Allee effect bifurcation in the γ-Ricker population model using the Lambert W function

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Abstract

- The main purpose of this talk is to present the dynamical study and the bifurcation structures of the **γ-Ricker population model**.
- Resorting to the **Lambert *W* function**, the analytical solutions of the positive fixed point equation for the γ-Ricker population model are explicitly presented and conditions for the existence and stability of these fixed points are established.
- Another main focus of this work is the definition and characterization of the **Allee effect bifurcation** for the γ-Ricker population model, which is not a pitchfork bifurcation.
- Consequently, we prove that the **phenomenon of Allee effect** for the γ-Ricker population model is associated to the asymptotic behavior of the Lambert *W* function in a neighborhood of zero.
- Numerical studies are included.

Introduction and motivation

- In [Ricker, 1954] is presented the classical discrete Ricker population model for modeling fish populations, given by the difference equation,

  $$x_{n+1} = r\, x_n\, e^{-\delta x_n},$$

  with $r > 0$ the density-independent death rate and $\delta > 0$ the carrying capacity parameter.
- In this population model is assumed that the survival function for generation n is density-dependent, while the birth or growth rate is density-independent.
- In several applications of this overcompensatory model to biology and ecology there are circumstances which lead to non constant density-dependent birth or growth functions. This phenomenon can be caused by several factors: difficulty to find mates, environmental modification, predator satiation, cooperative defense, among others.
- This model is classified in several studies as relatively inflexible, since it has only two parameters.

Introduction and motivation

- In this work it is considered the discrete-time population model whose dynamics of the population x_n, after n generations, is defined by the difference equation,

$$x_{n+1} = b(x_n)\ x_n\ s(x_n), \text{ with } n \in \mathbb{N} \tag{1}$$

  - $b(x_n) = x_n^{\gamma-1}$ is the per-capita birth or growth function (a cooperation or interference factor), with $\gamma > 0$ the cooperation parameter or Allee effect parameter;
  - $s(x_n) = e^{\mu - \delta x_n}$ is the survival function for generation n or the intraspecific competition, with $\mu > 0$ the density-independent death rate and $\delta > 0$ the carrying capacity parameter.
- We consider the γ-Ricker population model defined by Eq.(1) written in the form,

$$x_{n+1} = r\ x_n^{\gamma}\ e^{-\delta x_n} := f(x_n) \tag{2}$$

  where $r = e^{\mu} > 0$.
- Throughout this work, the parameters space is denoted by,

$$\Sigma_0 = \left\{ (r, \gamma, \delta) \in \mathbb{R}^3 :\ r, \gamma, \delta > 0 \text{ and } \gamma \neq 1 \right\}. \tag{3}$$

Fixed points of the γ-Ricker population model

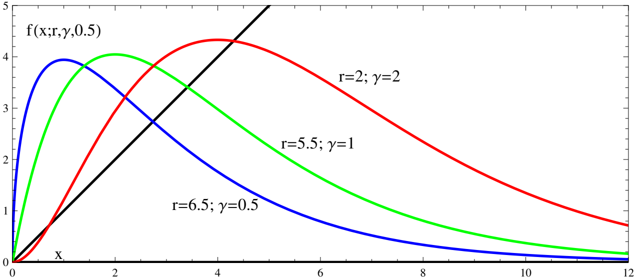


Figure: γ-Ricker population model $f(x; r, \gamma, \delta = 0.5)$, $f : [0, +\infty[\to [0, +\infty[$: the graphics corresponding to ($r = 6.5, \gamma = 0.5$) and ($r = 5.5, \gamma = 1$) are γ-Ricker population models without Allee effect; the graphic corresponding to ($r = 2, \gamma = 2$) is a γ-Ricker population model with Allee effect.

- The steady states of a population growth model are given by the positive fixed points, which are a significant part of the study of population dynamics.
- The fixed points equation of the γ-Ricker model is given by,

$$rx^{\gamma} e^{-\delta x} = x \;\Leftrightarrow\; x = 0 \;\vee\; rx^{\gamma-1} e^{-\delta x} = 1, \tag{4}$$

where $x = 0$ is the trivial solution.

Fixed points of the γ-Ricker population model

- In a neighborhood of the fixed point $x = 0$, the first derivative of the γ-Ricker model f verifies that,

$$\begin{cases} \lim\limits_{x \to 0^+} \dfrac{\partial f}{\partial x}(x; r, \gamma, \delta) = +\infty & , \text{ if } 0 < \gamma < 1 \\ \lim\limits_{x \to 0^+} \dfrac{\partial f}{\partial x}(x; r, \gamma, \delta) = r & , \text{ if } \gamma = 1 \\ \lim\limits_{x \to 0^+} \dfrac{\partial f}{\partial x}(x; r, \gamma, \delta) = 0 & , \text{ if } \gamma > 1 \end{cases} . \tag{5}$$

- Clearly, we can state that the stability of the fixed point $x = 0$ depends on the variation of the Allee effect parameter γ.
- Thus, the first derivative of the γ-Ricker model f is a discontinuous map at $x \to 0^+$, with respect to the Allee effect parameter γ.

Positive fixed points of the γ-Ricker population model defined as a Lambert W function

- On the other hand, in the Σ_0 parameters space, the equation of the positive fixed points can be written in an equivalent way as,

$$rx^{\gamma-1}e^{-\delta x} = 1 \Leftrightarrow -\frac{\delta x}{\gamma-1}e^{-\frac{\delta x}{\gamma-1}} = \frac{\delta}{1-\gamma}r^{\frac{1}{1-\gamma}}. \quad (6)$$

- Consequently, we obtain an equation written in the form $g(x)\, e^{g(x)} = y$, with

$$g(x) = -\frac{\delta x}{\gamma-1} \text{ and } y = \frac{\delta}{1-\gamma}r^{\frac{1}{1-\gamma}}. \quad (7)$$

- Thus, the equation of the positive fixed points of the γ-Ricker model, given by Eq.(6), is a Lambert W function defined by,

$$-\frac{\delta x}{\gamma-1} = W\left(\frac{\delta}{1-\gamma}r^{\frac{1}{1-\gamma}}\right). \quad (8)$$

Lambert W function

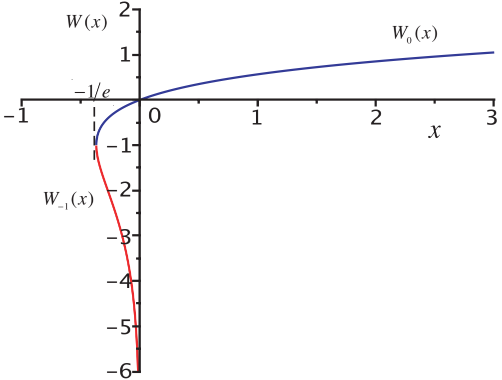


Figure: The two real branches of the Lambert W function, defined as the real analytic inverse of the function $W(x) = xe^x$: $W_0(x)$ (principal branch) and $W_{-1}(x)$ (other real branch).

- The Lambert W function is associated with the logarithmic function and arises from many models in the natural sciences, including a diversity of problems in physics, biological, ecological and evolutionary models, see [Lehtonen, 2016].

Fixed points of the γ-Ricker population model as analytical solutions of the Lambert W function

Proposition

Let $f : [0, +\infty[\to [0, +\infty[$ be the γ-Ricker model, defined by Eq.(19), in the Σ_0 parameters space, with $X(r, \gamma, \delta) = \frac{\delta}{1-\gamma} r^{\frac{1}{1-\gamma}}$ and let X^* be the set of the fixed points of f. In the (X^*, Σ_0) space it is verified that:

(i) *if $0 < \gamma < 1$, then Eq.(6) has one non-zero solution, given by the Lambert W function such that,*

$$x_0 = \frac{1-\gamma}{\delta} W_0 \left(X(r, \gamma, \delta) \right); \qquad (9)$$

(ii) *if $-\frac{1}{e} < X(r, \gamma, \delta) < 0$, then Eq.(6) has two non-zero solutions, given by the Lambert W function such that,*

$$x_0 = \frac{1-\gamma}{\delta} W_0 \left(X(r, \gamma, \delta) \right) \ \ and \ \ x_1 = \frac{1-\gamma}{\delta} W_{-1} \left(X(r, \gamma, \delta) \right). \qquad (10)$$

- If $X(r, \gamma, \delta) < -\frac{1}{e}$, for $\gamma > 1$, then the γ-Ricker model f has a single real fixed point $x = 0$. In this region $x_0, x_1 \in \mathbb{C}$ are complex and conjugate numbers. This region corresponds to an extinction region, in the Σ_0 parameters space.

Graphics of the Lambert W function

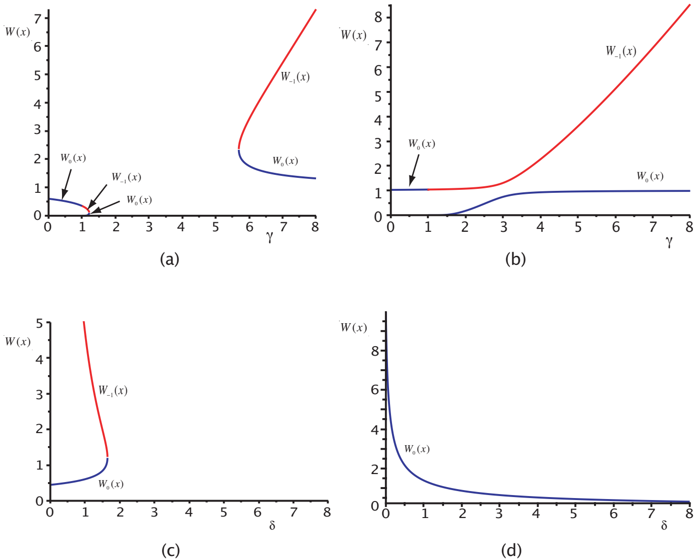


Figure: Graphics of the Lambert W function defined by Eq.(8): (a) $(r = 2, \delta = 2)$; (b) $(r = 8, \delta = 2)$; (c) $(r = 5, \gamma = 3)$; (d) $(r = 5, \gamma = 0.3)$.

Fold bifurcation of the non-zero fixed points of the γ-Ricker model

- The next result establishes the relationship between the double valued (or global minimum) of the Lambert W function and the fold bifurcation of the non-zero fixed points of the γ-Ricker model.

Corollary

Let $f : [0, +\infty[\to [0, +\infty[$ be the γ-Ricker model, defined by Eq.(19), in the Σ_0 parameters space, with $X(r, \gamma, \delta) = \frac{\delta}{1-\gamma} r^{\frac{1}{1-\gamma}}$. The set

$$S_{(1)_0} = \left\{ (r, \gamma, \delta) \in \Sigma_0 : X(r, \gamma, \delta) = -\frac{1}{e}, \textit{ for } \gamma > 1 \right\} \tag{11}$$

is a fold bifurcation surface of f relative to the fixed point $x = \frac{\gamma-1}{\delta}$.

- The fold bifurcation surface of f, for the non-zero fixed points, is defined by,

$$\begin{cases} f(x; r, \gamma, \delta) = x \\ \frac{\partial f}{\partial x}(x; r, \gamma, \delta) = 1 \end{cases} \Leftrightarrow \begin{cases} x = \frac{\gamma-1}{\delta}, \text{ for } \gamma > 1 \\ r = \varphi_1(x; \gamma, \delta) = \left(\frac{\gamma-1}{\delta}\right)^{1-\gamma} e^{\gamma-1} \end{cases}. \tag{12}$$

Stability of the positive fixed points of the γ-Ricker model

- The flip bifurcation surface of f, for the non-zero fixed points, is defined by,

$$\begin{cases} f(x;r,\gamma,\delta)=x \\ \frac{\partial f}{\partial x}(x;r,\gamma,\delta)=-1 \end{cases} \Leftrightarrow \begin{cases} x=\frac{\gamma+1}{\delta}, \text{ for } \gamma>0 \\ r=\psi_1(x;\gamma,\delta)=\left(\frac{1+\gamma}{\delta}\right)^{1-\gamma} e^{1+\gamma} \end{cases} . \quad (13)$$

- The stability results for the positive fixed points of the γ-Ricker model are summarized in the next proposition, where x_0 and x_1 are the analytical solutions of the Lambert W function, given by Proposition 1 (ii).

Proposition

Let $f:[0,+\infty[\to[0,+\infty[$ be the γ-Ricker model, defined by Eq.(19), with $r=\varphi_1(x;\gamma,\delta)$ and $r=\psi_1(x;\gamma,\delta)$ given by Eqs.(12) and (13), respectively, in the Σ_0 parameters space. If $\gamma>1$ and $r>\varphi_1(x;\gamma,\delta)$, then there exist two positive fixed points $0<x_1<x_0$. The fixed point x_1 is unstable and the fixed point x_0 is locally asymptotically stable if $r<\psi_1(x_0;\gamma,\delta)$ and is unstable if $r>\psi_1(x_0;\gamma,\delta)$.

Allee effect phenomenon

- Taking into account the above results, we can conclude that the Allee effect parameter $\gamma = 1$ represents a change in the bifurcation behavior in a neighborhood of the fixed point $x = 0$ of f. Therefore, the set defined by

$$\Theta_{AE} = \left\{ (r, \gamma, \delta) \in \mathbb{R}^3 : \; r, \gamma, \delta > 0 \text{ and } \; \gamma = \nu(r, \delta) = 1 \right\} \tag{14}$$

is a bifurcation plane that characterizes the stability of the fixed point $x = 0$.

- In the next result is characterized the birth of the Allee fixed points $x = x_1$.

Proposition

Let $f : [0, +\infty[\to [0, +\infty[$ be the γ-Ricker model, defined by Eq.(19), in the Σ_0 parameters space, where $X(r, \gamma, \delta) = \frac{\delta}{1-\gamma} r^{\frac{1}{1-\gamma}}$ and $S_{(1)_0}$ the fold bifurcation surface, defined by Eq.(11). In the (X^*, Σ_0) space it is verified that:

(i) *the set*

$$\hat{H}_{(1)_0} = \{ (r, \gamma, \delta) \in \Sigma_0 : r = \varphi_1(x; \gamma \to 1^+, \delta) \to 1^+ \} \tag{15}$$

is a fold bifurcation curve relative to the fixed point $x = 0$ of f. Moreover, it is verified that $\hat{H}_{(1)_0} \subset \Theta_{AE}$;

(ii) *the bifurcation relative to the $(1; j)$-cycle of f at the bifurcation plane Θ_{AE} is not a pitchfork bifurcation.*

Scheme of the Allee effect bifurcation

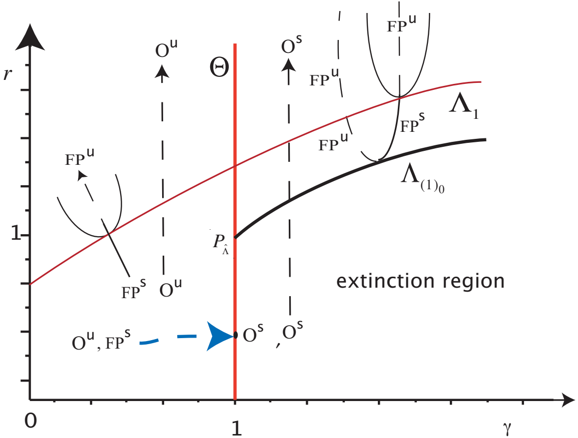


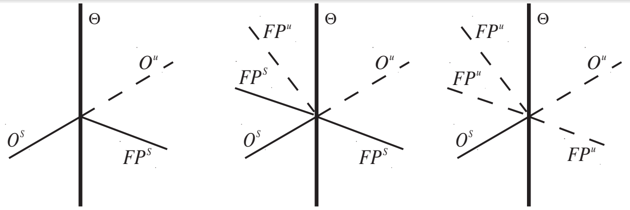
Figure: Scheme of the Allee effect bifurcation, in the $\Delta_{\gamma,r}$ parameter plane: $O^s \equiv$ stable origin, $O^u \equiv$ unstable origin, $FP^s \equiv$ stable fixed point, $FP^u \equiv$ unstable fixed point, Θ is the Allee effect bifurcation curve, see Definition 2, $\Lambda_{(1)_0}$ is a fold bifurcation curve of the 1-cycle (which is not from $x = 0$), Λ_1 is a flip bifurcation curve of the 1-cycle (which is not from $x = 0$), $P_{\hat{\Lambda}}$ is a point of the fold bifurcation curve $\hat{H}_{(1)_0}$.

Definition

Let $f : [0, +\infty[\to [0, +\infty[$ be the γ-Ricker model, defined by Eq.(19), in the Σ_0 parameters space, with $r = \psi_1(x; \gamma, \delta)$, given by Eq.(13). In the $(X^*; \Sigma_0)$ space, the Allee effect bifurcation occurs at the crossing of the bifurcation plane Θ_{AE}, given by Eq.(14), which is schemed in the following way,

$$\begin{cases} O^s \leftrightarrow O^u + FP^s & , \text{ if } 0 < r < 1 \\ O^s + FP^s + FP^u \leftrightarrow O^u + FP^s & , \text{ if } 1 < r < \psi_1(x; 1, \delta) \\ O^s + FP^u + FP^u \leftrightarrow O^u + FP^u & , \text{ if } r > \psi_1(x; 1, \delta) \end{cases} . \qquad (16)$$

The set Θ_{AE} is designated by the Allee effect bifurcation plane.



(a) (b) (c)

$\Delta_{\gamma,r}$ parameter plane - ($\delta = 2$)

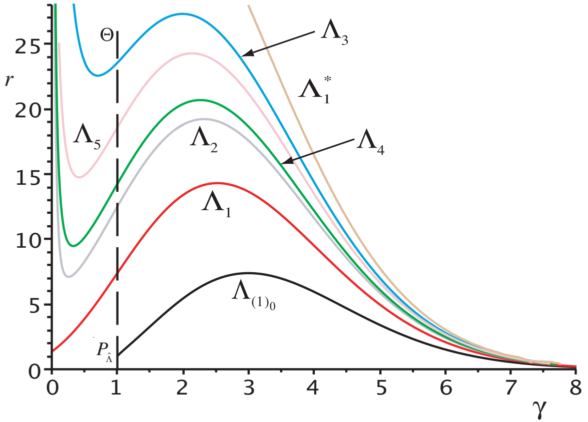


Figure: Bifurcation curves of the γ-Ricker population model $f^n(x; r, \gamma, 2)$, with $n = 1, 2, 3, 4, 5$, in the $\Delta_{\gamma,r}$ parameter plane: $\Lambda_{(1)_0}$ is the fold bifurcation curves of the cycle of order $n = 1$; Λ_n are the flip bifurcation curves of the cycles of order $n = 1, 2, 3, 4, 5$; Λ_1^* is the SBR bifurcation curve; Θ is the Allee effect bifurcation curve; $P_{\hat{\Lambda}}$ is the point of the fold bifurcation curve $\hat{H}_{(1)_0}$.

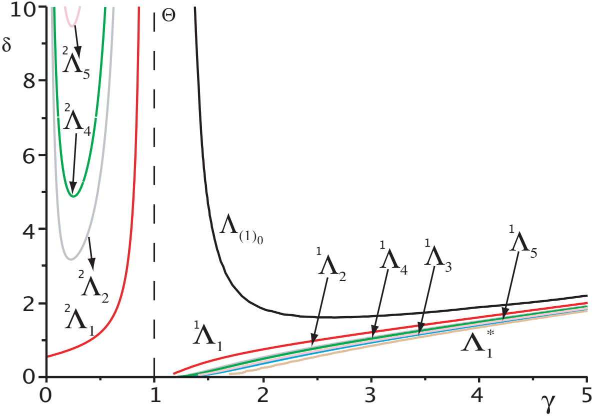


Figure: Bifurcation curves of the γ-Ricker population model $f^n(x;5,\gamma,\delta)$, with $n = 1,2,3,4,5$, in the $\Delta_{\gamma,\delta}$ parameter plane: $\Lambda_{(1)_0}$ is the fold bifurcation curves of the cycle of order $n = 1$; Λ_n^1 and Λ_n^2 are the flip bifurcation curves of the cycles of order $n = 1,2,3,4,5$; Θ is the Allee effect bifurcation curve.

$\Delta_{\delta,r}$ parameter plane - ($\gamma = 2$)

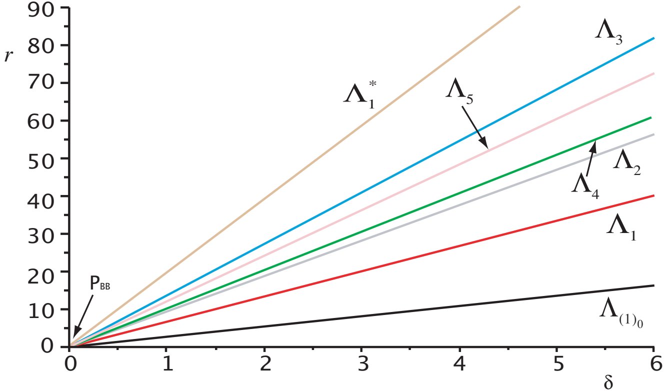


Figure: Bifurcation curves of the γ-Ricker population model $f^n(x; r, 2, \delta)$, with $n = 1, 2, 3, 4, 5$, in the $\Delta_{\delta,r}$ parameter plane: $\Lambda_{(1)_0}$ is the fold bifurcation curves of the cycle of order $n = 1$; Λ_n are the flip bifurcation curves of the cycles of order $n = 1, 2, 3, 4, 5$; Λ_1^* is the SBR bifurcation curve; P_{BB} is the big bang bifurcation point.

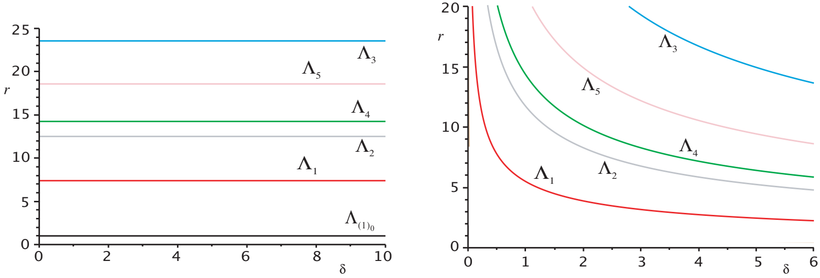


Figure: Bifurcation curves of the γ-Ricker population model $f^n(x; r, \gamma, \delta)$, with $n = 1, 2, 3, 4, 5$, in the $\Delta_{\delta,r}$ parameter plane: $\Lambda_{(1)_0}$ is the fold bifurcation curve of the cycle of order $n = 1$; Λ_n are the flip bifurcation curves of the cycles of order $n = 1, 2, 3, 4, 5$.

Results to appear in IJBC (June 2020)

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Bifurcation analysis of the γ-Ricker population model using the Lambert w function

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Future research

- **γ-Ricker population model with a Holling type II per-capita birth function**.
- Consider the discrete-time population model whose dynamics of the population x_n, after n generations, with $n \in \mathbf{N}$, is defined by the difference equation,

$$x_{n+1} = b(x_n)\ x_n^{\gamma-1}\ s(x_n) \tag{17}$$

with $\gamma > 0$ the cooperation or Allee's effect parameter. The per-capita birth or growth function is defined by,

$$b(x_n) = \frac{c x_n}{\beta + x_n} \tag{18}$$

a Holling's type II functional form or rectangular hyperbola.

- Generically, we study an extended γ-Ricker population model, defined by Eq.(17), written in the form,

$$x_{n+1} = r\ \frac{x_n^{\gamma}}{\beta + x_n}\ e^{-\delta x_n} := f(x_n) \tag{19}$$

where the per-capita birth or growth function $b(x_n)$ used is a Holling function of type II.

Acknowledgements and main references

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Main references:

- W.E. Ricker (1954) *Stock and recruitment*, J. Fish. Res. Board Canada, **11 (5)**, 559–623.
- J. Leonel Rocha and Abdel-Kaddous Taha (2020) *Bifurcation analysis of the γ-Ricker population model using the Lambert W function*, International Journal of Bifurcation & Chaos, to appear in June.
- J. Lehtonen (2016) *The Lambert W function in ecological and evolutionary models*, Methods Ecol. Evol., **7**, 1110–1118.

Sketch of the proof (not a pitchfork bifurcation)

- Consider a generic point of the bifurcation plane $(r, \gamma = 1, \delta) \in \Theta_{AE}$. For these parameter values, the fixed points of f are $x^* = 0$ and $x^* = \delta^{-1} \ln r$.
- The fixed point $x^* = 0$ is non-hyperbolic just for the bifurcation points $(r = 1, \gamma = 1, \delta) \in \Theta_{AE}$, i.e.,

$$\frac{\partial f}{\partial x}(x^*; r, \gamma = 1, \delta) = 1 \Leftrightarrow r = 1. \tag{20}$$

- For $x^* = 0$ and $(r = 1, \gamma = 1, \delta) \in \Theta_{AE}, \forall \delta > 0$, are verified the next conditions,

$$\frac{\partial f}{\partial r}(x^*; r = 1, \gamma = 1, \delta) = 0, \ \forall \delta > 0$$

and

$$\frac{\partial^2 f}{\partial x^2}(x^*; r = 1, \gamma = 1, \delta) = -2\delta \neq 0, \ \forall \delta > 0. \tag{21}$$

Considering the results on pitchfork bifurcation, see, for example, [Strogatz, 1994] and [Wiggins, 2003], Eq.(21) is a contradiction of that f has a pitchfork bifurcation at $x^* = 0$ and $(r = 1, \gamma = 1, \delta) \in \Theta_{AE}, \forall \delta > 0$; (nullity conditions).
- Also it is proved that there is not a pitchfork bifurcation of f at $x^* = \delta^{-1} \ln r$, for $(r = 1, \gamma = 1, \delta) \in \Theta_{AE}, \forall \delta > 0$.