .

*Proof.* a) If  $v = 0$ , then  $(1 - u)(u - M)(A + u^2) = 0$  or  $u = 0$ .

b) As  $Cu^2 - u + AC = 0$ , the equation has two different positive roots, if and only if,  $1 - 4C^2A > 0$ .

c) If  $1 - 4C^2A = 0$ , then  $P_4$  collapses with  $P_5$  at  $\bar{\Gamma}$  and we get

$$v_4 = \frac{1}{8C^4}(2C - 1)(1 - 2CM).$$

Moreover,  $0 < v_4$ , if and only if  $2C > 1 > 2CM$ , this is, if and only if  $C > \frac{1}{2}$  and  $M < \frac{1}{2C}$ .

d) Trivial.  $\square$

**Remark 1.** The analysis required to know whether singularities  $P_4 = (u_4, v_4)$  and  $P_5 = (u_5, v_5)$  lie at  $\bar{\Gamma}$ , will be shown below.

**Lemma 3.3.** a) For all parameter values  $P_0$  is an attractor.

Also, assuming that  $W^2 = 1 - 4C^2A < 0$ , then

b)  $P_M = (M, 0)$  is a saddle point and  $P_1 = (1, 0)$  is a local attractor.

c) There exists a separatrix curve dividing the behavior of the trajectories (see Figure 2).

*Proof.* a) The eigenvalues of the Jacobian matrix at  $P_0$  always have negative real part.

b(i) From the Jacobian matrix at  $P_M = (M, 0)$  we get

$$\det DY_\eta(M, 0) = BM(1 - M)(M^2 + A)(M - CM^2 - CA).$$

Assuming that  $M - CM^2 - CA > 0$ , as  $1 - 4C^2A < 0$ , the contradiction  $\frac{(1-2CM)^2}{4C^2} < 0$  is obtained. Thus,  $P_M = (M, 0)$  is a saddle point.

When  $M - CM^2 - CA = 0$  and  $1 - 4C^2A < 0$ , we obtain that  $(1 - 2CM)^2 < 0$ , and therefore  $P_M$  is a non-hyperbolic saddle point.

b(ii) From the Jacobian matrix at  $P_1$  we get

$$\det DY_\eta(1, 0) = -(1 + A)(1 - M)B(1 - C - CA).$$

Assuming that  $1 - C - CA > 0$  and given that  $1 - 4C^2A < 0$ , then the contradiction  $(1 - 2C)^2 < 0$  is obtained. Therefore,  $\det DY_\eta(1, 0) > 0$ , and  $P_1 = (1, 0)$  is a local attractor since  $\text{tr}DY_\eta(1, 0) < 0$ .

c) The stable manifold  $W^s(P_M)$  of the saddle point  $P_M$ , determines a separatrix curve, above which the trajectories have the point  $P_0$  as  $\omega$ -limit, and those starting below this separatrix go to  $P_1$ .  $\square$

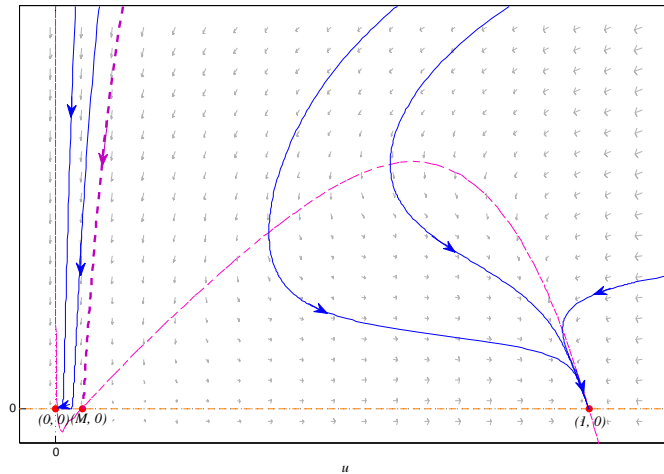


FIGURE 2.  $A = 0.5$ ,  $B = 1.0$ ,  $C = 0.8$ , and  $M = 0.05$ , the singularities  $(1, 0)$  and  $(0, 0)$  are attractor points; the stable manifold of  $(M, 0)$  determines a separatrix curve.

**Lemma 3.4.** Assuming that  $W^2 = 1 - 4C^2A = 0$ , then

a) The point  $P_4 = \left(\frac{1}{2C}, \frac{(2C-1)(1-2CM)}{8C^4}\right)$  is the unique singularity at the interior of  $\bar{\Gamma}$ , if and only if,  $2C - 1 > 0$  and  $1 - 2CM > 0$  and,

i) it is a saddle-node attractor [3], if and only if,  $3 - 4C - 4CM + 4C^2M > 0$ .

ii) it is a saddle-node repeller, if and only if,  $3 - 4C - 4CM + 4C^2M < 0$ .



iii) it is a cusp point and system (4) has a Bogdanov-Takens bifurcation [32, 43, 44], if and only if,  $M = \frac{4C-3}{4C(C-1)}$  and  $\frac{1}{2} \ll C < \frac{3}{4}$  or  $\frac{3}{2} \ll C$ .

If  $1 - 2CM = 0$ , the point  $P_4$  is a non hyperbolic saddle point and if  $2C - 1 = 0$  the point  $P_4$  is a non hyperbolic local attractor.

b) The point  $P_1$  is local attractor.

*Proof.* a) We have that  $v_4 = \frac{(2C-1)(1-2CM)}{8C^4} > 0$  if and only if  $2C - 1 > 0$  and  $1 - 2CM > 0$ .

In this case,  $P_1$  and  $P_0$  are both local attractors and  $P_M$  is a saddle point.

The Jacobian matrix at  $P_4$  is

$$DY_\eta(u_4, v_4) = \begin{pmatrix} -\frac{(1+4AC^2)(3-4C-4CM+4C^2M)}{16C^4} & -\frac{1}{2C} \\ 0 & 0 \end{pmatrix},$$

where  $\det DY_\eta(u_4, v_4) = 0$

and

$$\text{tr} DY_\eta(u_4, v_4) = -\frac{(1+4C^2A)((3-4C)-4C(1-C)M)}{16C^4}.$$

The sign of  $\text{tr} DY_\eta(u_4, v_4)$  depends on the sign of  $T = (3 - 4C) - 4C(1 - C)M$ .

i) If  $(3 - 4C) - 4C(1 - C)M > 0$ , then  $(\frac{1}{2C}, v_4)$  is a saddle-node attractor

ii) if  $(3 - 4C) - 4C(1 - C)M < 0$ , then  $(\frac{1}{2C}, v_4)$  is a saddle-node repellor

iii) Clearly, if  $(3 - 4C) - 4C(1 - C)M = 0$ , or  $0 < M = \frac{4C-3}{4C(C-1)} < 1$ , then,  $(u_4, v_4)$  is a cusp point.

This inequality it is fulfilled if and only if  $\frac{1}{2} < C < \frac{3}{4}$  or  $\frac{3}{2} < C$ , but since  $M$  must be small, then  $\frac{1}{2} \ll C < \frac{3}{4}$  or  $\frac{3}{2} \ll C$ .

On the other hand:

If  $2C - 1 = 0$ ,  $P_4$  coincides with  $P_1$  and it is a non hyperbolic local attractor.

If  $1 - 2CM = 0$ ,  $P_4$  coincides with  $P_M$  and it is a non hyperbolic saddle point.

b) As  $1 - C - CA = -\frac{(2C-1)^2}{4C}$  is negative for  $2C - 1 \neq 0$ , then  $P_1$  is a local attractor.  $\square$

**Theorem 3.5.** For the equilibrium points  $P_4$  and  $P_5$  we have that

a)  $P_4 \in \bar{\Gamma}$  and  $P_5 \in \bar{\Gamma}$ , if and only if  $A > \frac{M(1-CM)}{C}$  and  $A > \frac{1-C}{C}$ ;

moreover, in this case  $P_1$  is an attractor and  $P_M$  is a saddle point.

b)  $P_4 \in \bar{\Gamma}$  and  $P_5 \notin \bar{\Gamma}$ , if and only if,  $\frac{1-C}{C} > A > \frac{M(1-CM)}{C}$ ; in this case  $P_1$  and  $P_M$  are saddle points.

c)  $P_4 \notin \bar{\Gamma}$  and  $P_5 \in \bar{\Gamma}$  if and only if  $A < \frac{M(1-CM)}{C}$  and  $A > \frac{1-C}{C}$ ; then,  $P_M$  is a repellor and  $P_1$  is an attractor.

*Proof.* a) The equilibrium points  $P_4$  and  $P_5$  belong to  $\tilde{\Gamma}$  simultaneously, if and only if,

$M < u_4 < u_5 < 1$  (and  $v_4, v_5 > 0$ ), that is, if  $M < \frac{1}{2C}(1-W) < \frac{1}{2C}(1+W) < 1$ .

Since  $0 < A = \frac{1-W^2}{4C^2} < 1$ , then  $1 - W^2 > 0$  and  $1 - W^2 - 4C^2 < 0$ , this implies that:

i)  $2CM < 1 - W$  and  $1 - W < 2C$ , this is,  $1 - W - 2MC > 0$  and  $2C - 1 + W > 0$ ,

ii)  $2CM < 1 + W$  and  $1 + W < 2C$ , this is,  $1 + W - 2MC > 0$  and  $2C - 1 - W > 0$ .

Then,

$$v_4 = \frac{(1-W)}{8C^4} (2C - 1 + W)(1 - W - 2MC) \text{ and}$$

$$v_5 = \frac{(1+W)}{8C^4} (2C-1-W)(1+W-2MC) \text{ are both positives.}$$

From i) we have;  $1-2MC > W > 1-2C$

and from ii) we obtain;

$$2MC-1 < W < 2C-1.$$

Therefore,

$$1-2MC > W > 2MC-1 \text{ and } 2C-1 > W > 1-2C,$$

that is,

$$|1-2MC| > W$$

and

$$|2C-1| > W,$$

hence,

$$(1-2MC)^2 > 1-4AC^2$$

and

$$(2C-1)^2 > 1-4AC^2$$

that is,

$$CA-M+CM^2 > 0 \text{ and } C-1+CA > 0.$$

Therefore,

$$A > \frac{M(1-CM)}{C} \text{ and } A > \frac{1-C}{C}.$$

Furthermore, looking at the corresponding Jacobian matrix we have that  $P_1$  is an attractor and  $P_M$  is a saddle point.

b) The equilibrium point  $P_4 \in \tilde{\Gamma}$  and  $P_5 \notin \tilde{\Gamma}$ , if and only if,

$$M < u_4 < 1 < u_5, \text{ that is,}$$

$$M < \frac{1}{2C}(1-W) < 1 < \frac{1}{2C}(1+W),$$

this implies that

iii)  $2CM < 1-W$  and  $1-W < 2C$ , this is,  $1-W-2MC > 0$  and  $2C-1+W > 0$ ,

iv)  $2CM < 1+W$  and  $1+W > 2C$ , this is,  $1+W-2MC > 0$  and  $2C-1-W < 0$ .

Then,

$$v_4 = \frac{(1-W)}{8C^4} (2C-1+W)(1-W-2MC) > 0 \text{ and}$$

$$v_5 = \frac{(1+W)}{8C^4} (2C-1-W)(1+W-2MC) < 0.$$

From iii) we have that:

$$1-2MC > W > 1-2C$$

from iv) we obtain that:

$$W > 2MC-1 \text{ and } W > 2C-1.$$

Therefore,

$$|1-2MC| > W \text{ and } |1-2C| < W,$$

hence,

$$(1-2MC)^2 > 1-4AC^2 \text{ and } 1-4AC^2 > (1-2C)^2,$$

that is,

$$CA-M+CM^2 > 0 \text{ and } C-1+CA < 0.$$

Thus,

$$A > \frac{M(1-CM)}{C} \text{ and } A < \frac{1-C}{C}.$$

From the respective Jacobian matrices we have that the singularities  $P_1$  and  $P_M$  are saddle points.

- c) If  $M - CM^2 - CA > 0$ , then  $v_4 < 0$  and  $P_4 \notin \tilde{\Gamma}$ .  
 b) From a)  $P_5 \in \tilde{\Gamma}$ , if and only if,  $\frac{1-C}{C} < A < \frac{1}{4C^2}$  (see Figure 1).  $\square$

**Theorem 3.6.** *When the equilibrium point  $P_5 \in \tilde{\Gamma}$  is a saddle point and there exists a new separatrix curve for the trajectories determined by the heteroclinic that joins the singularities  $P_5$  with  $P_1$ .*

*Proof.* The Jacobian matrix at  $P_5$  is

$$DY_\eta(u_5, v_5) = \begin{pmatrix} Y_\eta 11(u_5, v_5) & -u_5 \\ -BWv_5 & 0 \end{pmatrix},$$

with  $\det DY_\eta(u_5, v_5) = -BWv_5u_5 < 0$ , hence  $P_5$  is a saddle point, independent of the sign of the  $\text{tr}DY_\eta(u_5, v_5) = Y_\eta 11(u_5, v_5)$ .

The stable manifold  $W^s(P_5)$  of  $P_5$  determines a separatrix curve which divides the behavior of the trajectories, implying the existence of a trajectory that joins the singularities  $P_5$  and  $P_1$ .  $\square$

**Theorem 3.7.** *If singularity  $P_4$  belongs to  $\tilde{\Gamma}$ , then we have that:*

- a)  $P_4$  is an attractor point (see Figures 2 and 4), if and only if  
 $(2C + 5 + 2MC)W - 5 + 4AC^2 + 2C + 4MC^2 + 8C^2 < 0$ ,  
 b)  $P_4$  is a repellor surrounded by a stable limit cycle (see Figures 3 and 5), if and only if  
 $(2C + 5 + 2MC)W - 5 + 4AC^2 + 2C + 4MC^2 + 8C^2 > 0$ ,  
 c) Assuming that  $P_5 \in \tilde{\Gamma}$  and  $P_4$  is a repellor, then the limit cycle disappears when it intersects the stable manifold of  $P_5$  (see Figures 6 and 7).

*Proof.* i) If singularity  $P_5 \in \tilde{\Gamma}$  then  $u_5 = \frac{1}{2C}(1+W) < 1$ , and  $\frac{1-C}{C} < A < \frac{1}{4C^2}$  (see Figure 1).

Then  $P_1 = (1, 0)$  is a stable equilibrium point.

ii) If  $P_5 \notin \tilde{\Gamma}$ , then  $A < \frac{1-C}{C} < \frac{1}{4C^2}$  and  $P_1$  is a hyperbolic saddle point. Thus, it appears the unstable manifold  $W^u(P_1)$ .

The Jacobian matrix at  $(u_4, v_4)$  is

$$DY_\eta(u_4, v_4) = \begin{pmatrix} Y_\eta 11(u_4, v_4) & -u_4 \\ BWv_4 & 0 \end{pmatrix},$$

As  $\det DY_\eta(u_4, v_4) = BWv_4u_4 > 0$ , then the nature of the equilibrium point  $(u_4, v_4)$  depends on

$$\begin{aligned} \text{tr}DY_\eta(u_4, v_4) &= Y_\eta 11(u_4, v_4) \\ &= -5u_4^4 + 4(1+M)u_4^3 - 3(M+A)u_4^2 + 2A(1+M)u_4 - MA - v_4 \\ &= \frac{1}{8} \frac{1}{C^4} \left( (1-W)^2 (-W^2 + (2C+5+2MC)W - 4 + 2C + 4MC^2 + 8C^2) \right) \\ &= \frac{1}{8} \frac{1}{C^4} \left( (1-W)^2 ((2C+5+2MC)W - 5 + 4AC^2 + 2C + 4MC^2 + 8C^2) \right) \end{aligned}$$

and

- a)  $P_4$  is an attractor, if and only if,  
 $(2C + 5 + 2MC)W - 5 + 4AC^2 + 2C + 4MC^2 + 8C^2 < 0$ ,  
 b)  $P_4$  is a repellor point, if and only if,  
 $(2C + 5 + 2MC)W - 5 + 4AC^2 + 2C + 4MC^2 + 8C^2 > 0$ .  
 c) Assuming that  $P_5 \in \tilde{\Gamma}$  and  $P_4$  is a repellor, we have that the limit cycle disappears when it intersects the stable manifold of  $P_5$  (see Figures 7 and 8).  $\square$

**Theorem 3.8.** *The equilibrium Point  $P_4$  is a first order weak (fine) focus [7], if and only if,*

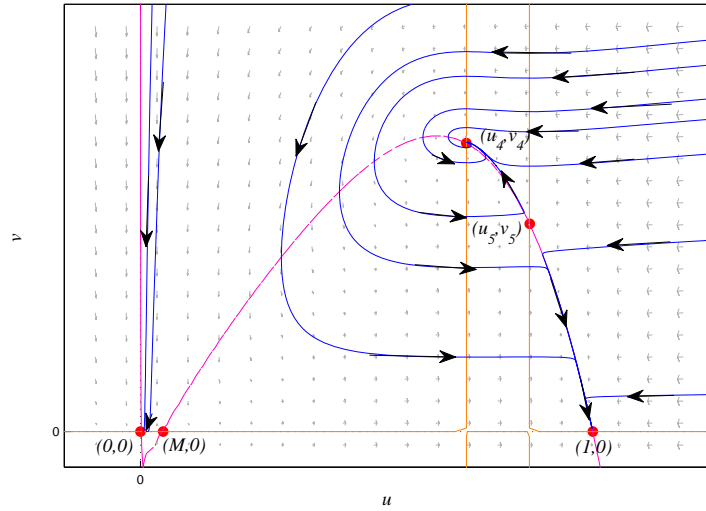


FIGURE 3. For  $A = .7$ ,  $B = 1$ ,  $C = 0.62$  and  $M = 0.05$ , the points  $(1, 0)$ ,  $(u_4, v_4)$  and  $(0, 0)$  are attractors. The positive singularity  $(u_5, v_5)$  is a saddle point.

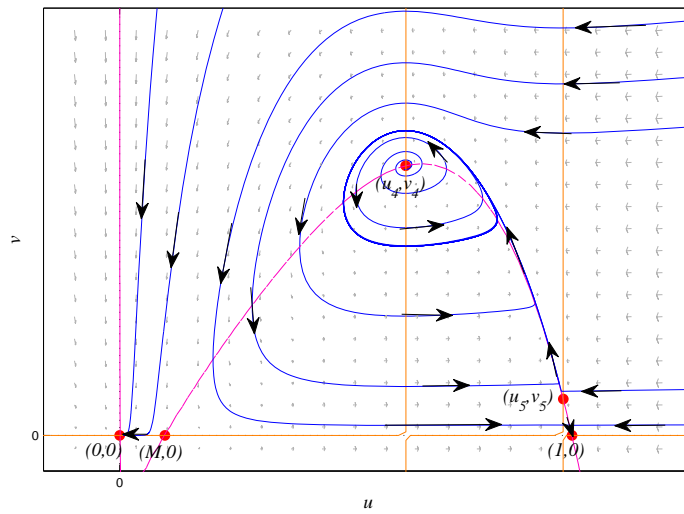


FIGURE 4. For  $A = .62$ ,  $B = 1$ ,  $C = 0.62$  and  $M = 0.05$ , the points  $(0, 0)$  and  $(1, 0)$  are attractor equilibrium points. The point  $(u_4, v_4)$  is a repeller surrounded by a limit cycle and  $(u_5, v_5)$  is a saddle point.

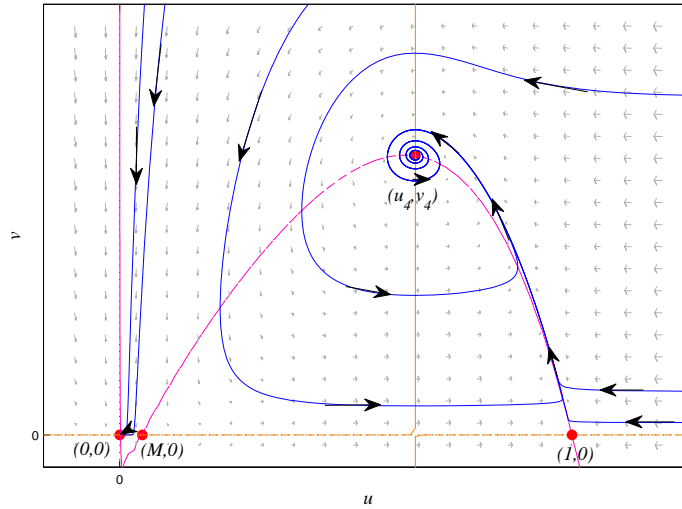


FIGURE 5. For  $A = .88$ ,  $B = 1$ ,  $C = 0.5$  and  $M = 0.05$ , the unique positive singularity  $(u_4, v_4)$  and  $(0, 0)$  are attractors;  $(1, 0)$  is a saddle point.

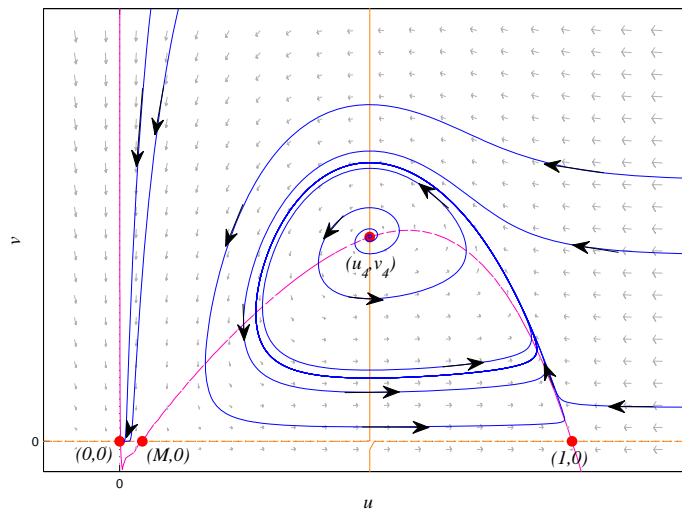


FIGURE 6. For  $A = .8$ ,  $B = 1$ ,  $C = 0.5$  and  $M = 0.05$ , the singularity  $(1, 0)$  is saddle point, the unique positive singularity  $(u_4, v_4)$  is a repeller surrounded by a unique limit cycle.

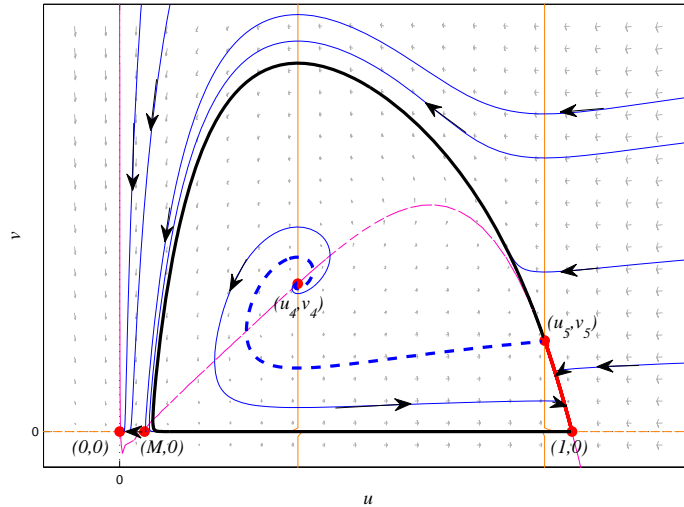


FIGURE 7. For  $A = .37$ ,  $B = 1$ ,  $C = 0.75$  and  $M = 0.05$ , the points  $(0,0)$  and  $(1,0)$  are attractors;  $(u_4, v_4)$  is repeller and  $(u_5, v_5)$  is a saddle point. There exist heteroclinic curves joining  $(u_4, v_4)$  with  $(1,0)$ ,  $(u_5, v_5)$  with  $(1,0)$  and  $(u_4, v_4)$  with  $(u_5, v_5)$ ; there exists no limit cycle.

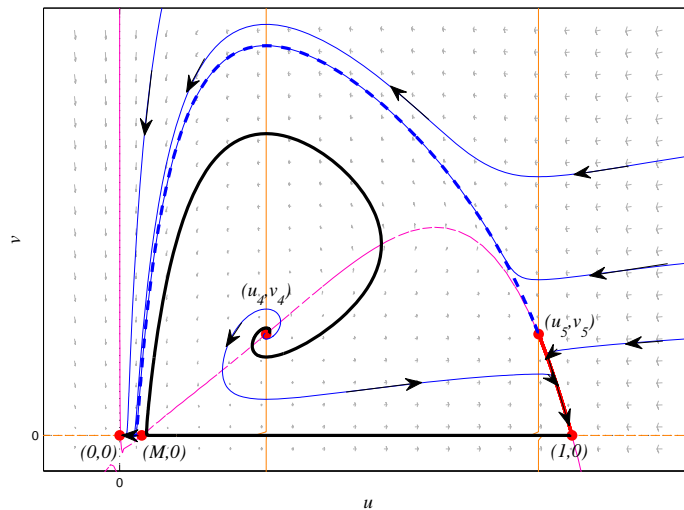


FIGURE 8. For  $A = .3$ ,  $B = 1$ ,  $C = 0.8$  and  $M = 0.05$ , the points  $(0,0)$  and  $(1,0)$  are attractors;  $(u_4, v_4)$  is a repeller and  $(u_5, v_5)$  is a saddle point. There exist heteroclinic curves joining  $(u_4, v_4)$  with  $(1,0)$ ,  $(u_5, v_5)$  with  $(1,0)$  and  $(u_5, v_5)$  with  $(M,0)$ .

$$C(4C^2A + 4C^2 - 1)M^2 + (-12C + 4C^2 + 20C^2A - 5 + 16C^3 + 16C^3A)M + 24C^2A + 15CA - 20C - 10 + 16C^3 + 8C^2 + 4C^3A^2 + 20C^3A = 0.$$

*Proof.*  $P_4$  is a weak focus, if and only if,

$$(2C + 5 + 2MC)W - 5 + 4AC^2 + 2C + 4MC^2 + 8C^2 = 0 \text{ or}$$

$$C(4C^2A + 4C^2 - 1)M^2 + (-12C + 4C^2 + 20C^2A - 5 + 16C^3 + 16C^3A)M + 24C^2A + 15CA - 20C - 10 + 16C^3 + 8C^2 + 4C^3A^2 + 20C^3A = 0.$$

If  $P_5 \in \tilde{\Gamma}$ , the above results hold for a subset of trajectories inside of the region defined by the separatrix curve which is determined by the horizontal stable manifold  $W^s(P_5)$  and under the separatrix curve determined by the stable manifold  $W^s(P_M)$ .

Then, depending on the the initial conditions, the trajectories have as  $\omega$ -limit either the point  $P_4$ , or a limit cycle which surrounds it, or the point  $P_1$  (see Figures 3 and 4).

If  $P_5 \notin \tilde{\Gamma}$ , the system behavior depends on the location of  $W^s(P_M)$  and  $W^u(P_1)$ . The above results hold for  $v^s \geq v^u$  that is,  $M \ll u_4 < 1$  and the nature of  $(u_4, v_4)$  depends on the sign of its trace (see Figures 5 and 6).

In order to determine the order of weakness, we calculate the Liapunov quantities [7], for a normal form [7] of system (4), translating the point  $(u_4, v_4) = (H, L)$  to origin  $(0, 0)$  [22, 24, 31] by means of the equalities  $u = U + H$  and  $v = V + L$ .

We recall that,

$u_4 = H = \frac{1}{2C}(1 - W)$  with  $W^2 = 1 - 4AC^2$ , with  $H$  satisfying the equation  $H - C(A + H^2) = 0$  and  $L = (1 - H)(H - M)(A + H^2)$ , we obtain the system  $Z_\nu$ :

$$\begin{cases} \frac{dU}{d\tau} = \left( (1 - (U + H))((U + H) - M)(A + (U + H)^2) - (V + L) \right) (U + H) \\ \frac{dV}{d\tau} = B \left( (U + H) - C(A + (U + H)^2) \right) (V + L) \end{cases}$$

The Jacobian matrix for vector field  $Z_\nu$  is

$$DZ_\nu(0, 0) = \begin{pmatrix} (-4H^3 + 3(1 + M)H^2 - 2(M + A)H + (1 + M)A)H & -H \\ BWL & 0 \end{pmatrix}$$

with  $\det DZ_\nu(0, 0) = HBWL > 0$  and the first Liapunov quantity is

$$\eta_1 = \text{tr} DZ_\nu(0, 0) = H((M - 2H + 1)A - H((2 - 3H)M + H(4H - 3))),$$

when,  $\text{tr} DZ_\nu(0, 0) = 0$ , we have  $A = \frac{H((2-3H)M - H(3-4H))}{M - 2H + 1}$  with

i)  $M - 2H + 1 < 0$  and  $(2 - 3H)M - H(3 - 4H) < 0$ , implying  $M < 2H - 1$  and  $M < \frac{H(3-4H)}{2-3H}$  or  $M < 2H - 1$  and  $M > \frac{H(3-4H)}{3H-2}$

ii)  $M - 2H + 1 > 0$  and  $(2 - 3H)M - H(3 - 4H) > 0$ , implying  $M > \frac{H(3-4H)}{2-3H}$ .

$$\frac{H(3-4H)}{2-3H} - (2H - 1) = 2 \frac{(1-H)^2}{2-3H}$$

Let  $F = \sqrt{\det DZ_\nu(0, 0)} = \sqrt{HBWL}$ . Using the matrix of Jordan [3]

$$J = \begin{pmatrix} 0 & -F \\ F & 0 \end{pmatrix} \text{ and the respective matrix of change of basis}$$

$$N = \begin{pmatrix} Z_{11} - \alpha & -F \\ Z_{21} & 0 \end{pmatrix}.$$

The change of variables is given by  $x = \frac{H}{F^2}V$ , and  $y = -\frac{1}{F}U$ , making

$W = \frac{A-H^2}{A+H^2}$ , for  $A > H^2$  and after of tedious algebraic calculus we obtain

$$\bar{Z}_\nu : \begin{cases} \frac{dx}{d\tau} = -Fy - \frac{BH^2}{A+H^2}Ly^2 - FB\frac{A-H^2}{A+H^2}xy - \frac{BH^2}{A+H^2}F^2xy^2 \\ \frac{dy}{d\tau} = Fx - F(-10H^3 + 6MH^2 + 6H^2 - 3HM - 3HA + A + MA)y^2 - \\ \frac{F^2}{H}xy + F^2(4H - M - 10H^2 + 4HM - A)y^3 - \\ F^3(1 - 5H + M)y^4 - F^4y^5 \end{cases}$$

rescaling the time by  $T = F\tau$  it becomes

$$\check{Z}_\nu : \begin{cases} \frac{dx}{dT} = -y - \frac{1}{F}\frac{BH^2}{A+H^2}Ly^2 - B\frac{A-H^2}{A+H^2}xy - \frac{BH^2}{A+H^2}Fxy^2 \\ \frac{dy}{dT} = x - (-10H^3 + 6MH^2 + 6H^2 - 3HM - 3HA + A + MA)y^2 - \\ \frac{F}{H}xy + F(4H - M - 10H^2 + 4HM - A)y^3 - \\ F^2(1 - 5H + M)y^4 - F^3y^5 \end{cases}$$

By using the Mathematica package [40] we obtain the second Liapunov quantity:

$$\eta_2 = -\frac{F}{A-H^2}f_1(A, H, M), \text{ where}$$

$$f_1(A, H, M) = -(M+1)A^2 + (H^2(9(M+1) - 26H))A + 6H^4 - 6H^3M(1-H).$$

Replacing  $A = \frac{H((2-3H)M - H(3-4H))}{M-2H+1}$ , it is obtained,

$$f_1(H, M) = \frac{2H^2}{(2H-M-1)^2}f_2(H, M) \text{ with}$$

$$f_2(H, M) = -(15H^2 - 12H + 2)M^3 - (1 - 4H)(21H^2 - 16H + 2)M^2 - H(162H^3 - 208H^2 + 85H - 12)M + H^2(104H^3 - 162H^2 + 84H - 15),$$

$f_1(A, H, M) < 0$  is incompatible with the conditions

$$\eta_1 = (M - 2H + 1)A - H((2 - 3H)M + H(4H - 3)) = 0 \text{ and } A > H^2.$$

Then,  $\eta_2$  can not change the sign; so  $P_4$  is a first order weak (fine) focus.  $\square$

Comparing with the results obtained in [22], we can conclude that the inclusion of the Allee effect in a Gause type predator-prey model with non-monotonic functional response decreases the number of limit cycles. But it is not a general property since the Gause type predator-prey model with sigmoid functional response considering the Allee effect increases the number of limit cycles [24, 31].

**Theorem 3.9.** Assume that  $\frac{1-C}{C} > A > \frac{M(1-CM)}{C}$ , then  $P_1$  and  $P_M$  are saddle points. Let  $W^s(P_M)$  and  $W^u(P_1)$  be the stable and unstable manifolds of  $P_M$  and  $P_1$  respectively, then there exists a subset of parameter values for which  $W^s(P_M) = W^u(P_1)$ , and an heteroclinic is originated, joining the saddle points  $P_1$  and  $P_M$ , and an invariant subregion  $\check{\Gamma} \subset \tilde{\Gamma}$  is determined.

*Proof.* If  $\frac{1-C}{C} > A > \frac{M(1-CM)}{C}$ , then  $P_1$  and  $P_M$  are saddle points and  $P_4$  is the unique point at the subregion  $\check{\Gamma} = \{(u, v) \in \tilde{\Gamma} / M < u < 1, 0 < v\}$ .

Let  $W^s(P_M)$ ,  $W^u(P_1)$  be the stable and unstable manifolds of  $P_M$  and  $P_1$ , respectively. It is clear that the  $\alpha$ -limit of  $W^s(P_M)$  and  $\omega$ -limit of  $W^u(P_1)$  are not at infinity on the direction of  $v$ -axis and under this conditions the  $\omega$ -limit of  $W^u(P_1)$  are not at  $u$ -axis; then there exist points  $(u^*, v^s) \in W^s(P_M)$  and  $(u^*, v^u) \in$



$W^u(P_1)$ , with  $v^s$  and  $v^u$  dependent on parameters, that is,  $v^s = s(A, B, C, M)$  and  $v^u = u(A, B, C, M)$ .

It can be seen that, if  $M < u^* \ll 1$ , then  $v^s < v^u$  and if  $M \ll u^* < 1$ , then  $v^s > v^u$ . Since the vector field  $Y_\eta$  is continuous with respect to the parameters, then the stable manifold  $W^s(P_M)$  intersects the unstable manifold  $W^u(P_1)$ .

Then, there exist  $(u_e^*, v_e^*) \in \tilde{\Gamma}$ , such that  $v^{*s} = v^{*u}$  and the equation  $s(A, B, C, M) = u(A, B, C, M)$  defines a surface in the parameter space  $(\mathbb{R}_+^3) \times ]-1, 1[$ , for which the heteroclinic curve exists and it has a bounded invariant subregion  $\check{\Gamma} \subset \tilde{\Gamma}$ , whose frontier is determined by the subinterval  $[M, 1]$  and the heteroclinic (Figure 9).  $\square$

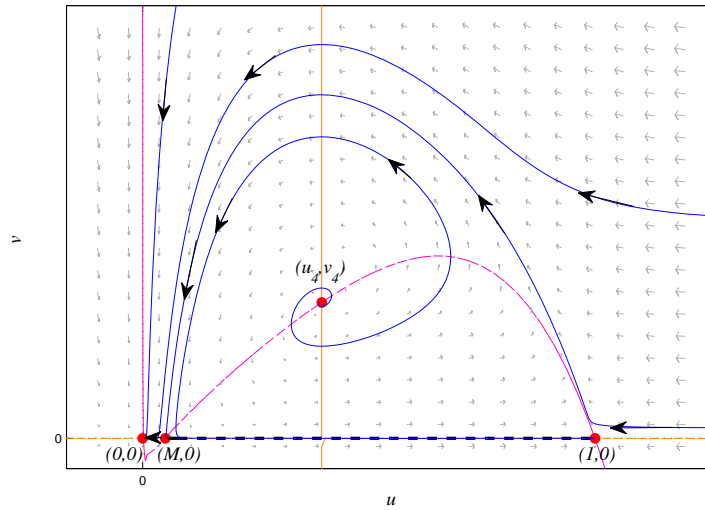


FIGURE 9.  $A = 0.635$ ,  $B = 1$ ,  $C = 0.5$  and  $M = 0.05$ , the heteroclinic curve joining the singularities  $(1, 0)$  and  $(M, 0)$  is shown.

Hereafter, let  $(u^*, v^s) \in W^s(P_M)$  and  $(u^*, v^u) \in W^u(P_1)$ , where  $v^s$  and  $v^u$  are functions of the parameters  $A, B, C$  and  $M$ .

**Theorem 3.10.** *Assuming that  $v^s < v^u$  and  $M < u_4 \ll 1$ , then the equilibrium point  $P_4$  is a repeller; the equilibrium point  $P_0$  is a global attractor, and there exists a heteroclinic curve joining them.*

*Proof.* If  $v^s < v^u$ , then the stable manifold  $W^s(P_M)$  lies below the unstable manifold  $W^u(P_1)$ . For uniqueness of solutions, the trajectories from the point  $(u_4, v_4)$ , can not intersect  $W^u(P_1)$  and since  $(M, 0)$  and  $(1, 0)$  are saddle points, by Poincaré-Bendixon Theorem they must have the point  $(0, 0)$  or a limit cycle as  $\omega$ -limit, when  $\text{tr}DY_\eta(u_e, v_e) > 0$ .

On the other hand, the limit cycles that appear by Hopf bifurcation increases until they disappear when the heteroclinic curve joining the points  $(M, 0)$  and  $(1, 0)$  is broken. Then there exists a subset of the parameter space for which the point  $(0, 0)$  is globally asymptotically stable.

Moreover, there exists one trajectory originated on  $(u_4, v_4)$  and ending on  $(0, 0)$ , forming a new heteroclinic curve (Figure 9); moreover, two heteroclinic curves joining the equilibrium points  $(M, 0)$  with  $(1, 0)$  and  $(u_4, v_4)$  with  $(M, 0)$  can exist for a determined parameter subset (Figure 10).  $\square$

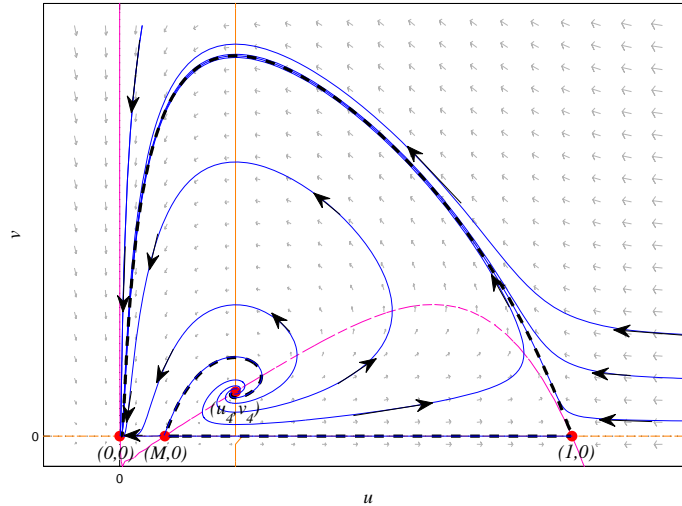


FIGURE 10.  $A = 0.4$ ,  $B = 1$ ,  $C = 0.55$  and  $M = 0.05$ . The singularity  $(0, 0)$  is a global attractor and there exist four heteroclinic curves joining  $(u_4, v_4)$  with  $(0, 0)$ ,  $(u_4, v_4)$  with  $(M, 0)$ ,  $(1, 0)$  with  $(0, 0)$  and  $(M, 0)$  with  $(1, 0)$ .

**3.2. A special case of weak Allee effect.** When  $M = 0$  in system (4) (that is,  $m = 0$  in system (3)) we have the following system:

$$Y_v : \begin{cases} \frac{du}{d\tau} = ((1-u)(A+u^2)u - v)u \\ \frac{dv}{d\tau} = B(u - C(A+u^2))v \end{cases} \quad (5)$$

For vector field  $Y_v$  or system (5) we have a similar result for the model with strong Allee effect that we summarize in the following :

**Theorem 3.11.** *a) For all parameter values at  $\bar{\Gamma}$  there exist the singularities  $P_0 = (0, 0)$  and  $P_1 = (1, 0)$ .*

*b) The origin is a saddle-node point having a separatrix curve determined by the stable manifold  $W^s(P_0)$  and it is an attractor for any trajectory laying above the separatrix.*

*c) If  $1 - 4C^2A < 0$ , there exist no equilibrium points at the interior of  $\bar{\Gamma}$ , whereas  $P_0 = (0, 0)$  and  $P_1 = (1, 0)$  are both local attractors.*

*e) If  $1 - 4C^2A = 0$ , there exists a unique equilibrium point at the interior of  $\bar{\Gamma}$   $P_4 = (\frac{1}{2C}, \frac{2C-1}{8C^4})$  if and only if,  $C > \frac{1}{2}$  and*

*1) is a saddle-node attractor, if  $3 - 4C > 0$ .*

*2) is a saddle-node repeller, if  $3 - 4C < 0$ .*

*3) the point  $P_4 = (u_4, v_4)$  is a cusp point [32] only for  $C = \frac{3}{4}$  and*

$$DY_v \left( \frac{2}{3}, \frac{16}{81} \right) = \begin{pmatrix} 0 & -\frac{2}{3} \\ 0 & 0 \end{pmatrix}$$

f) If  $1 - 4C^2A > 0$  then singularities  $P_4 = (u_4, v_4)$  and  $P_5 = (u_5, v_5)$  exist at  $\bar{\Gamma}$ .

1) The equilibrium points  $P_4$  and  $P_5$  belong to  $\bar{\Gamma}$  simultaneously if and only if  $A > \frac{1-C}{C}$ ; moreover, in this case  $P_1$  is an attractor.

2) The equilibrium point  $P_4 \in \bar{\Gamma}$  and  $P_5 \notin \bar{\Gamma}$ , if and only if,  $\frac{1-C}{C} > A$ ; in this case  $P_1$  is a saddle point.

g) Assuming that  $P_4 \in \bar{\Gamma}$ , then

1)  $P_4$  is an attractor point if and only if,

$$4C^3A^2 + C(24C + 15 + 20C^2)A + 2(2C + 1)(4C^2 - 5) > 0,$$

2)  $P_4$  is repeller surrounded by a stable limit cycle if and only if,

$$4C^3A^2 + C(24C + 15 + 20C^2)A + 2(2C + 1)(4C^2 - 5) < 0,$$

3)  $P_4$  is an order one weak focus if and only if,

$$4C^3A^2 + C(24C + 15 + 20C^2)A + 2(2C + 1)(4C^2 - 5) = 0,$$

This equality is fulfilled if  $A < 1$  and  $40C^3 + 32C^2 - 5C - 10 > 0$ .

h) Assume that  $\frac{1-C}{C} > A$ . Let  $W^s(P_0)$  and  $W^u(P_1)$  be the stable and unstable manifolds of  $P_0$  and  $P_1$  respectively, then there exists a subset of parameter values for which  $W^s(P_0) = W^u(P_1)$ , and a heteroclinic curve is originated which joins the saddle points  $P_1$  and  $P_0$ , and an invariant subregion  $\check{\Gamma} \subset \bar{\Gamma}$  is determined.

i) Let  $(u^*, v^s) \in W^s(P_0)$  and  $(u^*, v^u) \in W^u(P_1)$ , where  $v^s$  and  $v^u$  are functions of the parameters  $A, B$  and  $C$ . Assuming that  $v^s < v^u$  and  $0 < u_4 \ll 1$ , we have that the equilibrium point  $P_4$  is a repeller, the equilibrium point  $P_0$  is a global attractor, and there exists a heteroclinic curve joining them.

*Proof.* e1) Through the substitution  $u \rightarrow z + \frac{2}{3}$ ,  $v \rightarrow w + \frac{16}{81}$  [20] and by time rescaling, we can translate this point to the origin obtaining the vector field  $\bar{Z}$ . In order to prove that the origin of the vector field  $\bar{Z}$  is a cusp, it is sufficient to show that the Takens normal form of this singularity has codimension two, since it is the unique topological type in this codimension.

g3) In the case when

$$4C^3A^2 + C(24C + 15 + 20C^2)A + 2(2C + 1)(4C^2 - 5) = 0.$$

The first Liapunov quantities are

$$\text{tr}DZ_\nu(0,0) = (-4H^3 + 3H^2 - 2AH + A)H = 0,$$

and

$$\eta_2 = -\frac{Ef_2(A,H)}{A-H^2}.$$

with

$$f_2(A,H) = -A^2 - H^2(26H - 9)A + 6H^4.$$

The conditions for the existence of a limit cycle are

$$-A^2 - H^2(26H - 9)A + 6H^4 > 0 \text{ and } T = -4H^3 + 3H^2 - 2AH + A > 0,$$

and  $A > H^2$ , are not compatibles, then  $(u_4, v_4)$  is an order one weak (fine) focus [7].  $\square$

**4. Concluding remarks.** In this work we have analyzed the dynamics of a system, representing the ecological interaction between one prey population subjected to Allee effect and its specialist predator, which exhibits a non-monotonic functional response. The analysis was carried out on a simpler, topologically equivalent system. Our main purpose is to understand how an increasingly recognized ecological process

(Allee effect) affects the population dynamics in interaction with other plausible non-linearities, here the inhibited functional response.

If a non-monotonic functional response is considered for the standard Gause model, there exist up to two interior equilibrium points [32, 42, 44] and there exists a subset of parameter values for which a unique positive equilibrium point is surrounded by two limit cycles [22].

The resulting dynamics, when the two modifications described above are added simultaneously to the classical Gause model reveals that long-term behavior includes coexistence, extinction of predators or extinction of both prey and predators, depending on parameter values and initial conditions. For system (3) the origin  $(0, 0)$  is a local attractor equilibrium point for all parameter values; orbits starting from above the threshold curve determined by the stable manifold  $W^s(m, 0)$  of the equilibrium point  $(m, 0)$  have  $(0, 0)$  as its  $\omega$ -limit, implying the possibility of extinction of both populations. Below the separatrix, the invariance region  $\Gamma$  can contain up to two positive equilibria or a limit cycle surrounding a positive equilibrium point.

When two equilibrium points  $(x_1, y_1)$  and  $(x_2, y_2)$  exist within  $\Gamma$  where  $x_1 < x_2$ , the point  $(x_2, y_2)$  is a saddle point and  $(K, 0)$  is a local attractor. In this case,  $(x_1, y_1)$  can be an attractor point or a repeller surrounded by a stable limit cycle. Therefore, we have demonstrated that for some parameter values the system presents three simultaneous attractors: the point  $O = (0, 0)$ , the point  $(K, 0)$ , and either the point  $(x_1, y_1)$  or its associated periodic attractor.

If  $(x_2, y_2) \in \Gamma$ , and the stable manifold  $W^s(m, 0)$  is above the unstable manifold  $W^u(K, 0)$ , both populations coexist if initial conditions are near  $(K, 0)$ , but if population sizes are under the separatrix curve determined by  $W^s(x_2, y_2)$  the prey tends to reach its carrying capacity and predators go to extinction.

For some parameter values, there exists a unique singularity  $(x_1, y_1)$  at the interior of the first quadrant, in which case  $(x_2, y_2) \notin \Gamma$  and  $(K, 0)$  is a saddle point. The point  $(x_1, y_1)$  can be a repeller surrounded by a limit cycle, whose amplitude can be large enough as to touch the heteroclinic curve formed by the intersection of the stable manifold  $W^s(m, 0)$  and the unstable manifold  $W^u(K, 0)$ . When this heteroclinic breaks, we get one of two results: the stable manifold  $W^s(m, 0)$  can rest below the unstable manifold  $W^u(K, 0)$  and a subregion of invariance appears; otherwise  $W^s(m, 0)$  can rest above  $W^u(K, 0)$  and all trajectories have the point  $(0, 0)$  as their  $\omega$ -limit, that is, the singularity  $(0, 0)$  is a global attractor.

If there exists no equilibrium point at the interior of the first quadrant, i.e. if  $p^2 - 4ac^2 < 0$ , predators always tend to extinction, whereas the prey can either go to extinction since the origin is an attractor or attain its maximum size  $K$ , depending on which side of the separatrix curve initial conditions are.

Based on previous works, for instance in [22, 32, 42, 44], it is possible to postulate that the dynamics of system (3) is strongly influenced by Allee effect which determines the existence of the separatrix and the attracting nature of the origin implying the extinction of both populations, and by the non-monotonic functional response which determines the existence of two positive equilibrium points having a behaviour that is similar to those having no Allee effect.

Furthermore, the uniqueness of limit cycles in our system of interest is proved but this limit cycle can disappear when parameters vary and an heteroclinic curve joining the singularities  $(m, 0)$  and  $(K, 0)$  is formed.

However, we cannot assure that the Allee effect increases or diminishes the number of limit cycles since a different situation respect to our results has been observed

when a Gause type predator-prey model with a sigmoid functional response and the Allee effect on prey population is analyzed [24, 31]. For this system, the existence of two limit cycles is showed, differencing with the model without Allee effect for which the uniqueness of limit cycle is proved.

Then, for a general theory, models must be studied using other mathematical forms to express the Allee effect [22], or else, assume predators have an alternative food.

Accepting that ordinary differential equations (ODE) are a good tool to predict the behavior of species interactions, parodying Coleman [10], the problem is: Find a predator-prey or other interacting system in nature, or construct one in the laboratory, having three attracting sets for the same set of the parameter values.

This means that for a fixed set of parameters and different populations sizes of prey affected by the Allee effect and predators consuming them to a non-monotonic rate, it must occur: i) both populations can go to extinction, ii) the population of predators disappear and the prey goes to their maximum carrying capacity, or iii) the populations sizes oscillate around a fixed point.

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