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Multiple stability and uniqueness of the limit cycle in a Gause-type predator–prey model considering the Allee effect on prey

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ABSTRACT

In this work, a bidimensional differential equation system obtained by modifying the well-known predator–prey Rosenzweig–MacArthur model is analyzed by considering prey growth influenced by the Allee effect.

One of the main consequences of this modification is a separatrix curve that appears in the phase plane, dividing the behavior of the trajectories. The results show that the equilibrium in the origin is an attractor for any set of parameters. The unique positive equilibrium, when it exists, can be either an attractor or a repeller surrounded by a limit cycle, whose uniqueness is established by calculating the Lyapunov quantities. Therefore, both populations could either reach deterministic extinction or long-term deterministic coexistence.

The existence of a heteroclinic curve is also proved. When this curve is broken by changing parameter values, then the origin turns out to be an attractor for all orbits in the phase plane. This implies that there are plausible conditions where both populations can go to extinction. We conclude that strong and weak Allee effects on prey population exert similar influences on the predator–prey model, thereby increasing the risk of ecological extinction.

1. Introduction

In this work, we analyze a Gause-type predator–prey model derived from the reasonably realistic and well-known Rosenzweig–MacArthur model [1,2], where the Allee effect on the prey growth equation [3–5], has been incorporated. Our main goals involve describing the system dynamics and establishing the number of limit cycles that the system can exhibit.

It is well known that a classical Gause-type predator–prey model [6,7] is represented by the second-order differential equation system:

$$X : \begin{cases} \dfrac{dx}{dt} = x\,g(x) - h(x)\,y \\ \dfrac{dy}{dt} = (\psi(x) - c)\,y, \end{cases} \tag{1}$$

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where $x = x(t)$ and $y = y(t)$ indicate the prey and predator population sizes at time $t > 0$; functions $g(x)$, $h(x)$ and $\psi(x)$ have appropriate properties [7,8], representing the prey growth rate, functional response or the trophic function of the predator [9] and numerical response, respectively; function $f(x) = x\,g(x)$ is the prey population growth rate in the absence of predators.

The problem of determining the conditions that guarantee the uniqueness of a limit cycle [7], the global stability of the unique positive equilibrium in predator–prey systems [10], or the nonexistence of limit cycles [8], has been extensively studied over the last few decades starting with the work by Cheng [11].

The existence of limit cycles in predator–prey systems may be used to explain many real-world oscillatory phenomena. For a wide class of predator–prey models, those satisfying the so-called Kolmogorov conditions, May [12] claimed that a unique stable limit cycle must occur. However, it is possible to construct a predator–prey model satisfying the Kolmogorov conditions for which many periodic solutions inside an annular region bounded by two limit cycles exist [13].

However, it is not an easy task to study the quantity of limit cycles that can be originated throughout the bifurcation of a center-focus [14]. This problem is related to the well-known Hilbert 16th Problem for polynomial systems [15], and it is a question that has remained unanswered for the predation model, particularly for the Gause-type model described by system (1) [16].

On the other hand, *Allee effect* is an ecological phenomenon caused by any mechanism leading to a positive relationship between individual fitness and the abundance of conspecifics [5]. Distinct ecological mechanisms producing Allee effects are known, such as: reduction in matting success, suppressed social thermoregulation, reduced anti-predator defense, and reduced feeding efficiency [17]. Nevertheless, other causes may also generate these phenomena (see Table 1 in [18] or Table 2.1 in [19]).

Recent ecological research suggests the possibility that two or more Allee effects can be generated by mechanisms acting simultaneously on a single population (see Table 2 in [18]). The combined influence of some of these phenomena is known as *multiple Allee effect* [20,18,19].

The Allee effect is an important and interesting phenomenon for both ecologists and mathematicians. From an ecological point of view, the Allee effect increases the risk of population extinction, as supported by recent developments in ecology and conservation [3,19].

A combination of fluctuating population size and Allee effect has been invoked to explain the extinction of some animal species [5]. Although this phenomenon has attracted attention among scientists within different subfields of ecology, such as metapopulation dynamics, biological invasions, [19] or epidemiology, only some studies have analyzed the community consequences of Allee effect using bidimensional differential equation systems [21,22].

Careful mathematical analyses of simple models can reveal much about the dynamics of populations subjected to the Allee effect [5,23], where a new equilibrium point changing the structural stability of the system often appears [24,25].

The Allee effect can be divided into two main types, depending on how strong the per capita growth rate is depleted at low population sizes. These two types are called *strong Allee effect* [26–28] or *critical depensation* [29–31], and *weak Allee effect* [17,27] or *noncritical depensation* [29–31]. The strong Allee effect implies the existence of a threshold population level $m > 0$ [23,32], below which the population becomes extinct. This requires the population growth dx/dt to be negative for $x < m$, and positive if $x > m$, where $x = x(t)$ indicates the population size.

Many algebraic forms have been used to describe the Allee effect [33,22,4,26], although most of them are topologically equivalent [34]. However, some of these forms may produce a change in the quantity of limit cycles surrounding a positive equilibrium point in predator–prey models [24].

Oscillatory behavior in predator–prey (consumer–resource) interaction has been an important topic in Population Dynamics [27], since the persistence of ecological populations and communities over time is intimately related to their ability to maintain abundance distant from low numbers. In nature, fluctuating populations are prone to stochastic extinction when they go through phases of low abundance. Therefore, it is of great concern from a managing perspective, albeit technically challenging, to establish conditions under which populations are predicted to exhibit oscillatory behavior, especially if the Allee effect influences the prey population.

Our analyses show the consequences of both strong and weak Allee effects on the dynamics of the Rosenzweig–MacArthur predator–prey model are similar, when the simplest mathematical form for this effect is incorporated to the model. Remarkably, a heteroclinic curve appears, which increases the probability of deterministic extinction for both species. In addition, we establish the existence of a unique limit cycle surrounding the positive equilibrium point and conditions under which both populations go to extinction.

This paper is organized as follows: In the next section, we present the model, and a model topologically equivalent to the Gause-type predator–prey model is obtained. Section 3 deals with the main properties of the new model whose proofs are given in the Appendix; in Section 4 some simulation are shown and a brief discussion is formulated in Section 5.

2. The model

Using the most simple and common model in continuous time for representing the growth of the prey population influenced by the Allee effect and the hyperbolic functional response, the Gause-type predator–prey model is described by the following differential equation system:

$$X_\mu : \begin{cases} \dfrac{\mathrm{d}x}{\mathrm{d}t} = \left(r \left(1 - \dfrac{x}{K}\right)(x - m) - \dfrac{q\,y}{a + x} \right) x \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = \left(\dfrac{p\,x}{a + x} - c \right) y \end{cases} \tag{2}$$

with $\mu = (r, K, q, a, p, c, m) \in \mathbb{R}^6_+ \times \mathbb{R}$, and for ecological reasons $a, m < K$.

The equation representing the growth of prey in the absence of predators is

$$\frac{\mathrm{d}x}{\mathrm{d}t} = r\left(1 - \frac{x}{K}\right)(x - m)x,$$

where $m > 0$ is the minimum viable prey population, i.e., the threshold below which the population goes to extinction yet in absence of predators (strong Allee effect). If $m \leq 0$, equation represents the weak Allee effect. When $m = 0$, implies the collapse of the singularities m and 0. If $m < 0$, then the equation represents a compensatory growth function [29,31]; therefore, system (2) have a similar dynamics than the Rosenzweig–MacArthur model, and it will not be analyzed in this work; we only consider the special case of weak Allee effect when $m = 0$.

In system (2), the parameter r represents the intrinsic growth rate of the prey, meanwhile K is the prey carrying capacity. Function $h(x) = \frac{q\,x}{x+a}$, is the hyperbolic functional response, a particular case of Holling type II functional response [1,2]; in this function q is the maximum consumption rate of predators and a is the half saturation parameter. Finally, the parameter p is the efficiency of converting consumed prey into new predators, and c is the natural per capita mortality rate of predators.

System (2) is of Kolmogorov type [6,35]; so, the axes are invariant sets and it is defined in the first quadrant, i.e., in the set $\Omega = \{(x, y) \in \mathbb{R}^2 / \, x \geq 0, \; y \geq 0\}$.

The equilibrium points of system (2) or singularities of the vector field X_μ are $O = (0, 0)$, $P_K = (K, 0)$, $P_m = (m, 0)$ and $P_e = (x_e, y_e)$, where $x_e = \frac{ac}{p-c}$ and $y_e = \frac{r}{q}(1 - \frac{x_e}{K})(x_e - m)(a + x_e)$. The equilibrium P_m is a direct consequence of the Allee effect on prey.

On the other hand, equilibrium P_e arises due to predation and its existence is guaranteed in the interior of the first quadrant when $p > c$. Therefore, species are able to coexist if the conversion efficiency of predators is higher than their natural mortality, provided that the prey population level is maintained over the threshold m.

In order to simplify the calculus, we follow the methodology used in [36,37], changing the variables and rescaling the time through the function $\varphi : \Omega \times \mathbb{R} \longrightarrow \Omega \times \mathbb{R}$, such that

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

thus, $\det D\varphi(u, v, \tau) = \frac{K(a+Ku)}{q} > 0$. Then, φ is a diffeomorphism [14], for which the vector field X_μ in the new coordinate system is topologically equivalent to the vector field $Y_\eta = \varphi \circ X_\mu$, which takes the form $Y_\nu = P(u, v)\frac{\partial}{\partial u} + Q(u, v)\frac{\partial}{\partial v}$ [38]. The associated fourth-order polynomial system is given by

$$Y_\eta : \begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}\tau} = ((1 - u)(u - M)(A + u) - v)u \\ \dfrac{\mathrm{d}v}{\mathrm{d}\tau} = S\,(u - E)v \end{cases} \tag{3}$$

where $\eta = (A, E, S, M) \in \mathbb{R}^3_+ \times [0, 1[$, with $A = \frac{a}{K}$, $E = \frac{ac}{K(p-c)}$, $S = \frac{p-c}{rK}$ and $M = \frac{m}{K}$. Moreover, $p - c > 0$ and $0 < A < 1$; M can be zero on a particular case of weak Allee effect.

Since φ is a diffeomorphism, the vector field (3) has the same qualitative behavior than the original system (2) [38]. System (3) is defined on the set

$$\hat{\Omega} = \{(u, v) \in \mathbb{R}^2 / \, u \geq 0, \; v \geq 0\}.$$

The equilibrium points of system (3) are: $O = (0, 0)$, $Q_M = (M, 0)$ and $Q_1 = (1, 0)$, which always lie in $\hat{\Omega}$. The existence of $Q_e = (E, v_e)$ in $\hat{\Omega}$, where $v_e = (1 - E)(E - M)(A + E) > 0$, is guaranteed if $0 < M < E < 1$.

The corresponding Jacobian matrix is

$$D\,Y_\eta(u, v) = \begin{pmatrix} D\,Y_\eta(u, v)_{11} & -\,u \\ Sv & S(u - E) \end{pmatrix}$$

with

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

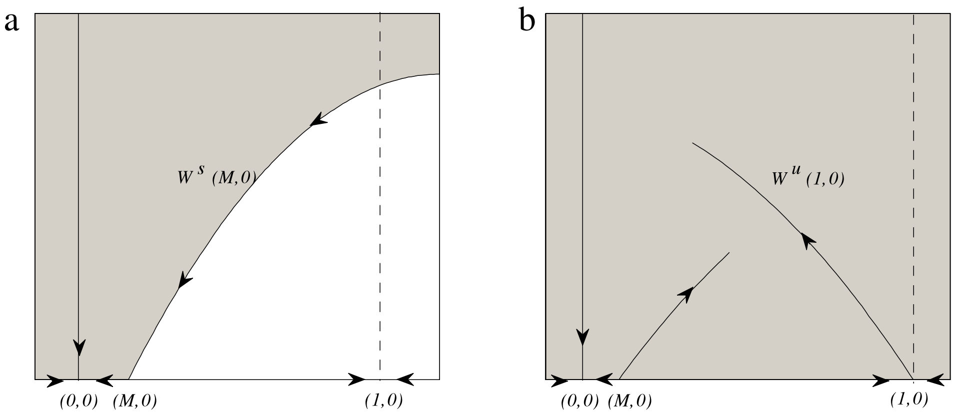

Fig. 1. The trajectories with initial conditions in the dark zones have the point (0, 0) as their ω-*límit*, for $E > 1$ (a) or $0 < E < M$ (b).

3. Main results

The following results were obtained for system (3); the proofs are given in the Appendix.

Lemma 1. (a) *The set* $\bar{\Gamma} = \{(u, v) \in \hat{\Omega} / 0 \le u \le 1,\ v \ge 0\}$ *is an invariant region.*
(b) *The solutions are bounded.*

Lemma 2. *Nature of equilibrium points over the axes*

(2.1) *The equilibrium point* $Q_1 = (1, 0)$ *is*
 (2.1.1) *a hyperbolic attractor, if and only if* $E > 1$.
 (2.1.2) *a hyperbolic saddle point, if and only if* $0 < M < E < 1$.
 (2.1.3) *a non-hyperbolic attractor, if and only if* $E = 1$.
(2.2) *The point* $Q_M = (M, 0)$ *is*
 (2.2.1) *a hyperbolic saddle point, if and only if* $M < E$.
 (2.2.2) *a hyperbolic repeller, if and only if* $E < M$.
 (2.2.3) *a non-hyperbolic repeller, if and only if* $M = E$.
(2.3) *The equilibrium point* $O = (0, 0)$ *is a hyperbolic attractor for any set of parameter values.*

The stable and unstable manifolds of Q_M and Q_1 are denoted by $W^s(M, 0)$ and $W^u(1, 0)$ respectively. Then we note that:

(a) If $E > 1$, then there are three equilibrium points O, Q_1 and Q_M in the invariant region $\bar{\Gamma}$. The equilibrium points O and Q_1 are local attractors, while Q_M is a saddle point. Moreover, there exists a separatrix curve for the trajectories in $\bar{\Gamma}$ determined by $W^s(M, 0)$, the stable manifold of the saddle point Q_M, which divides the behaviors of the trajectories (Fig. 2(a)).
(b) If $E = 1$, then Q_e coincides with Q_1 and a non-hyperbolic local attractor is obtained; the point O is a local attractor and Q_M a saddle point. The behavior of the trajectories in $\bar{\Gamma}$ is determined by $W^s(M, 0)$.
(c) If $E < M$ then there are three equilibrium points in the invariant region: Q_1 is a saddle point, Q_M is a repeller, and O is a global attractor for the trajectories in $\bar{\Gamma}$ (Fig. 2(b)).
(d) If $E = M$ then Q_e collapses with Q_M, being a non-hyperbolic repeller, and O is a global attractor.

Then, the stable manifold $W^s(M, 0)$ divides $\bar{\Gamma}$ into two subregions; one of them denoted by Λ is limited by $W^s(M, 0)$, the straight line $u = 1$, and the x-axis. When $E > 1$, Q_e lies outside the first quadrant and the trajectories with initial conditions inside Λ have the point Q_1 as ω-*límit* (Fig. 1(a)), whereas the orbits starting out of Λ (above the manifold $W^s(M, 0)$) have the point $(0, 0)$ as their ω-*límit* (Fig. 1(b)).

In the following, we assume that $0 < M < E < 1$, and hence the existence of a unique equilibrium point Q_e in the interior of the first quadrant is guaranteed, more precisely in the subregion $\hat{\Gamma} = \{(u, v) \in \bar{\Gamma} / M < u < 1, v \ge 0\}$. Moreover, the equilibrium point O is a local attractor and the singularities Q_1 and Q_M are saddle points.

Lemma 3. *Let* $W^s(M, 0)$ *and* $W^u(1, 0)$ *be the stable and unstable manifolds of* Q_M *and* Q_1 *respectively; then, a subset of parameter values for which* $W^s(M, 0) = W^u(1, 0)$ *exists, giving rise to a heteroclinic joining the saddle points* Q_1 *and* Q_M.

For $0 < M < E < 1$ we have that $\det D\,Y_\nu(E, v_e) > 0$, then the nature of the equilibrium point Q_e is dependent on the sign of the trace of the Jacobian matrix evaluated in this point. Whether Q_e is a node or a focus depends on the quantity:

$$\begin{aligned} P &= (\operatorname{tr} DY_\nu(E,\ v_e))^2 - 4 \det D\,Y_\nu(E,\ v_e) \\ &= (-3E^2 - 2EA + 2E + A)^2 - 4S(1 - E)(A + E). \end{aligned}$$

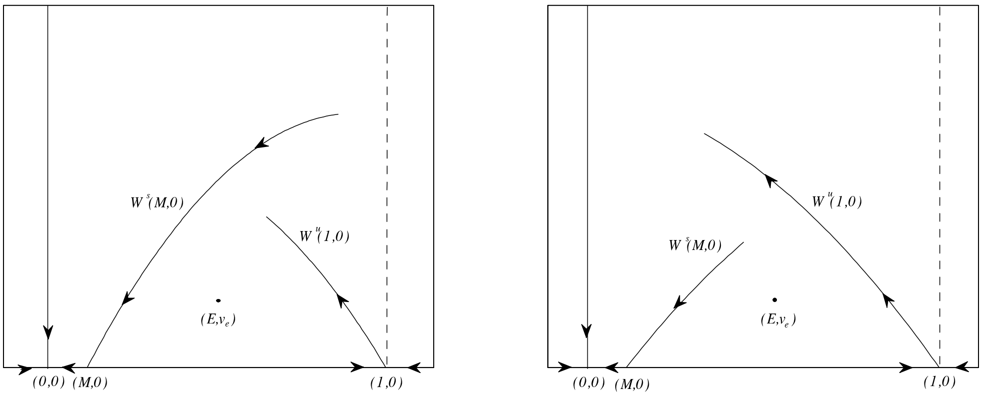

Fig. 2. Different positions of the stable manifold W^s of saddle point $(M, 0)$ and the unstable manifold W^u of saddle point $(1, 0)$, when $0 < M < E < 1$.

Theorem 4. *Let us assume that* $(u^*, v^s) \in W^s(M, 0)$ *and* $(u^*, v^u) \in W^u(1, 0)$, *where* v^s *and* v^u *are functions of the parameters* A, E, S *and* M. *Let us further assume that* $v^s \geq v^u$.

(a) *If* $A > \frac{-3E^2+2EM+2E-M}{2E-M-1}$, *then the trace is negative and the equilibrium* Q_e *is a local attractor.*

If $S > \frac{(-3E^2-2EA+2E+A)^2}{4(2)(A+E)}$, *then* Q_e *is an attracting focus, and*

if $S < \frac{(-3E^2-2EA+2E+A)^2}{4(2)(A+E)}$, *then* Q_e *is an attracting node.*

(b) *If* $A < \frac{-3E^2+2EM+2E-M}{2E-M-1}$, *then the trace is positive and the equilibrium* Q_e *is a repeller.*

(b1) *If* $S > \frac{(-3E^2-2EA+2E+A)^2}{4(2)(A+E)}$, *then* Q_e *is an unstable focus surrounded by a stable limit cycle.*

(b2) *If* $S < \frac{(-3E^2-2EA+2E+A)^2}{4(2)(A+E)}$, *then* Q_e *is an unstable node and the limit cycle disappears. In this last case, the singularity* $(0, 0)$ *is globally asymptotically stable.*

(c) *If* $A = \frac{-3E^2+2EM+2E-M}{2E-M-1} < 1$, *then* $\operatorname{tr} D\,Y_\nu(E, v_e) = 0$ *and the equilibrium point is a weak focus of order one* [14].

Note that for system (3) there is a unique stable limit cycle and there are not unstable limit cycles in the interior of the first quadrant, which is in disagreement with previous results [22].

Theorem 5. *Let* $(u^*, v^s) \in W^s$ *and* $(u^*, v^u) \in W^u$, *where* v^s *and* v^u *are functions of the parameters* A, E, S *and* M. *Assuming that* $v^s < v^u$ *and* $M < E \ll 1$, *then the equilibrium point* Q_e *is a repeller node and the equilibrium point* $(0, 0)$ *is a global attractor. Then, there exists a new heteroclinic curve linking the points* Q_e *and* $(0, 0)$.

3.1. A particular case of weak Allee effect

Considering $m = 0$ in the model (2), the following system is obtained:

$$Y_\eta : \begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}\tau} = ((1-u)(A+u)u - v)u \\ \dfrac{\mathrm{d}v}{\mathrm{d}\tau} = S\,(u-E)v \end{cases} \tag{4}$$

whose equilibrium points are $O = (0, 0)$, $Q_1 = (1, 0)$, and $Q_e = (E, (1-E)(A+E)E)$. In this case, the equilibrium point $(m, 0)$ of system (2) coincides with $(0, 0)$.

For the vector field Y_η we have:

Theorem 6. 1. *The origin is a saddle-node point; moreover, it is an attractor for any trajectory that lies above a separatrix curve determined by a stable manifold* $W^s(0, 0)$ *originated in the non-hyperbolic equilibrium point* (0.0).

2. *For the equilibrium points* Q_1 *and* Q_e, *we have that:*

(a) *if* $E > 1$, *then* Q_e *lies in the fourth quadrant and the singularity* Q_1 *is a local attractor,*
(b) *if* $0 < E < 1$, *then* Q_e *belongs to the first quadrant and the singularity* Q_1 *is a saddle point,*
(c) *if* $E = 1$, *then the singularity* Q_e *collapses with* Q_1, *being a saddle-node point.*

In the following we suppose that $0 < E < 1$ and let

$$\begin{aligned} P &= (\operatorname{tr} D\,Y_\nu(E, v_e))^2 - 4 \det D\,Y_\nu(E, v_e) \\ &= (-3E^2 - 2EA + 2E + A)^2 - 4S(1-E)(A+E). \end{aligned}$$

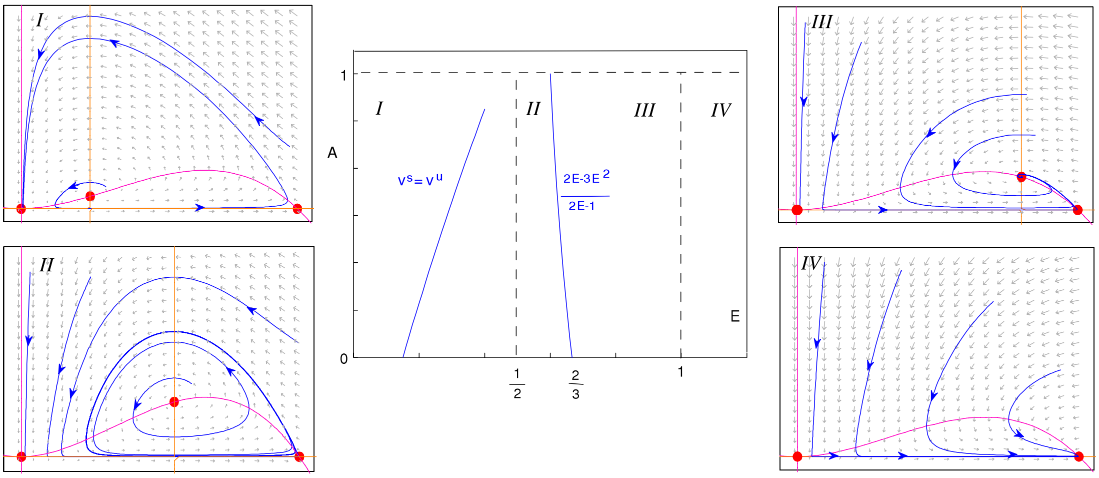

Fig. 3. The bifurcation diagram for the weak Allee effect in the parameter space E, A, where $(E, A) \in]0, 1[\times]0, 1[$, with the constraints $v^s = s(A, E, S, M) = v^u = u(A, E, S, M)$ and $\operatorname{tr} DY_\eta(E, v_e) = 0$.

Theorem 7. *Let $(u, v^s) \in W^s(0, 0)$ be, the stable manifold of O and $(u, v^u) \in W^u(1, 0)$, the unstable manifold of Q_1.*

7.1 *Assuming that $v^s > v^u$ we obtain that:*

(a) *If $A > \frac{2E-3E^2}{2E-1}$, the singularity Q_e is a local attractor.*

  (a1) *if $S > \frac{1}{4}\frac{(3E^2+2EA-2E-A)^2}{(1-E)(A+E)}$, the point Q_e is an attracting focus, and*

  (a2) *if $S < \frac{1}{4}\frac{(3E^2+2EA-2E-A)^2}{(1-E)(A+E)}$, the point Q_e is an attracting node.*

(b) *If $A < \frac{2E-3E^2}{2E-1}$, the singularity Q_e is a repeller.*

  (b1) *If $S > \frac{(-3E^2-2EA+2E+A)^2}{4(2)(A+E)}$, then Q_e is an unstable focus surrounded by a stable limit cycle.*

  (b2) *If $S < \frac{(-3E^2-2EA+2E+A)^2}{4(2)(A+E)}$, then Q_e is an unstable node and the limit cycle disappears. In this last case the singularity $(0, 0)$ is globally asymptotically stable.*

(c) *If $A = \frac{2E-3E^2}{2E-1}$ and $S > \frac{1}{4}\frac{(3E^2+2EA-2E-A)^2}{(1-E)(A+E)}$, Q_e is a weak focus of order one.*

7.2 *If $v^s < v^u$, then the point Q_e is a repeller, the limit cycle disappears and the origin is globally asymptotically stable; then, an heteroclinic curve is obtained, joining Q_e with $(0, 0)$.*

The bifurcation diagram of system (4) for the special case of weak Allee effect with $M = 0$ is shown in Fig. 3.

3.2. Some simulations

In Fig. 4 we present a set of simulations in order to illustrate the dynamic consequences of the strong Allee effect in the Rosenzweig–MacArthur model. We note that the point $(0, 0)$ is a local attractor for all parameter values. The results are similar to those obtained for the weak Allee effect, according to the bifurcation diagram shown in Fig. 4.

In Fig. 4a, the interior equilibrium (E, v_e) acts as a local attractor, where predators and preys can coexist in stable conditions, provided initial conditions below the separatrix curve.

In Fig. 4b the unique interior equilibrium is a repeller (an unstable focus) with a stable limit cycle around it, with predators and prey exhibiting an oscillatory behavior.

In Fig. 4c the unique interior equilibrium is a repeller and the limit cycles have disappeared, which means the prey and predator populations will ultimately go to extinction.

In Fig. 4d the equilibrium is located outside the invariant region, which means the predator population will ultimately tend to extinction, provided initial conditions below the separatrix curve.

4. Discussion

In this work we analyzed a deterministic predator–prey model derived from the Rosenzweig–MacArthur model that includes Allee effect in the prey population. It was verified that the Allee effect exerts a large influence on the long-term community stability. Whenever the threshold density m is positive, the singularity $(0, 0)$ is a locally asymptotically stable equilibrium point of the system for any set of parameter values. Therefore, there is a set of initial conditions for which both populations will disappear.

In our study system, the community extinction is driven by the existence of a separatrix curve, which is determined by the stable manifold of the saddle equilibrium point $(m, 0)$. In the case of the weak Allee effect, the non-hyperbolic equilibrium

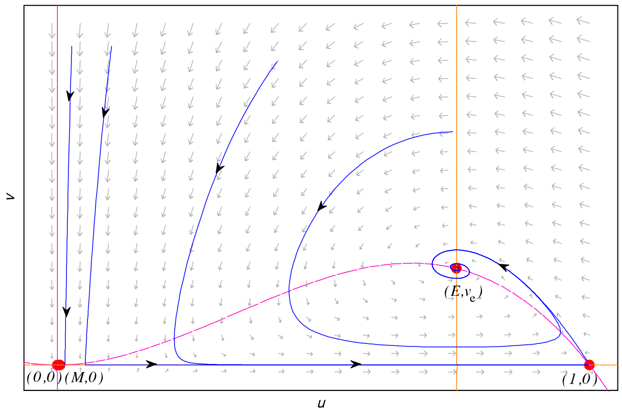

Fig. 4a. Coexistence or extinction of both species. For $A = 0.01, S = 1, E = 0.75$ and $M = 0.005$, the unique positive singularity (E, v_e) and the point (0, 0) are local attractors, $(M, 0)$ and (1, 0) are saddle points. The stable manifold $W^s(M, 0)$ determines a separatrix curve dividing the behavior of trajectories at the phase plane.

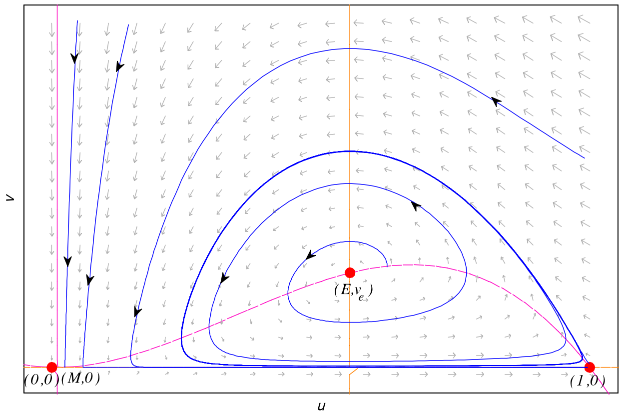

Fig. 4b. Periodicity or extinction of two species. For $A = 0.01, S = 1, E = 0.55$ and $M = 0.005$, the singularity (0, 0) is a local attractor; (E, v_e) is a repeller surrounded by a limit cycle; (1, 0) and $(M, 0)$ are saddle points; the stable manifold $W^s(M, 0)$ determines a separatrix curve dividing the behavior of trajectories in the phase plane.

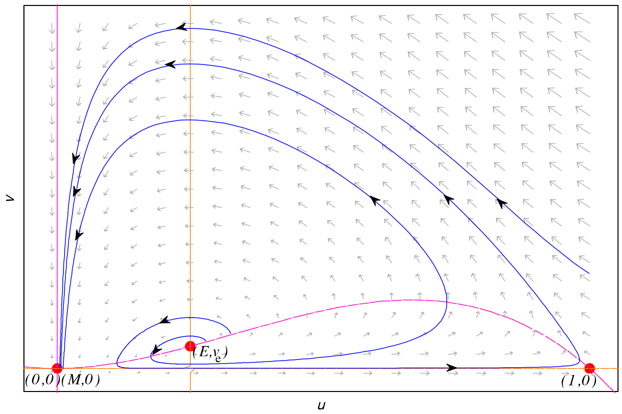

Fig. 4c. Extinction of two species. For $A = 0.01$, $S = 1$, $E = 0.25$ and $M = 0.005$; the singularity (0, 0) is a global attractor equilibrium point; (E, v_e) is a repeller, the limit cycle has disappeared; (1, 0) and $(M, 0)$ are saddle points and the stable manifold $W^s(M, 0)$ is below the unstable manifold $W^u(1, 0)$.

(0, 0) generates the separatrix curve. Then, two trajectories starting at opposite sides of the separatrix will have different *ω-limits* [39]. This implies, independent of the prey–predator ratio, the population trajectories starting above this separatrix will approach the equilibrium point (0, 0) and therefore will go extinct. Conversely, trajectories starting below the separatrix will approach either a steady state or a periodic oscillation, avoiding deterministic extinction.

Even though the weak Allee effect does not generate a new equilibrium point, its effect on the dynamics is remarkably similar to that found for the strong Allee effect, i.e., the deterministic extinction is predicted for a subset of parameters values, specially for low x/y ratios. Moreover, the separatrix curve observed with the strong Allee effect is preserved when (0, 0) and $(M, 0)$ collapse and the origin is a non-hyperbolic equilibrium point.

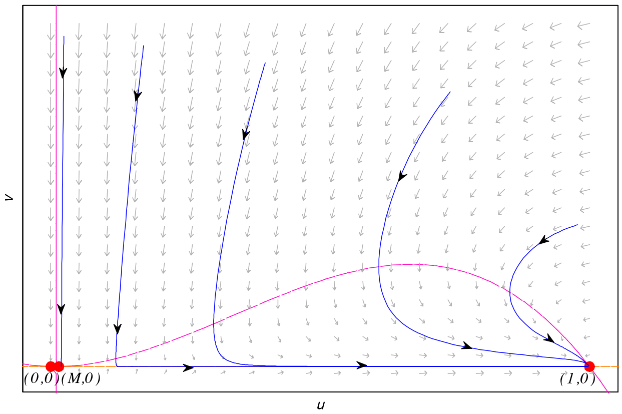

Fig. 4d. Extinction of predators or extinction of two species. For $A = 0.01$, $S = 1$, $E = 1.2$ and $M = 0.005$, the singularity $(0, 0)$ and the point $(1, 0)$ are local attractors, $(M, 0)$ is a saddle point. The singularity (E, v_e) is outside the invariant region $\bar{\Gamma}$. The stable manifold $W^s(M, 0)$ is below the unstable manifold $W^u(1, 0)$.

There is an invariant subregion $\tilde{\Lambda}$, limited by the stable manifold $W^s(m, 0)$, the straight line $x = K$ and the x-axis, where the dynamics is similar to that of the original Rosenzweig–MacArthur model.

A new interesting consequence of the Allee effect is the existence of a heteroclinic curve, for a set of parameter values, formed by the intersection of the unstable and the stable manifolds of singularities $(M, 0)$ and $(1, 0)$, respectively. With $A < \frac{1}{2}$, decreasing the value of parameter E (Fig. 2), the amplitude of the limit cycle increases, up to a limit where it coincides with the heteroclinic, and then a further increase in E destroys the periodic oscillation. Consequently, the point $(0, 0)$ is globally asymptotically stable, being ω-*limit* for all trajectories of the system. This situation has dramatic consequences on the fate of the ecological community, since both populations become extinct.

The model here analyzed does not satisfy the conditions for global stability of the unique positive equilibrium (x_e, y_e) reported by Xiao and Zhang [8]. This disagreement rests on the existence of a separatrix curve in the phase plane of the model studied here.

There are conditions of the parameter values for which the interior equilibrium point is unstable and surrounded by a unique stable limit cycle. The uniqueness of the limit cycle was demonstrated by calculating the Lyapunov quantities [14], a result that contradicts a proposition stated in [22]. Then, for a set of parameters values, both community extinction and population oscillations can result from different initial conditions.

Roughly speaking, Allee effect – either weak or strong – generates a basin of attraction where population trajectories inside it will invariably reach extinction. This result may seem intuitive as an extension of the case of single populations exhibiting a strong Allee effect, but it is not so when the Allee effect is weak since no additional equilibria appear in the one-dimensional case. The risk of extinction not only increases for those populations whose densities start within the extinction basin, but also for trajectories living within the coexistence basin.

The existence of a limit cycle therein impose a double risk for the persistence of populations exposed to a stochastic world. First, oscillating populations may reach low numbers at certain times, which can result in extinction after suffering a moderate stochastic perturbation. Second, oscillating populations can approach the separatrix curve at certain times, which can result in a jump into the extinction basin driven by a stochastic perturbation, namely passive noise [40].

Given the Allee effect is being increasingly identified in natural populations, and their dynamic consequences at the population and community levels are of deep concern, further empirical studies are needed as is presented in [28] to test theoretical predictions such as the ones revealed here.

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Appendix

Proof of Lemma 1. (a) Clearly, the u-axis and the v-axis are invariant sets, because the system is of Kolmogorov type. If $u = 1$, we have that

$$Y_\eta : \begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}\tau} = -v \\ \dfrac{\mathrm{d}v}{\mathrm{d}\tau} = S\,(u - E)v. \end{cases}$$

Then the vector field Y_η points to the inside of region $\bar{\Gamma}$, whatever the sign of $\frac{\mathrm{d}v}{\mathrm{d}\tau}$.

(b) In order to prove the boundedness of solutions, the Poincaré compactification [14] is used to study the behavior of point $(0, \infty)$. 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 $\frac{du}{d\tau} = -\frac{1}{v^2}\frac{dv}{d\tau}$. After simplifications, a new system $\breve{Z}$ is obtained where the nature of the point $(0, 0)$ of $\breve{Z}$ determines the nature of $(0, \infty)$.

Using the blowing up method [14,38], it is shown that $(0, 0)$ is a non-hyperbolic saddle point and, as a consequence, the point $(0, \infty)$ is a saddle point. □

Proof of Lemma 2. The Jacobian matrix [39] in Q_M, Q_1 and O are

$$D\,Y_\eta(M, 0) = \begin{pmatrix} M(1-M)(M+A) & -M \\ 0 & S(M-E) \end{pmatrix},$$

$$D\,Y_\eta(1, 0) = \begin{pmatrix} -(1-M)(1+A) & -1 \\ 0 & S(1-E) \end{pmatrix}$$

$$D\,Y_\eta(0, 0) = \begin{pmatrix} -AM & 0 \\ 0 & -SE \end{pmatrix},$$

(a) Clearly, the eigenvalues of $D\,Y_\eta(0, 0)$ are both negative, then O is a local attractor (locally asymptotically stable), since

$$\det D\,Y_\eta(0, 0) = AMSE > 0 \quad \text{and} \quad \operatorname{tr} D\,Y_\eta(0, 0) = -AM - SE < 0.$$

If $E > 1$, then Q_e is in the fourth quadrant and

$$\det D\,Y_\eta(M, 0) = SM(1-M)(M+A)(M-E) < 0;$$

thus, Q_M is a saddle point.
Since $\det D\,Y_\eta\,(1, 0) = -S(1+A)(1-M)(1-E) > 0$ and
$\operatorname{tr} D\,Y_\eta(1, 0) = -(1-M)(1+A) + S(1-E) < 0$;
then, Q_1 is an attractor.
Therefore, the behavior of the trajectories of the system in $\bar{\Omega}$, depend on their relative position with respect to the separatrix curve, determined by $W^s(M, 0)$ the stable manifold of Q_M. When the trajectories are above $W^s(M, 0)$, their *ω-limit* is the equilibrium point O, and if the trajectories are below $W^s(M, 0)$, then their *ω-limit* is the point Q_1.

(b) If $E = 1$, then the singularity Q_e collapses with Q_1, and $\det D\,Y_\eta(1, 0) = 0$. Applying the Center Manifold theorem [14] we can show that Q_1 is a non-hyperbolic local attractor. Moreover, Q_M is a saddle point and O is a local attractor (locally asymptotically stable), and the behavior of the trajectories is similar to case (a).

(c) If $E < M$, then $v_e < 0$, the equilibrium point Q_e is in the fourth quadrant, Q_M is a repeller since $\det DY_\eta(M, 0) > 0$ and $\operatorname{tr} D\,Y_\eta(M, 0) > 0$, whereas Q_1 is a saddle point because $\det DY_\eta(1, 0) < 0$ and O is a global attractor (globally asymptotically stable).

(d) If $E = M$, then Q_e collapses with Q_M, and $\det D\,Y_\eta(M, 0) = 0$. Applying the Center Manifold theorem we can show that Q_M is a non-hyperbolic local repeller. Moreover, Q_1 is still a saddle point and $(0, 0)$ is a global attractor. □

In the following, we suppose that $0 < M < E < 1$, and the existence of a unique equilibrium point Q_e in the interior of the first quadrant is guaranteed, more precisely in the subregion

$$\bar{\Gamma} = \{(u, v) \in \Gamma / 0 < M < u < 1, v \geq 0\}.$$

Moreover, O is a local attractor, the singularities Q_1 and Q_M are saddle points and $W^s(M, 0)$ and $W^u(1, 0)$ are the stable and unstable manifolds [14] of Q_M and Q_1, respectively.

Proof of Lemma 3. Let $W^s(M, 0)$, $W^u(1, 0)$ be the stable and unstable manifolds of Q_M and Q_1, respectively. It is then clear the *α-limit* of $W^s(M, 0)$ and *ω-limit* of $W^u(1, 0)$ are not at infinity on the direction of v-axis, nor the *ω-limit* of $W^u(1, 0)$ is over the u-axis; then, there are points $(u^*, v^s) \in W^s(M, 0)$ and $(u^*, v^u) \in W^u(1, 0)$, with v^s and v^u, depending on the parameter value, such that $v^s = s(A, E, S, M)$ and $v^u = u(A, E, S, M)$.

It can be that if $0 < M < u^* \ll 1$, then $v^s < v^u$ and if $M \ll u^* < 1$, then $v^s > v^u$. Since the vector field Y_η is continuous with respect to the parameters values, then the stable manifold $W^s(M, 0)$ intersects the unstable manifold $W^u(1, 0)$.

Hence, there exists $(u^*, v^*) \in \bar{\Gamma}$ such that $v^{*s} = v^{*u}$ and the equation

$$s(A, E, S, M) = u(A, E, S, M)$$

defines a surface in the parameters space, for which the heteroclinic curve exists. □

If $v^s > v^u$, an invariant subregion Λ, determined by stable manifold $W^s(M, 0)$, the straight $u = 1$ and the u-axis, exists. As the nature of the equilibrium point Q_e depends only on $\operatorname{tr} D\,Y_\nu(E, v_e)$, because $\det D\,Y_\nu(E, v_e)$ is always positive; then, the point Q_e can be an attractor or a repeller surrounded by at least one limit cycle (Poincaré–Bendixson theorem), or else it is a weak focus [14] in the subregion Λ.

$$\breve{\Gamma} = \{(u, v) \in \Gamma / M < u < 1, 0 < v \leq v^s\}.$$

The conditions for the nature of the point Q_e are established in the proof of Theorem 4.

Proof of Theorem 4. In the point Q_e, the Jacobian matrix is

$$D\,Y_\eta(E, v_e) = \begin{pmatrix} E(-3E^2 - 2EA + 2EM + 2E + AM + A - M) & -E \\ S(1-E)(E-M)(A+E) & 0 \end{pmatrix}.$$

Hence

$$\det D\,Y_\nu(E, v_e) = SE(1-E)(E-M)(A+E) > 0$$

and

$$\operatorname{tr} D\,Y_\nu(E, v_e) = E(-3E^2 - 2EA + 2EM + 2E + AM + A - M),$$

the behavior of (E, v_e) is determined by

$$T = (-2E + M + 1)A - 3E^2 + 2EM + 2E - M.$$

We have that:

(a) $\operatorname{tr} D\,Y_\eta(E, v_e) < 0$, if and only if, $A > \frac{-3E^2+2EM+2E-M}{2E-M-1}$ $(T < 0)$ and the singularity Q_e is a local attractor.

(b) $\operatorname{tr} D\,Y_\eta(E, v_e) > 0$, if and only if, $A > \frac{-3E^2+2EM+2E-M}{2E-M-1}$ and Q_e is a repeller and by the Poincaré–Bendixson theorem at least one limit cycle surrounding the point (E, v_e) exists; the trajectories under the separatrix determined by $W^s(M, 0)$ tend to this limit cycle.

When $v^s = v^u$, the limit cycle collapses with the heteroclinic that joins both saddle points.

(c) $\operatorname{tr} D\,Y_\eta(E, v_e) = 0$ if and only if $A = \frac{-3E^2+2EM+2E-M}{2E-M-1} < 1$.

To determine the weakness of Q_e we employ the translation to origin given by

$$u \to U + E \quad \text{and} \quad v \to V + v_e, \quad \text{with } v_e = \frac{(1-E)^2(E-M)^2}{2E-M-1},$$

obtaining the system

$$Z_\eta : \begin{cases} \dfrac{dU}{d\tau} = ((1-U-E)(U+E-M)(A+U+E) - (V+v_e))(U+E) \\ \dfrac{dV}{d\tau} = S\,U(V+v_e). \end{cases}$$

The Jordan form associated to $D\,Z_\eta(0, 0)$ is

$$J = \begin{pmatrix} \alpha & -H \\ H & \alpha \end{pmatrix}$$

with $\alpha = \operatorname{tr} D\,Z_\eta(0, 0) = 0$ and $H = \det DZ_\eta(0, 0)$ where

$$H^2 = SE\frac{(1-E)^2(E-M)^2}{2E-M-1}$$

and the matrix for the change of variables [39] is

$$N = \begin{pmatrix} Z11 - \alpha & -H \\ Z21 & 0 \end{pmatrix} = \begin{pmatrix} 0 & -H \\ \dfrac{H^2}{E} & 0 \end{pmatrix}.$$

Then the vector field Z_η becomes

$$\bar{Z}_\eta : \begin{cases} \dfrac{dx}{d\tau} = -Hy - HSxy \\ \dfrac{dy}{d\tau} = Hx - \dfrac{H^2}{E}xy + H(2)\dfrac{E}{2E-M-1}y^2 - H^2\dfrac{1-4E+5E^2-4EM+M^2+M}{2E-M-1}y^3 + H^3y^4. \end{cases}$$

Making a time rescaling given by $T = H\tau$, we have the canonical system

$$\breve{Z}_\eta : \begin{cases} \dfrac{dx}{dT} = -y - Sxy \\ \dfrac{dy}{dT} = x - \dfrac{H}{E}xy + (2)\dfrac{E}{2E-M-1}y^2 - H\dfrac{1-4E+5E^2-4EM+M^2+M}{2E-M-1}y^3 + H^2y^4. \end{cases}$$

Using the Mathematica software [41] to calculate the focal values for the vector field $\check{Z}_\eta$, the second Lyapunov quantity [14] is given by

$$L_2 = -\frac{(3)H}{8(3)} = -\frac{H}{8(3)} f(M, E),$$

where $L_2 < 0$, since

$$f(M, E) = 2 - 9E + 12E^2 + 2M - 9EM + 2M^2 > 0$$

for all E such as

$$\frac{1+M}{2} < E < \frac{1}{3}(M + 1 + \sqrt{M^2 - M + 1}).$$

Thus, Q_e is a weak focus of order one and system (3) has a unique limit cycle. □

Proof of Theorem 5. If $v^s < v^u$, then the stable manifold $W^s(M, 0)$ is below the unstable manifold $W^u(1, 0)$, and $0 < M < E \ll 1$. Due to uniqueness of solutions, the trajectories withdrawing from the point Q_e cannot intersect $W^u(M, 0)$ and they must have as ω-*limit* the point O, since Q_M and Q_1 are saddle points.

On the other hand, the limit cycle that appears by Hopf bifurcations increases until intersects the heteroclinic curve joining the points Q_M and Q_1, and disappearing when this curve is broken.

Then, there exists a subset on the parameters space for which the point O is globally asymptotically stable.

Moreover, there exists a trajectory originated on Q_e and ending on O, forming a new heteroclinic curve. □

Proof of Theorem 6. When $M = 0$, we have the weak Allee effect

(1) In this case the Jacobian matrix in O is

$$DY_\eta(0, 0) = \begin{pmatrix} 0 & 0 \\ 0 & -SE \end{pmatrix}.$$

Applying the Central Manifold Theorem we obtain the behavior of a saddle-node. There is a separatrix curve originated for the collapse of the points O and Q_M of system (3), dividing the behavior of the trajectories which have different ω-*limit*. Then, for all parameter values, O is a local attractor for all the trajectories with initial conditions above the separatrix curve.

(2) As the Jacobian matrix in Q_1 is

$$DY_\eta(1, 0) = \begin{pmatrix} -(1+A) & -1 \\ 0 & S(1-E) \end{pmatrix},$$

the equilibrium point Q_1 will have the same characteristics of the strong Allee effect depending on the sign of $1 - E$. □

Proof of Theorem 7. In the point Q_e, the Jacobian matrix is

$$DY_\eta(E, v_e) = \begin{pmatrix} -4E^3 + 3E^2(1-A) + 2AE - v_e & -E \\ Sv_e & 0 \end{pmatrix}$$

with $v_e = \frac{(1-E)^2E^2}{2E-1}$. As $v_e > 0$, then $\det DY_\eta(E, v_e) > 0$ and the nature of Q_e depends on

$$\operatorname{tr} DY_\eta(E, v_e) = -A(2E - 1) + E(2 - 3E).$$

Q_e has the same nature as the equivalent point in system (3) that is.

If $A > \frac{2E-3E^2}{2E-1}$, the singularity Q_e is an attractor.

If $A < \frac{2E-3E^2}{2E-1}$, the singularity Q_e is a repeller surrounded by a limit cycle (Theorem of Poincaré–Bendixson), when $v^s > v^u$.

If $A = \frac{2E-3E^2}{2E-1}$, the singularity Q_e is a weak focus.

Using the Mathematica software [41] we obtain that the second Lyapunov quantity [14] is $L_2 = -\frac{(3)H}{8(3)}$, with $H^2 = SE\frac{(1-E)^2E^2}{2E-1}$, which is clearly negative for $E > \frac{1}{2}$. For system (3), the uniqueness of limit cycle, when it exists, is assured.

This limit cycle increased when the parameters changed until to intersect the heteroclinic joining Q_1 and O.

7.2. When $E \to 0$, the point Q_e is a repeller node. The heteroclinic that joined the saddle points Q_1 and O is broken (also disappearing the limit cycle); then, the origin O will be globally asymptotically stable. □

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