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STABILITY AND BIFURCATION ANALYSIS OF A NON–LINEAR GINZBURG–TANEYHILL POPULATION MODEL WITH MINIMAL MATERNAL QUALITY

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Dedicated to the 65th birthday of the dear Professor Mehmed Nurkanović

ABSTRACT. In this paper, we investigate the stability and Neimark-Sacker bifurcation of a Ginzburg–Taneyhill model under the assumption of minimal maternal quality. The analysis begins with an examination of the existence and classification of equilibrium points, followed by a detailed study of their local stability. We show that the system undergoes a Neimark–Sacker bifurcation under certain parameter conditions, leading to the emergence of an invariant closed curve. Numerical simulations are presented to illustrate and confirm the theoretical results.

1. INTRODUCTION

In this paper, we investigate the following system of difference equations:

$$\begin{cases} x_{t+1} = \frac{1}{R(R-1)} + \frac{(Mx_t)^\beta}{1+Rx_t y_t}, \\ y_{t+1} = Rx_t y_t, \end{cases} \tag{1.1}$$

where x_t is the average quality of the individuals (maternal effect) and y_t represents population size at t generation and $M, R > 1$ with $0 < \beta \neq 1$.

The study of biological models and the mathematical description of relationships between generations of certain species began roughly a century ago. Most of these studies are based on the theory of discrete dynamical systems, which provides a framework for describing the interactions between two or more species.

In their work [4], Ginzburg and Taneyhill also introduced a two-dimensional system of interactions. However, this model does not represent a classical example of interspecific interaction; instead, it describes the relationship between two characteristics within a single population. One of these characteristics represents

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the population ratio between two successive generations, while the other dimension reflects the average quality of individuals within the population – a concept associated with the maternal effect. The maternal effect refers to female fecundity and the ability of offspring to survive from birth to adulthood. This ability is influenced by several factors, including food availability, environmental conditions, and genetic predispositions. In essence, the quality of the offspring is directly linked to the quality of the mother – i.e., the maternal effect. These assumptions can be represented by the following system of equations:

$$\begin{cases} x_{t+1} = \varphi(x_t, N_{t+1}), \\ N_{t+1} = N_t f(x_t), \end{cases} \tag{1.2}$$

where f is a monotonically increasing function of x_t that describes the net reproductive rate of an individual of quality x, and $\varphi(x_t, N_{t+1})$ is an increasing function of x (representing the maternal effect) and a decreasing function of N_{t+1}. As the population increases within a given area, the resources required for survival become limited. This leads to stronger competition among individuals, which can reduce reproductive success and overall population size. In ecological terms, such density-dependent effects play a crucial role in regulating population dynamics, preventing unlimited growth and maintaining ecological balance within the habitat. Note that the argument N of the first equation is evaluated at the same generation as x on the left side. This follows from the assumption that individual quality is affected by the population density in the current generation — a mathematically crucial assumption of the model.

In the same paper, the authors proposed a specific example with parametrization:

$$\begin{cases} x_{t+1} = x_t \frac{M}{1+N_{t+1}}, \\ N_{t+1} = N_t R \frac{x_t}{1+x_t}, \end{cases}$$

where parameter R represents the maximum reproductive rate given any quality x, and M is the maximum possible increase in average quality. This model has been designed to explain population behavior of some forest insects (Lepidopera) and biologically speaking it has to be valid $R, M > 1$. The authors proposed this model and gave some graphical explanation of the behavior without detailed mathematical analysis. In [5], the authors evaluated the fixed points and the Jacobian matrix, showing that the interior point is elliptic and that the model is area-preserving in logarithmic coordinates, suggesting that KAM theory could be applied. However, a detailed analysis was not conducted. In [13], the following system was considered:

$$\begin{cases} x_{n+1} = x_n g(y_{n+1}), \\ y_{n+1} = y_n f(x_n), \end{cases}$$

which actually represents one class of the Ginzburg–Taneyhill model, where

$$\varphi(x_t, N_{t+1}) = x_n g(y_{n+1}) \quad \text{and} \quad y_{n+1} = N_{t+1}.$$

In that paper, the authors performed a KAM analysis of this general model for an interior point and provided results used in the special case when

$$f(x_n) = \frac{Rx_n}{1+x_n} = R\left(1 - \frac{1}{1+x_n}\right) \text{ and } g(y_{n+1}) = \frac{M}{1+y_{n+1}}$$

which represents a completion of the analysis of the interior equilibrium stability, extending the work previously initiated by [5] on the Ginzburg–Taneyhill model.

In the aforementioned studies, the maternal effect was assumed to be linear and that the system itself is conservative, with the stability of the interior equilibrium analyzed using KAM theory (also see [1]). In paper [4], the authors also proposed a model in which maternal effect is non-linear and minimum quality x exists and it is incorporated explicitly into a differentiable form of $\varphi(x, N)$. An example is given by

$$\varphi(x_t, N_{t+1}) = k + \frac{(Mx_t)^{\beta}}{1+N_{t+1}},$$

where k is a small number representing the minimum quality. They have made the assumption that k is equal to the equilibrium quality divided by the maximum rate of numerical increase R, meaning that species with higher potential growth rates have a smaller minimum quality. Accordingly, they set $k = \frac{1}{R(R-1)}$ and this, it turns out, is a convenient form mathematically concerning the bifurcation behavior of the model. They stated that Hopf-type bifurcation will arise with the emergence of stable cycles in the form of an invariant Hopf curve. Thus, both the non-linearity and growth parameters can control the bifurcation behavior of the model. Hence, $\varphi(x_t, N_{t+1})$ takes the form

$$\varphi(x_t, N_{t+1}) = \frac{1}{R(R-1)} + \frac{(Mx_t)^{\beta}}{1+N_{t+1}},$$

and System (1.2) becomes

$$\begin{cases} x_{t+1} = \frac{1}{R(R-1)} + \frac{(Mx_t)^{\beta}}{1+N_{t+1}}, \\ N_{t+1} = N_t f(x_t). \end{cases} \tag{1.3}$$

In this paper, we will focus on a detailed analysis of System (1.3) under the assumption that $f(x_t)$ is a linear function, namely $f(x_t) = Rx_t$. Using this assumption and introducing the notation $N_t = y_t$ System (1.3) takes the form (1.1).

The paper is structured to provide a systematic overview of the conditions under which the considered system exhibits the existence of equilibrium points. For the identified points, a comprehensive analysis of local stability has been conducted, both for the boundary and the interior equilibrium points. We establish the existence of the Neimark-Sacker bifurcation, with a complete mathematical procedure illustrating the emergence of the invariant curve. We follow the algorithm from Theorem 1 and Corollary 1 in [7, 9] (see also [2, 3, 6, 10–12]). Finally, numerical simulations (see [8]) and graphical representations serve as illustrative confirmations of the obtained theoretical results, providing a visual insight into the complex dynamics of the analyzed models and linking the theoretical considerations with observations obtained through computational experiments.

2. THE EQUILIBRIUM POINTS

Because of the biological interpretation, we consider only non-negative equilibrium points. The equilibrium points $(\overline{x},\overline{y})$ of System (1.1) satisfy the following system of algebraic equations

$$\begin{cases} \overline{x} = \frac{1}{R(R-1)} + \frac{(M\overline{x})^{\beta}}{1+R\overline{x}\overline{y}}, \\ \overline{y} = R\overline{x}\overline{y}. \end{cases} \tag{2.1}$$

We consider two cases: $\overline{y}=0$ and $\overline{y}\neq 0$.

If $\overline{y}=0$, we examine the existence of boundary equilibria of the form $E_{\overline{x}}=(\overline{x},0)$. From the first equation of system (2.1) we have

$$\overline{x}-(M\overline{x})^{\beta}-\frac{1}{R(R-1)}=0. \tag{2.2}$$

Denote by

$$h(x)=x-(Mx)^{\beta}-\frac{1}{R(R-1)}.$$

To find possible boundary equilibrium points, it is necessary to find the zeros of the function $h(x)$ for $x>0$. Notice $h(0)=-\frac{1}{R(R-1)}<0$ since $R>1$. Furthermore, $h'(x)=1-\beta M^{\beta}x^{\beta-1}$, $h''(x)=-\beta(\beta-1)M^{\beta}x^{\beta-2}$, and the stationary point x_s of the function $h(x)$ satisfies the equality $M^{\beta}x_s^{\beta-1}=\frac{1}{\beta}$, i.e., $x_s=\left(\beta M^{\beta}\right)^{\frac{1}{1-\beta}}>0$.

The following lemma specifies the number of boundary equilibrium points according to the value of the positive parameter β.

Lemma 2.1. *Let $R,M>1$, and $x_s=\left(\frac{1}{\beta M^{\beta}}\right)^{\frac{1}{\beta-1}}$.*

(i) *If $\beta>1$ and $M^{\beta}>\frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1}$, then System (1.1) has no boundary equilibrium points.*

(ii) *If $0<\beta<1$ or $\left(\beta>1 \text{ and } M^{\beta}=\frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1}\right)$, then System (1.1) has one boundary equilibrium.*

(iii) *If* $\beta > 1$ *and* $M^{\beta} < \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1}$, *then System (1.1) has two boundary equilibrium points* $E_{\bar{x}_1} = (\bar{x}_1, 0)$ *and* $E_{\bar{x}_2} = (\bar{x}_2, 0)$, *such that* $\bar{x}_1 < x_s < \bar{x}_2$, *and*

$$\bar{x}_{1,2} \in I = \left(\frac{1}{R(R-1)}, M^{\frac{-\beta}{\beta-1}}\right) \subset (0,1). \tag{2.3}$$

Proof. If $0 < \beta < 1$, then $h''(x) > 0$. Since $h(0) < 0$, by the convexity and continuity of the function $h(x)$, we conclude that function $h(x)$ has exactly one zero, i.e., there exists one boundary equilibrium.

If $\beta > 1$, then $h''(x) < 0$. Since $h(0) < 0$, by the concavity and continuity of the function $h(x)$, and given that it has one positive stationary point, three cases are possible: $h(x_s) > 0$, $h(x_s) = 0$, or $h(x_s) < 0$, corresponding to two, one, or no boundary equilibrium points, respectively. Notice

$$h(x_s)\left\{\begin{array}{c} > \\ = \\ < \end{array}\right\} 0 \Longleftrightarrow M^{\beta}\left\{\begin{array}{c} < \\ = \\ > \end{array}\right\} \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1}.$$

From (2.2) we conclude that

$$(M\bar{x})^{\beta} = \bar{x} - \frac{1}{R(R-1)} > 0,$$

i.e.,

$$\bar{x} > \frac{1}{R(R-1)}.$$

Also from (2.2), we conclude that $\bar{x} - (M\bar{x})^{\beta} > 0$, hence

$$M^{\beta}\bar{x}^{\beta} < \bar{x} \Longrightarrow \bar{x}^{\beta-1} < M^{-\beta} \Longrightarrow \bar{x} < M^{\frac{-\beta}{\beta-1}}.$$

Since $M^{\frac{-\beta}{\beta-1}} < 1$, (2.3) is satisfied. □

Example 2.1. *For* $M = 2$, $R = 5$ *and* $\beta = 0.5$, *and from (2.2) we obtain one boundary equilibrium* $E_{\bar{x}} = (2.0988, 0)$.

Example 2.2. *For* $M = 1.2$, $R = 3.5$, *and* $\beta = 2$, *we have* $M^{\beta} = 1.44 < 2.1875 = \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1}$, *and hence there are two boundary equilibrium points. Furthermore, from (2.2) we obtain that the boundary equilibrium points are* $E_{\bar{x}_1} = (0.144, 0)$ *and* $E_{\bar{x}_2} = (0.552, 0)$.

Example 2.3. *For* $M = \sqrt{3}$, $R = 4$, *and* $\beta = 2$, *we have* $M^{\beta} = \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1} = 3$, *and hence there is one boundary equilibrium. Furthermore, from (2.2) we have* $E_{\bar{x}} = \left(\frac{1}{6}, 0\right)$.

Example 2.4. *For $M = 1.2$, $R = 2.5$, and $\beta = 2$, we have $M^{\beta} = 1.44 > 0.9375 = \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1}$, and there are no boundary equlibrium points.*

If $\bar{y} \neq 0$, then System (1.1) has an interior equilibrium $E_{+} = \left(\frac{1}{R}, \left(\frac{M}{R}\right)^{\beta}\frac{R(R-1)}{R-2} - 1\right)$ for

$$\left(\frac{M}{R}\right)^{\beta}\frac{R\,(R-1)}{R-2} > 1. \tag{2.4}$$

Notice that (2.4) implies $\frac{R(R-1)}{R-2} > 0$, which, together with $R > 1$, implies that $R > 2$.

The following lemma describes the conditions for the existence of an interior equilibrium point.

Lemma 2.2. *System (1.1) has an interior equilibrium $E_{+} = \left(\frac{1}{R}, \left(\frac{M}{R}\right)^{\beta}\frac{R(R-1)}{R-2} - 1\right)$ if*

(i) *$M \geq R > 2$ and $\beta > 0$;*

(ii) *$1 < M < R$ and $\beta < \beta_c = \frac{\ln\frac{R(R-1)}{R-2}}{\ln\frac{R}{M}}$.*

Proof. (i) From (2.4) we obtain $\frac{M}{R} > \left(\frac{R-2}{R(R-1)}\right)^{\frac{1}{\beta}}$. Since, $\frac{R-2}{R(R-1)} < 1$, condition (2.4) is true whenever $M \geq R$.

(ii) If $1 < M < R$ and $R > 2$, then $0 < \frac{M}{R} < 1$, hence from (2.4) by taking the logarithm of the last equality we obtain $\beta \ln\left(\frac{M}{R}\right) > -\ln\frac{R-2}{R(R-1)}$, and from $0 < \frac{M}{R} < 1$ the statement follows. □

3. LOCAL STABILITY OF EQUILIBRIUM POINTS

The map associated with System (1.1) has the following form

$$T\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \frac{1}{R(R-1)} + \frac{(Mx)^{\beta}}{1+Rxy} \\ Rxy \end{pmatrix}. \tag{3.1}$$

Notice that $T\begin{pmatrix} 0 \\ y \end{pmatrix} = \begin{pmatrix} \frac{1}{R(R-1)} \\ 0 \end{pmatrix}$ for $y \geq 0$ and $n \geq 1$, and that the y-axis is an invariant set under the mapping T.

The Jacobian marix of the map T defined by (3.1) is:

$$J_T\,(x,y) = \begin{pmatrix} M^{\beta}\frac{\beta x^{\beta-1}(1+Rxy)-Rx^{\beta}y}{(1+Rxy)^2} & \frac{-RM^{\beta}x^{\beta+1}}{(1+Rxy)^2} \\ Ry & Rx \end{pmatrix}.$$

3.1. **Local stability of boundary equilibrium points**

The Jacobian of the map T at the boundary equilibrium points $E_{\overline{x}} = (\overline{x}, 0)$ is given by

$$J(\overline{x}, 0) = \begin{pmatrix} \beta M^{\beta}\overline{x}^{\beta-1} & -RM^{\beta}\overline{x}^{\beta+1} \\ 0 & R\overline{x} \end{pmatrix},$$

whose eigenvalues are

$$\lambda_1 = R\overline{x} \text{ and } \lambda_2 = \beta M^{\beta}\overline{x}^{\beta-1}.$$

Notice that $\lambda_1, \lambda_2 > 0$.

Case $0 < \beta < 1$:

For $\beta \in (0,1)$, we have $\lambda_1 > 1$ and $\lambda_2 < 1$, hence the boundary equilibrium is unstable (a saddle point). Indeed, from (2.2), i.e.,

$$\overline{x} - (M\overline{x})^{\beta} = \frac{1}{R(R-1)},$$

since $R > 1$, we conclude

$$\overline{x} - (M\overline{x})^{\beta} > 0,$$

so

$$\overline{x} > (M\overline{x})^{\beta} \Longrightarrow \overline{x}^{1-\beta} > M^{\beta} \Longrightarrow \overline{x} > M^{\frac{\beta}{1-\beta}}.$$

Also, since $\frac{\beta}{1-\beta} > 0$, it follows that $M^{\frac{\beta}{1-\beta}} > 1$ because $M > 1$, and thus we conclude that $\overline{x} > M^{\frac{\beta}{1-\beta}} > 1$. Therefore, $\lambda_1 = R\overline{x} > 1$.
Consider the second eigenvalue λ_2,

$$\begin{aligned} \lambda_2 = \beta M^{\beta}\overline{x}^{\beta-1} &= \frac{\beta}{\overline{x}}(M\overline{x})^{\beta} = \frac{\beta}{\overline{x}}\left(\overline{x} - \frac{1}{R(R-1)}\right) \\ &= \beta - \frac{\beta}{\overline{x}}\frac{1}{R(R-1)}. \end{aligned}$$

To prove that $\lambda_2 < 1$, assume the contrary, i.e., that $\lambda_2 > 1$. Now

$$\beta - \frac{\beta}{\overline{x}}\frac{1}{R(R-1)} > 1 \Longleftrightarrow \beta - 1 > \frac{\beta}{\overline{x}}\frac{1}{R(R-1)},$$

which is impossible since $\beta - 1 < 0$ and $\frac{\beta}{\overline{x}}\frac{1}{R(R-1)} > 0$. Thus, we have shown that the boundary equilibrium is a saddle point.

Case $\beta > 1$:

In the following analysis, we consider the cases of one and two boundary equilibrium points.

1) First, assume that $h(x_s) = 0$.

Then there exists one boundary equilibrium $E_{\bar{x}} = (\bar{x}, 0) = (x_s, 0)$ with $\bar{x} = x_s = \left(\frac{1}{\beta M^\beta}\right)^{\frac{1}{\beta-1}}$ such that

$$\frac{1}{R(R-1)} < \bar{x} < M^{\frac{-\beta}{\beta-1}}.$$

The Jacobian of the map T at this equilibrium has eigenvalues $\lambda_1 = R\bar{x}$ and $\lambda_2 = \beta M^\beta x_s^{\beta-1} = 1$. This implies that $E_{\bar{x}}$ is non-hyperbolic. It is obvious that $E_{\bar{x}}$ is unstable if $\lambda_1 > 1$. If $\lambda_1 < 1$, or equivalently $1 - R\bar{x} > 0$, note that the eigenspace E^s is in the direction of the eigenvector

$$\left(\frac{R\bar{x}^2}{\beta(1-R\bar{x})}, \quad 1 \right).$$

Also, the positive x-axis is invariant under the map T and it is in the same direction as the eigenspace E^c. Thus, the positive x-axis is a center manifold W^c, so the boundary equilibrium $E_{\bar{x}}$ of the map T is stable, but not asymptotically stable.

If we make the substitution $\frac{(\beta-1)R(R-1)}{\beta} = t$, then we have

$$\begin{aligned} h(x_s) = 0 &\Longleftrightarrow M^\beta = \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1} \Longleftrightarrow M^\beta = \frac{1}{\beta}t^{\beta-1} \\ &\Longleftrightarrow \beta M^\beta = t^{\beta-1}, \end{aligned}$$

i.e.,

$$\frac{1}{\beta M^\beta} = \frac{1}{t^{\beta-1}} = t^{-(\beta-1)}. \tag{3.2}$$

Now, by (3.2) we have

$$\begin{aligned} \lambda_1 < 1 &\Longleftrightarrow x_s R = \left(\frac{1}{\beta M^\beta}\right)^{\frac{1}{\beta-1}} R < 1 \\ &\Longleftrightarrow \left(t^{-(\beta-1)}\right)^{\frac{1}{\beta-1}} R < 1 \Longleftrightarrow t^{-1}R < 1 \Longleftrightarrow R < t. \end{aligned}$$

That is, we get

$$\lambda_1 < 1 \Longleftrightarrow 1 < \frac{t}{R} = \frac{(\beta-1)(R-1)}{\beta} \Longleftrightarrow R > \frac{2\beta-1}{\beta-1}.$$

So for $\beta > 1$ conditions $R > \frac{2\beta-1}{\beta-1}$ and $M^\beta = \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1}$ imply $\lambda_1 < 1$.

Example 3.1. *If $\beta = 2$, then $R > 3$, so let $R = 3.5$, $M = \sqrt{2.1875}$. Then $x_s = \left(\frac{1}{\beta M^\beta}\right)^{\frac{1}{\beta-1}} = 0.2285714286$, $h(x_s) = \frac{\beta-1}{\beta}x_s - \frac{1}{R(R-1)} = 0$ and $x_s R = 0.8 < 1$.*

If $\lambda_1 = \lambda_2 = 1$, i.e., if $\bar{x}$ satisfies the following three equalities:

$$R\bar{x} = 1,\ \beta M^{\beta}\bar{x}^{\beta-1} = 1,\ \bar{x} - (M\bar{x})^{\beta} = \frac{1}{R(R-1)} \tag{3.3}$$

the equilibrium $E_{\bar{x}} = (\bar{x}, 0)$ is a 1-1 resonant fixed point of T. From the reasoning above if $R\bar{x} = 1$, then $R = \frac{2\beta-1}{\beta-1}$, i.e., $\beta = \frac{R-1}{R-2}$. Also, from $M^{\beta} = \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1}$ we obtain

$$M = \left(\frac{R-2}{R-1}\right)^{\frac{R-2}{R-1}} R^{\frac{1}{R-1}}.$$

Example 3.2. *If we take* $R = 3$, *then* $\beta = 2$, $M = \left(\frac{1}{2}(3)^1\right)^{\frac{1}{2}} = \sqrt{\frac{3}{2}} \approx 1.225$, *and* $\bar{x} = x_s = \frac{1}{3}$. *The Jacobian matrix at the boundary equilibrium point* $E_{\bar{x}}$ *is*

$$J(\bar{x}, 0) = \begin{pmatrix} 1 & -\frac{R-2}{R(R-1)} \\ 0 & 1 \end{pmatrix} = \begin{pmatrix} 1 & -\frac{1}{6} \\ 0 & 1 \end{pmatrix},$$

with eigenvalues $\lambda_{1,2} = 1$.

2) Now, assume that $h(x_s) > 0$.

In this case System (1.1) has two equilibrium points $E_{\bar{x}_1} = (\bar{x}_1, 0)$ and $E_{\bar{x}_2} = (\bar{x}_2, 0)$ such that $\bar{x}_1 < x_s < \bar{x}_2$, i.e., $M^{\beta} < \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1} = a(R, \beta)$.
Using $\beta M^{\beta} x_s^{\beta-1} = 1$, i.e., $(Mx_s)^{\beta} = \frac{x_s}{\beta}$ we get

$$\begin{aligned} h(x_s) > 0 &\Longleftrightarrow x_s - (Mx_s)^{\beta} - \frac{1}{R(R-1)} > 0 \\ &\Longleftrightarrow x_s - \frac{x_s}{\beta} > \frac{1}{R(R-1)} \Longleftrightarrow x_s > \frac{\beta}{\beta-1}\frac{1}{R(R-1)}. \end{aligned}$$

The eigenvalues of the equilibrium points $E_{\bar{x}_i}$, $i = 1, 2$ are $\lambda_{1,2}(\bar{x}_i)$, where $\lambda_1(\bar{x}_i) = R\bar{x}_i$ and $\lambda_2(\bar{x}_i) = \beta M^{\beta}\bar{x}_i^{\beta-1} = \beta\frac{M^{\beta}\bar{x}_i^{\beta}}{\bar{x}_i} = \frac{\beta}{\bar{x}_i}\left(\bar{x}_i - \frac{1}{R(R-1)}\right)$, i.e., $\lambda_2(\bar{x}_i) = \beta\left(1 - \frac{1}{\bar{x}_i R(R-1)}\right)$.
$\lambda_2(\bar{x}_i)$ is a strictly increasing functions of $\bar{x}_i$ ($\frac{\lambda_2(\bar{x}_i)}{d\bar{x}_i} = \frac{\beta}{\bar{x}_i^2}\frac{1}{R(R-1)} > 0$), and

$$\lambda_2(x_s) = \beta M^{\beta} x_s^{\beta-1} = \beta M^{\beta}\left(\left(\frac{1}{\beta M^{\beta}}\right)^{\frac{1}{\beta-1}}\right)^{\beta-1} = 1.$$

Now, from $\bar{x}_2 > x_s$ it follows that $\lambda_2(\bar{x}_2) > \lambda_2(x_s)$, i.e., $\lambda_2(\bar{x}_2) > 1$. Similarly, $\bar{x}_1 < x_s$ implies $\lambda_2(\bar{x}_1) < \lambda_2(x_s)$, i.e., $\lambda_2(\bar{x}_1) \in (0, 1)$.

Further stability depends on $\lambda_1(\bar{x}_i)$ and classification depends on $h(\frac{1}{R})$ which determines where $\frac{1}{R}$ lies.

$$h\left(\frac{1}{R}\right) = \frac{1}{R} - \left(M\frac{1}{R}\right)^{\beta} - \frac{1}{R(R-1)} = \frac{R-2}{R(R-1)} - \left(\frac{M}{R}\right)^{\beta}$$
$$= \frac{1}{R^{\beta}}\left(R^{\beta-1}\frac{R-2}{(R-1)} - M^{\beta}\right).$$

Let us define the threshold value $b(R,\beta)$ by

$$b(R,\beta) = \begin{cases} R^{\beta-1}\frac{R-2}{R-1}, & R > 2, \\ \text{non-positive}, & 1 < R \leq 2, \end{cases}$$

and observe that $b(R,\beta) > 0$ for $R > 2$, whereas for $1 < R \leq 2$ we have $b(R,\beta) \leq 0$. The order of points $\bar{x}_1 < x_s$ is satisfied since $\bar{x}_1$ is the unique zero of function $h(x)$ on the interval $(0,x_s)$. If $h(\frac{1}{R}) > 0$, then $\bar{x}_1 < \frac{1}{R}$ or equivalently $\lambda_1(\bar{x}_1) < 1$. Indeed, since $h(x)$ is an increasing function on the interval $(0,x_s)$ and since $\bar{x}_1$ is the unique zero of $h(x)$ on $(0,x_s)$ that means that if $h\left(\frac{1}{R}\right) > 0$, then the value $\frac{1}{R}$ is on the right side of $\bar{x}_1$, i.e., $\bar{x}_1 < \frac{1}{R}$, i.e.,

$$h\left(\frac{1}{R}\right) > 0 \Longleftrightarrow M^{\beta} < b(R,\beta).$$

Stability of the smaller root $\bar{x}_1$ can be analyzed in two cases.

In the case $R > 2$ (threshold $b(R,\beta)$ exists) if $M^{\beta} < \min\{a(R,\beta), b(R,\beta)\}$, then $\lambda_1(\bar{x}_1) < 1$ and $\lambda_2(\bar{x}_1) < 1$. Consequently, the equilibrium $(\bar{x}_1,0)$ is locally asymptotically stable. Note that since $M > 1$ then $b(R,\beta) > 1$ must hold. If $M^{\beta} = b(R,\beta)$, then for one of $\bar{x}_i$ we have $\bar{x}_i = \frac{1}{R}$ i.e., $\lambda_1(\bar{x}_i) = 1$. Moreover if $R < \frac{2\beta-1}{\beta-1}$, then $\frac{1}{R} < x_s$ and the equilibrium with $\bar{x} = \frac{1}{R}$ is the smaller root $\bar{x}_1$. But if $R > \frac{2\beta-1}{\beta-1}$, then $\frac{1}{R} > x_s$ and the equilibrium with $\bar{x} = \frac{1}{R}$ is the larger root $\bar{x}_2$. If $0 < b(R,\beta) < M^{\beta} < a(R,\beta)$, then $h\left(\frac{1}{R}\right) < 0$ which implies $\bar{x}_1 > \frac{1}{R}$ i.e., $\lambda_1(\bar{x}_1) > 1$ and $\lambda_2(\bar{x}_1) < 1$, and $(\bar{x}_1,0)$ is a saddle point.

In the case $1 < R \leq 2$, we have $b(R,\beta) \leq 0$, and consequently $h\left(\frac{1}{R}\right) < 0$, which implies $\bar{x}_1 > \frac{1}{R}$. Hence, $\lambda_1(\bar{x}_1) > 1$ and $\lambda_2(\bar{x}_1) < 1$, so the equilibrium $(\bar{x}_1,0)$ is a saddle point.

For the larger root $\bar{x}_2$, $\lambda_2(\bar{x}_2) > 1$ always holds and generically $\lambda_1(\bar{x}_2) = R\bar{x}_2 > 1$. Hence $(\bar{x}_2,0)$ is always unstable. But $\lambda_2(\bar{x}_2)$ can be equal to 1, i.e., $R\bar{x}_2 = 1$ if $M^{\beta} = b(R,\beta)$ and $R > \frac{2\beta-1}{\beta-1}$, and $(\bar{x}_2,0)$ becomes non-hyperbolic.

The previous consideration proves the following lemma.

Lemma 3.1. *Let $R > 1, M > 1$,*

$$x_s = \left(\frac{1}{\beta M^{\beta}}\right)^{\frac{1}{\beta-1}}, \; a(R,\beta) = \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1} \; \text{and } b(R,\beta) = R^{\beta-1}\frac{R-2}{R-1}.$$

The following statements hold:

(1) *If* $0 < \beta < 1$, *then there exists a boundary equilibrium* $E_{\bar{x}} = (\bar{x}, 0)$, *which is a saddle.*

(2) *If* $\beta > 1$ *and* $M^{\beta} > a(R,\beta)$, *then there is no boundary equilibrium points.*

(3) *If* $\beta > 1$ *and* $M^{\beta} = a(R,\beta)$, *then there exists a boundary equilibrium* $E_{\bar{x}} = (\bar{x}, 0) = (x_s, 0)$, *which is non-hyperbolic with one eigenvalue equal to* 1.

(i): *If* $R > \frac{2\beta-1}{\beta-1}$, *then* E_{x_s} *is stable.*

(ii): *If* $R = \frac{2\beta-1}{\beta-1}$, *then* E_{x_s} *is a 1-1 resonant fixed point.*

(iii): *If* $R < \frac{2\beta-1}{\beta-1}$, *then* E_{x_s} *is unstable.*

(4) *If* $\beta > 1$ *and* $M^{\beta} < a(R,\beta)$, *then there are two boundary equilibrium points* $E_{\bar{x}_1} = (\bar{x}_1, 0)$ *and* $E_{\bar{x}_2} = (\bar{x}_2, 0)$, *where* $\bar{x}_1 < x_s < \bar{x}_2$.

(i): *If* $R > 2$ *and* $M^{\beta} < \min\{a(R,\beta), b(R,\beta)\}$, *then*
$\lambda_1(\bar{x}_1) < 1$ *and* $\lambda_2(\bar{x}_1) < 1$ *and point the* $E_{\bar{x}_1} = (\bar{x}_1, 0)$ *is a sink,*
$\lambda_1(\bar{x}_2) > 1$ *and* $\lambda_2(\bar{x}_2) > 1$ *and point the* $E_{\bar{x}_2} = (\bar{x}_2, 0)$ *is unstable.*

(ii): *If* $R > 2$ *and* $M^{\beta} = b(R,\beta)$ *and* $R < \frac{2\beta-1}{\beta-1}$, *then*
$\lambda_1(\bar{x}_1) = 1$ *and* $\lambda_2(\bar{x}_1) < 1$ *and the point* $E_{\bar{x}_1} = (\bar{x}_1, 0)$ *is non-hyperbolic,*
$\lambda_1(\bar{x}_2) > 1$ *and* $\lambda_2(\bar{x}_2) > 1$ *and the point* $E_{\bar{x}_2} = (\bar{x}_2, 0)$ *is unstable.*

(iii): *If* $R > 2$ *and* $M^{\beta} = b(R,\beta)$ *and* $R > \frac{2\beta-1}{\beta-1}$, *then*
$\lambda_1(\bar{x}_1) < 1$ *and* $\lambda_2(\bar{x}_1) < 1$ *and the point* $E_{\bar{x}_1} = (\bar{x}_1, 0)$ *is a sink,*
$\lambda_1(\bar{x}_2) = 1$ *and* $\lambda_2(\bar{x}_2) > 1$ *and the point* $E_{\bar{x}_2} = (\bar{x}_2, 0)$ *is non-hyperbolic.*

(iv): *If* $R > 2$ *and* $0 < b(R,\beta) < M^{\beta} < a(R,\beta)$, *then*
$\lambda_1(\bar{x}_1) > 1$ *and* $\lambda_2(\bar{x}_1) < 1$ *and the point* $E_{\bar{x}_1} = (\bar{x}_1, 0)$ *is a saddle,*
$\lambda_1(\bar{x}_2) > 1$ *and* $\lambda_2(\bar{x}_2) > 1$ *and the point* $E_{\bar{x}_2} = (\bar{x}_2, 0)$ *is unstable.*

(v): *If* $1 < R \leq 2$ *and* $M^{\beta} < a(R,\beta)$, *then*
$\lambda_1(\bar{x}_1) > 1$ *and* $\lambda_2(\bar{x}_1) < 1$ *and the point* $E_{\bar{x}_1} = (\bar{x}_1, 0)$ *is a saddle,*
$\lambda_1(\bar{x}_2) > 1$ *and* $\lambda_2(\bar{x}_2) > 1$ *and the point* $E_{\bar{x}_2} = (\bar{x}_2, 0)$ *is unstable.*

Example 3.3. *If* $R = 4$ *and* $\beta = 3$, *then* $a(R,\beta) = \frac{1}{\beta}\left(\frac{(\beta-1)R(R-1)}{\beta}\right)^{\beta-1} = \frac{64}{3}$, $b(R,\beta) = R^{\beta-1}\frac{R-2}{R-1} = \frac{32}{3}$, *and* $M^{\beta} < \frac{32}{3} \Rightarrow M < \sqrt[3]{\frac{32}{3}} \approx 2.20285$. *For* $M = 2.2 < b(R,\beta)$ *the equilibrium points are* $(0.105, 0)$ *and* $(0.251, 0)$ *with* $\lambda_1(\bar{x}_1) = 0.3656$, $\lambda_2(\bar{x}_1) = 0.2674$, $\lambda_1(\bar{x}_2) = 1.00117$ *and* $\lambda_2(\bar{x}_2) = 2.00117$.

3.2. **Local stability of interior equilibrium points**

From the point of view of application, the investigation of local and global stability of the interior equilibrium E_+ is particularly important. The Jacobian matrix of the map T at positive the equilibrium point E_+ is

$$J_T(E_+) = \begin{pmatrix} \frac{M^\beta}{R^\beta} R \frac{\beta(1+\bar{y})-\bar{y}}{(1+\bar{y})^2} & -\frac{M^\beta}{R^\beta}\frac{1}{(1+\bar{y})^2} \\ R\bar{y} & 1 \end{pmatrix},$$

where $\bar{y} = \left(\frac{M}{R}\right)^\beta \frac{R(R-1)}{R-2} - 1$. If we make the substitution $1+\bar{y} = A$, then $A = \left(\frac{M}{R}\right)^\beta \frac{R(R-1)}{R-2}$, and $A > 1$ holds. Now the Jacobian matrix of the map T at the positive equilibrium point E_+ becomes

$$J_T(E_+) = \begin{pmatrix} \frac{R-2}{R-1}\left(\beta - 1 + \frac{1}{A}\right) & -\frac{1}{A}\frac{R-2}{R(R-1)} \\ R(A-1) & 1 \end{pmatrix}. \tag{3.4}$$

The characteristic polynomial of the matrix (3.4) is

$$P(\lambda) = \lambda^2 - trJ_T(E_+)\lambda + \det J_T(E_+),$$

where

$$trJ_T(E_+) = 1 + \frac{R-2}{R-1}\left(\beta - 1 + \frac{1}{A}\right)$$

and

$$\det J_T(E_+) = \beta\frac{R-2}{R-1}.$$

The eigenvalues of $J_T(E_+)$ are

$$\lambda_\pm = \frac{1}{2}\left(1 + \frac{R-2}{R-1}\left(\beta - 1 + \frac{1}{A}\right) \pm \sqrt{\left(1 + \frac{R-2}{R-1}\left(\beta - 1 + \frac{1}{A}\right)\right)^2 - 4\beta\frac{R-2}{R-1}}\right).$$

Lemma 3.2. *If $R > 2$ and $\beta > 0$, then System (1.1) has a unique positive equilibrium point $E_+ = \left(\frac{1}{R}, \left(\frac{M}{R}\right)^\beta \frac{R(R-1)}{R-2} - 1\right)$, which is:*

(1) locally asymptotically stable if $\beta < \beta_0$,
(2) a repeller if $\beta > \beta_0$,
(3) non–hyperbolic with conjugate complex eigenvalues if $\beta = \beta_0$,

where

$$\beta_0 = \frac{R-1}{R-2} (= \beta_{critical}).$$

Proof. (1) The equilibrium point E_+ is locally asymptotically stable if the next three conditions are met

(i) $1 - trJ_T(E_+) + DetJ_T(E_+) > 0$,
(ii) $1 + trJ_T(E_+) + DetJ_T(E_+) > 0$,
(iii) $1 - DetJ_T(E_+) > 0$.

The condition (i) is equivalent to

$$1-\left(1+\frac{R-2}{R-1}\left(\beta-1+\frac{1}{A}\right)\right)+\beta\frac{R-2}{R-1}>0$$
$$\Longleftrightarrow \frac{R-2}{R-1}\left(\frac{A-1}{A}\right)>0,$$

which is true since $R>2$ and $A>1$.

Let us now consider condition (ii):

$$1+\left(1+\frac{R-2}{R-1}\left(\beta-1+\frac{1}{A}\right)\right)+\beta\frac{R-2}{R-1}>0$$
$$\Longleftrightarrow 2+\frac{R-2}{R-1}\left(2\beta+\frac{1}{A}-1\right)>0.$$

Since $\frac{R-2}{R-1}=c>0$ we get

$$c\left(2\beta+\frac{1}{A}-1\right)>-2$$
$$\Longleftrightarrow 2\beta+\frac{1}{A}-1>-\frac{2}{c}$$
$$\Longleftrightarrow \frac{1}{A}>-2\frac{R-1}{R-2}+1-2\beta$$
$$\Longleftrightarrow \frac{1}{A}>-\frac{R}{R-2}-2\beta.$$

The last inequality is true because $\frac{1}{A}>0$, $R>2$, and $\beta\geq 0$.

From the condition (iii) $1-\beta\frac{R-2}{R-1}>0$ must hold which implies $\beta<\frac{R-1}{R-2}$. So, this part of the lemma holds.

(2) If $\beta>\frac{R-1}{R-2}$, then $\det J_T(E_+)>1$ is satisfied. Also, since $1+DetJ_T(E_+)>0$, the other conditions for the repeller coincide with the first two conditions from (1), and it has been shown that they are satisfied.

(3) Let now $\beta=\frac{R-1}{R-2}$. Notice $\beta=\frac{R-2+1}{R-2}=1+\frac{1}{R-2}>1$ for $R>2$. Then

$$TrJ_T(E_+)=2-\frac{1}{\beta}\left(\frac{A-1}{A}\right)$$

and

$$DetJ_T(E_+)=1.$$

The eigenvalues of $J_T(E_+)$ are

$$\lambda_{\pm}=1-\frac{A-1}{2A\beta}\pm i\frac{\sqrt{(A-1)(4A\beta-(A-1))}}{2A\beta}$$

and

$$
\begin{aligned}
|\lambda_{\pm}|^2 &= \left(1 - \frac{A-1}{2A\beta}\right)^2 + \frac{(A-1)(4A\beta-(A-1))}{(2A\beta)^2} \\
&= 1 - \frac{A-1}{A\beta} + \left(\frac{A-1}{2A\beta}\right)^2 + \frac{(A-1)(4A\beta-(A-1))}{(2A\beta)^2} \\
&= 1 - \frac{A-1}{A\beta} + \left(\frac{A-1}{2A\beta}\right)^2 + \frac{A-1}{A\beta} - \left(\frac{A-1}{2A\beta}\right)^2 = 1,
\end{aligned}
$$

so E_+ is non-hyperbolic equilibrium point. Also, $(A-1)(4A\beta-(A-1)) > 0$ for $A > 1$ and $\beta > 1$. Indeed,

$$4A\beta - (A-1) = A(4\beta - 1) + 1 > 0$$

because $\beta > 1$. This leads us to the conclusion that in the non-hyperbolic case the eigenvalues are always conjugate complex numbers. □

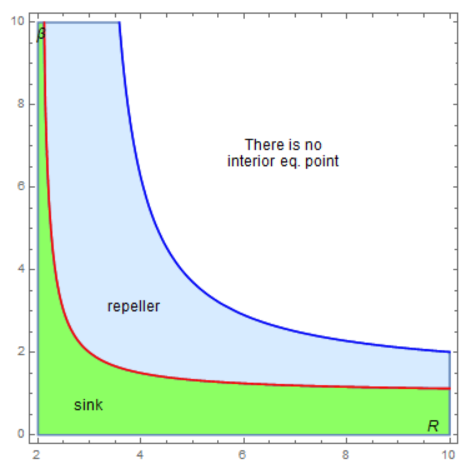


FIGURE 1. Parametric spaces of local dynamics of the interior equilibrium E_+ for $M = 2$ in the $R\beta$-plane.

Figure 1 shows areas of local stability of the interior equilibrium point E_+ in the $R\beta$-plane for $M = 2$, $R > 2$, and $\beta > 0$. In the blue area the equilibrium is a repeller, in the green area the equilibrium is locally asymptotically stable and on the red curve that separates them, the equilibrium is non-hyperbolic with eigenvalues that are complex conjugate numbers. Figure 2 shows the equilibrium points (the interior equilibrium E_+ or the boundary equilibrium points $E_{\overline{x}}$) that exist in the corresponding regions for the same parameter values, i.e., $M = 2$, $R > 2$, and $\beta > 0$.

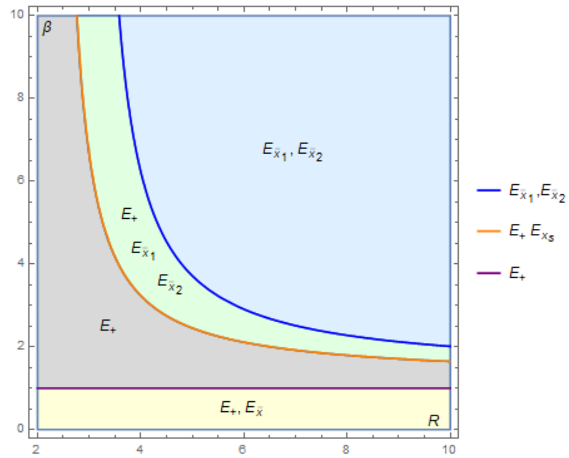


FIGURE 2. Existence of the interior equilibrium and the boundary equilibrium points for $M=2$ in the $R\beta$-plane.

Let us define

$$\Psi = \{(\beta, R, M) : h(x_s) = 0 \wedge \beta > 1 \wedge R > 2 \wedge M > 1\},$$
$$\Phi = \{(\beta, R, M) : \beta = \beta_{critical} \wedge \beta > 1 \wedge R > 2 \wedge M > 1\},$$
$$\Omega = \left\{(\beta, R, M) : \left(\frac{M}{R}\right)^{\beta} \frac{R(R-1)}{R-2} - 1 = 0 \wedge \beta > 1 \wedge R > 2 \wedge M > 1\right\}.$$

Let us note that for $M=2$, Ψ, Φ, and Ω correspond to the orange, red, and blue curves, respectively, as shown in Figures 1 and 2. From (3.3) and the discussion immediately below (3.3), it follows that Ψ and Φ intersect at the 1–1 resonant fixed points. Furthermore, by substituting $\beta = \beta_{critical}$ into $R = \left(\beta M^{\beta}\right)^{\frac{1}{\beta-1}}$, we obtain:

$$R = \left(\frac{R-1}{R-2} M^{\frac{R-1}{R-2}}\right)^{\frac{1}{\frac{R-1}{R-2}-1}} \Longleftrightarrow R = \left(\frac{R-1}{R-2} M^{\frac{R-1}{R-2}}\right)^{R-2}$$
$$\Longrightarrow R = \left(\frac{R-1}{R-2}\right)^{R-2} M^{R-1},$$

since $\beta, M > 1$, and $R > 2$. On the other hand, by substituting $\beta = \beta_{critical}$ into $\left(\frac{M}{R}\right)^{\beta} \frac{R(R-1)}{R-2} - 1 = 0$, we obtain:

$$\left(\frac{M}{R}\right)^{\beta} \frac{R(R-1)}{R-2} - 1 = 0 \Longleftrightarrow \left(\frac{M}{R}\right)^{\frac{R-1}{R-2}} \frac{R(R-1)}{R-2} - 1 = 0$$
$$\Longleftrightarrow \left(\frac{M}{R}\right)^{\frac{R-1}{R-2}} = \frac{R-2}{R(R-1)} \Longleftrightarrow \frac{R-1}{R-2} M^{\frac{R-1}{R-2}} = R^{\frac{R-1}{R-2}-1}$$

$$\Longleftrightarrow \frac{R-1}{R-2} M^{\frac{R-1}{R-2}} = R^{\frac{1}{R-2}} \Longrightarrow R = \left(\frac{R-1}{R-2}\right)^{R-2} M^{R-1},$$

since $\beta, M > 1$, and $R > 2$. This implies that Ψ, Φ, and Ω intersect at the 1–1 resonant fixed points.

4. Neimark–Sacker bifurcation

In this section, we prove that the system exhibits Neimark-Sacker bifurcation. We discuss the existence of Neimark-Sacker bifurcation for the unique positive equilibrium and compute asymptotic approximation of the invariant curve near the positive equilibrium point E_+ of the System (1.1).

First we need to shift the positive equilibrium point to the origin. By change of variable $u_t = x_t - \bar{x}$ and $v_t = y_t - \bar{y}$ the point $(\bar{x}, \bar{y})$ will be shifted to $(0,0)$ and the transformed system is given by

$$\begin{cases} u_{t+1} = \frac{1}{R(R-1)} + \frac{M^{\beta}(u_t+\bar{x})^{\beta}}{1+R(u_t+\bar{x})(v_t+\bar{y})} - \bar{x}, \\ v_{t+1} = R\left(u_t + \bar{x}\right)\left(v_t + \bar{y}\right) - \bar{y}. \end{cases} \tag{4.1}$$

The corresponding map for this system is given by

$$K\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \frac{1}{R(R-1)} + \frac{M^{\beta}(u+\bar{x})^{\beta}}{1+R(u+\bar{x})(v+\bar{y})} - \bar{x} \\ R\left(u+\bar{x}\right)\left(v+\bar{y}\right) - \bar{y} \end{pmatrix} \tag{4.2}$$

and the Jacobian marix of the map K at (u, v) is

$$J_K(u,v) = \begin{pmatrix} M^{\beta} \frac{\beta(u+\bar{x})^{\beta-1}(1+R(u+\bar{x})(v+\bar{y})) - (u+\bar{x})^{\beta} R(v+\bar{y})}{(1+R(u+\bar{x})(v+\bar{y}))^2} & -\frac{M^{\beta} R(u+\bar{x})^{\beta+1}}{(1+R(u+\bar{x})(v+\bar{y}))^2} \\ R\left(v+\bar{y}\right) & R\left(u+\bar{x}\right) \end{pmatrix}.$$

For the point $(0,0)$,

$$\begin{aligned} J_K(0,0) &= \begin{pmatrix} M^{\beta} \frac{\beta \bar{x}^{\beta-1}(1+R\bar{x}\bar{y}) - \bar{x}^{\beta} R\bar{y}}{(1+R\bar{x}\bar{y})^2} & -\frac{M^{\beta} R\bar{x}^{\beta+1}}{(1+R\bar{x}\bar{y})^2} \\ R\bar{y} & R\bar{x} \end{pmatrix} \\ &= \begin{pmatrix} M^{\beta} R^{1-\beta}\left(\frac{\beta}{1+\bar{y}} - \frac{\bar{y}}{(1+\bar{y})^2}\right) & -\frac{M^{\beta}}{R^{\beta}} \frac{1}{(1+\bar{y})^2} \\ R\bar{y} & 1 \end{pmatrix}. \end{aligned}$$

Using substitutions $A = \bar{y} + 1$ i.e., $A = M^{\beta} R^{1-\beta} \frac{R-1}{R-2}$ and $A > 1$, the above matrix becomes

$$J_K(0,0) = \begin{pmatrix} \frac{R-2}{R-1}\left(\beta - 1 + \frac{1}{A}\right) & -\frac{1}{A} \frac{R-2}{R(R-1)} \\ R\left(A-1\right) & 1 \end{pmatrix} \tag{4.3}$$

with the corresponding characteristic equation

$$\lambda^2 - \left(1 + \frac{R-2}{R-1}\left(\beta - 1 + \frac{1}{A}\right)\right)\lambda + \beta\frac{R-2}{R-1} = 0,$$

and eigenvalues

$$\lambda_{\pm} = \frac{\beta A(R-2) + R + A - 2 \pm i\sqrt{4A^2\beta(R-2)(R-1) - (\beta A(R-2) + R + A - 2)^2}}{2A(R-1)}.$$

Furthermore, we have

$$|\lambda(\beta)|^2 = \lambda(\beta)\cdot\overline{\lambda(\beta)} = \beta\frac{R-2}{R-1}, \text{ i.e., } |\lambda(\beta)| = \sqrt{\beta\frac{R-2}{R-1}}. \tag{4.4}$$

To study Neimark–Sacker bifurcation, we need the following lemma.

Lemma 4.1. *Let* $A_0 = M^{\beta_0}R^{1-\beta_0}\frac{R-1}{R-2}$, $R > 2$, $M > 1$, *and* $\beta_0 = \frac{R-1}{R-2}$.*Then* K *has an equilibrium point at* $(0,0)$ *and the eigenvalues of the Jacobian matrix of* K *at* $(0,0)$ *are* λ *and* $\overline{\lambda}$, *where*

$$\lambda(\beta_0) = \frac{2\beta_0 A_0 - (A_0 - 1) + i\Lambda}{2\beta_0 A_0},$$

and

$$\Lambda = \sqrt{(A_0 - 1)(4\beta_0 A_0 - (A_0 - 1))}.$$

Moreover, $\lambda(\beta_0)$ *satisfies the following:*

(a) $\lambda^k(\beta_0) \neq 1$ *for* $k = 1,2,3,4$*;*

(b) $d = d(\beta_0) = \frac{d}{d\beta}|\lambda(\beta)|_{|\beta=\beta_0} = \frac{R-2}{2(R-1)} > 0$*;*

(c) The eigenvectors associated to $\lambda(\beta_0)$ *are*

$$\mathbf{q}(\beta_0) = \begin{pmatrix} 1 & \frac{R(1-A_0-i\Lambda)}{2} \end{pmatrix}^T$$

and

$$\mathbf{p}(\beta_0) = \begin{pmatrix} \frac{4\beta_0 A_0 - (A_0-1) + i\Lambda}{2(4\beta_0 A_0 - (A_0 - 1))} & \frac{i\Lambda}{R(A_0-1)(4\beta_0 A_0 - (A_0-1))} \end{pmatrix},$$

such that $Sq(\beta_0) = \lambda q(\beta_0)$, $p(\beta_0)S = \lambda p(\beta_0)$ *and* $p(\beta_0)q(\beta_0) = 1$, *where* $S = J_K(0,0)|_{\beta=\beta_0}$.

Proof. Let $A_0 = M^{\beta_0}R^{1-\beta_0}\frac{R-1}{R-2}$, $R > 2$ and $\beta_0 = \frac{R-1}{R-2}$. Notice that $A_0 > 1$ and $\beta_0 = 1 + \frac{1}{R-2} > 1$. Then for $\beta = \beta_0$ from (4.3) we obtain

$$S = J_K(0,0)|_{\beta=\beta_0} = \begin{pmatrix} 1 - \frac{1}{\beta_0} + \frac{1}{\beta_0 A_0} & -\frac{1}{\beta_0 A_0 R} \\ R(A_0 - 1) & 1 \end{pmatrix}$$

and the eigenvalues of the matrix S are

$$\lambda(\beta_0) = \frac{2\beta_0 A_0 - (A_0 - 1) \pm i\Lambda}{2\beta_0 A_0}, \tag{4.5}$$

where

$$\Lambda = \sqrt{(A_0-1)(4\beta_0 A_0-(A_0-1))}.$$

From (4.4) we have

$$|\lambda(\beta_0)| = \sqrt{\beta_0\frac{R-2}{R-1}} = \sqrt{\frac{R-1}{R-2}\frac{R-2}{R-1}} = 1,$$

and notice that $\lambda(\beta_0) \neq 1$ since $A_0 > 1$, $R > 2$ and $\beta_0 > 1$. By straightforward calculation for $\beta = \beta_0$ we obtain

$$\lambda^2(\beta_0) = \frac{(A_0-1)^2+2\beta_0A_0(\beta_0A_0-2A_0+2))}{2\beta_0^2A_0^2}+i\frac{(2\beta_0A_0-A_0+1))\Lambda}{2\beta_0^2A_0^2},$$

$$\lambda^3(\beta_0) = \frac{(2\beta_0A_0-A_0+1)\left((A_0-1)^2+\beta_0A_0(\beta_0A_0-4A_0+4))\right)}{2\beta_0^3A_0^3} + \frac{i\Lambda(\beta_0A_0-A_0+1)(3\beta_0A_0-A_0+1)}{2\beta_0^3A_0^3}$$

$$\lambda^4(\beta_0) = 1-\frac{(A_0-1)(A_0(2\beta_0-1)+1)^2(4\beta_0A_0-A_0+1)}{2\beta_0^4A_0^4} + i\frac{(2\beta_0A_0-A_0+1))\left((A_0-1)^2+2\beta_0A_0(\beta_0A_0-2A_0+2))\right)\Lambda}{2\beta_0^4A_0^4}.$$

One can see that $|\lambda(\beta_0)| = 1$ and $\lambda^k(\beta_0) \neq 1$ for $k = 1,2,3,4$. Indeed, assume that the imaginary part of $\lambda^2(\beta_0)$ is equal to zero, i.e., $2\beta_0A_0-A_0+1 = 0$ or equivalently$\frac{A_0R+R-2}{R-2} = 0$. Then we get $A_0 = -\frac{R-2}{R} < 0$ which is impossible, so $\lambda^2(\beta_0) \neq 1$. Also, let us assume that the imaginary part of $\lambda^3(\beta_0)$ is equal to zero, i.e $\beta_0A_0-A_0+1 = 0$ or $3\beta_0A_0-A_0+1 = 0$. Using $\beta_0 = \frac{R-1}{R-2}$ then from the first condition we get that $A_0\frac{R-1}{R-2}-A_0+1 = 0$, or equivalently $A_0 = -(R-2)$. From the second condition $3\beta_0A_0-A_0+1 = 0$ we get that $3A_0\frac{R-1}{R-2}-A_0+1 = 0$ i.e., $A_0 = -\frac{R-2}{2R-1}$. In both cases $A_0 < 0$ which is impossible. So, $\lambda^3(\beta_0) \neq 1$. And from the previous conclusion, it follows that $\lambda^4(\beta_0) \neq 1$ as well. From (4.4) we get

$$\frac{d}{d\beta}|\lambda(\beta)| = \frac{R-2}{2(R-1)}\sqrt{\frac{R-1}{\beta(R-2)}}$$

and

$$\frac{d}{d\beta}|\lambda(\beta)|_{|\beta=\beta_0} = \frac{R-2}{2(R-1)}.$$

Vectors

$$\mathbf{q}(\beta_0) = \begin{pmatrix} 1 \\ \frac{R(1-A_0-i\Lambda)}{2} \end{pmatrix}$$

and

$$\mathbf{p}(\beta_0) = \begin{pmatrix} \frac{4\beta_0 A_0 - (A_0-1)+i\Lambda}{2(4\beta_0 A_0-(A_0-1))} & \frac{i\Lambda}{R(A_0-1)(4\beta_0 A_0-(A_0-1))} \end{pmatrix},$$

where

$$\Lambda = \sqrt{(A_0-1)\left(4\beta_0 A_0-(A_0-1)\right)},$$

satisfy $\mathbf{p}S = \lambda\mathbf{p}$, $S\mathbf{q} = \lambda\mathbf{q}$, and $\mathbf{pq} = 1$, which is easy to verify. □

Let $\beta = \beta_0 + \eta$, where η is a sufficiently small positive parameter and $d\beta = d\eta$. From Lemma 4.1, we can transform System (4.1) into the normal form

$$K(\beta, \mathbf{x}) = \mathcal{K}(\beta, \mathbf{x}) + O\left(\|\mathbf{x}\|^5\right),$$

and there are smooth functions $a(\beta)$, $b(\beta)$ and $\omega(\beta)$ so that in polar coordinates, the function $\mathcal{K}(\beta, \mathbf{x})$ is given by

$$\begin{pmatrix} r \\ \theta \end{pmatrix} = \begin{pmatrix} |\lambda(\beta)| - a(\beta) r^3 \\ \theta + \omega(\beta) + b(\beta) r^2 \end{pmatrix}.$$

Now, we compute $a(\beta_0)$ following the procedure in [9]. Notice that $\beta = \beta_0$ if and only if $\eta = 0$. First, we compute K_{20}, K_{11} and K_{02} defined in [9]. For $\beta = \beta_0$, we have

$$K\begin{pmatrix} u \\ v \end{pmatrix} = S\begin{pmatrix} u \\ v \end{pmatrix} + H\begin{pmatrix} u \\ v \end{pmatrix},$$

where

$$H\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \frac{1}{R(R-1)} + \frac{M^{\beta_0}(u+\bar{x})^{\beta_0}}{1+R(u+\bar{x})(v+\bar{y})} - \bar{x} + \frac{1}{\beta_0 A_0 R} v - \left(1 - \frac{1}{\beta_0} + \frac{1}{\beta_0 A_0}\right) u \\ R(u+\bar{x})(v+\bar{y}) - \bar{y} - v - R(A_0-1)u \end{pmatrix}.$$

System (4.1) is equivalent to

$$K\begin{pmatrix} u_n \\ v_n \end{pmatrix} = S\begin{pmatrix} u_n \\ v_n \end{pmatrix} + H\begin{pmatrix} u_n \\ v_n \end{pmatrix}.$$

Define the basis of $\mathbb{R}^2$ by $\Phi = (\mathbf{q}, \overline{\mathbf{q}})$, where $\mathbf{q}(\beta_0) = \begin{pmatrix} 1 & \frac{R(1-A_0-i\Lambda)}{2} \end{pmatrix}^T$. We can represent

$$\begin{aligned}
\begin{pmatrix} u \\ v \end{pmatrix} &= \Phi \begin{pmatrix} z \\ \bar{z} \end{pmatrix} = (\mathbf{q}, \overline{\mathbf{q}}) \begin{pmatrix} z \\ \bar{z} \end{pmatrix} = \mathbf{q}z + \overline{\mathbf{q}}\bar{z} \\
&= \begin{pmatrix} 1 \\ \frac{R(1-A_0-i\Lambda)}{2} \end{pmatrix} z + \begin{pmatrix} 1 \\ \frac{R(1-A_0+i\Lambda)}{2} \end{pmatrix} \bar{z} \\
&= \begin{pmatrix} z + \bar{z} \\ \frac{R((1-A_0-i\Lambda)z + (1-A_0+i\Lambda)\bar{z})}{2} \end{pmatrix}.
\end{aligned}$$

Let $H\left(\Phi\left(\begin{array}{c} z \\ \bar{z} \end{array}\right)\right) = \frac{1}{2}\left(g_{20}z^2 + 2g_{11}z\bar{z} + g_{02}^2\bar{z}\right) + O\left(|z|^3\right)$. We have

$$H\left(\Phi\left(\begin{array}{c} z \\ \bar{z} \end{array}\right)\right) = H\left(\begin{array}{c} z+\bar{z} \\ \frac{R((1-A_0-i\Lambda)z+(1-A_0+i\Lambda)\bar{z})}{2} \end{array}\right),$$

so

$$H\left(\Phi\left(\begin{array}{c} z \\ \bar{z} \end{array}\right)\right) = \left(\begin{array}{c} h_1(z,\bar{z}) \\ h_2(z,\bar{z}) \end{array}\right),$$

where

$$\begin{aligned} h_1(u,v) &= \frac{1}{R(R-1)} + \frac{M^{\beta_0}(z+\bar{z}+\frac{1}{R})^{\beta_0}}{1+R\left(\frac{R((1-A_0-i\Lambda)z+(1-A_0+i\Lambda)\bar{z})}{2} + A_0 - 1\right)\left(z+\bar{z}+\frac{1}{R}\right)} \\ &\quad -\frac{1}{R} + \frac{1}{\beta_0 A_0 R}\left(\frac{R((1-A_0-i\Lambda)z+(1-A_0+i\Lambda)\bar{z})}{2}\right) \\ &\quad -\left(1-\frac{1}{\beta_0}+\frac{1}{\beta_0 A_0}\right)(z+\bar{z}), \end{aligned}$$

and

$$\begin{aligned} h_2(u,v) &= R\left(\frac{R((1-A_0-i\Lambda)z+(1-A_0+i\Lambda)\bar{z})}{2} + A_0 - 1\right)\left(z+\bar{z}+\frac{1}{R}\right) \\ &\quad -(A_0-1) - \frac{R((1-A_0-i\Lambda)z+(1-A_0+i\Lambda)\bar{z})}{2} - R(A_0-1)(z+\bar{z}), \end{aligned}$$

Denote $i\Lambda = \Delta$. Since

$$g_{20} = \frac{\partial^2}{\partial z^2} H\left(\Phi\left(\begin{array}{c} z \\ \bar{z} \end{array}\right)\right)\Bigg|_{z=0},$$

$$g_{11} = \frac{\partial^2}{\partial z \partial \bar{z}} H\left(\Phi\left(\begin{array}{c} z \\ \bar{z} \end{array}\right)\right)\Bigg|_{z=0},$$

$$g_{02} = \frac{\partial^2}{\partial \bar{z}^2} H\left(\Phi\left(\begin{array}{c} z \\ \bar{z} \end{array}\right)\right)\Bigg|_{z=0}$$

we get

$$g_{20} = \left(\begin{array}{c} \frac{R(A_0(A_0((\beta_0-4)\beta_0+2)+\beta_0(\Delta+3)-3)+\Delta+1)}{A_0^2\beta_0} \\ -R^2(A_0-1+\Delta) \end{array}\right),$$

$$g_{11} = \left(\begin{array}{c} \frac{R\left(A_0\beta_0^2+A_0-\beta_0-1\right)}{A_0\beta_0} \\ (1-A_0)R^2 \end{array}\right),$$

$$g_{02} = \left(\begin{array}{c} \frac{R(A_0(A_0((\beta_0-4)\beta_0+2)-\beta_0(\Delta-3)-3)-\Delta+1)}{A_0^2\beta_0} \\ R^2(1-A_0+\Delta) \end{array}\right),$$

and using

$$\begin{aligned} K_{20} &= \left(\lambda^2 I - S\right)^{-1} g_{20}, \\ K_{11} &= (I - S)^{-1} g_{11}, \\ K_{02} &= \left(\overline{\lambda}^2 I - S\right)^{-1} g_{02}, \end{aligned}$$

we obtain

$$K_{20} = \begin{pmatrix} \frac{R\left(A_0^2\left(4\beta_0^2+\beta_0-1\right)-A_0\left(2\beta_0^2(\Delta+2)-3\beta_0\Delta+\Delta-2\right)-\beta_0(3\Delta+1)+\Delta-1\right)}{2(A_0-1)(A_0(3\beta_0-1)+1)} \\ \frac{\Delta R^2(A_0(3\beta_0-1)+\beta_0+1)-R^2(A_0(A_0\beta_0(2\beta_0(\beta_0+2)-5)+A_0+2\beta_0(\beta_0+2)-2)+\beta_0+1)}{A_0(6\beta_0-2)+2} \end{pmatrix},$$

$$K_{11} = \begin{pmatrix} R \\ \beta_0 R^2 (A_0\beta_0 - 1) \end{pmatrix},$$

and

$$K_{02} = \begin{pmatrix} \frac{R\left(A_0^2\left(4\beta_0^2+\beta_0-1\right)+A_0\left(2\beta_0^2(\Delta-2)-3\beta_0\Delta+\Delta+2\right)+\beta_0(3\Delta-1)-\Delta-1\right)}{2(A_0-1)(A_0(3\beta_0-1)+1)} \\ -\frac{R^2(\Delta(A_0(3\beta_0-1)+\beta_0)+A_0(A_0\beta_0(2\beta_0(\beta_0+2)-5)+A_0+2\beta_0(\beta_0+2)-2)+\beta_0+\Delta+1)}{A_0(6\beta_0-2)+2} \end{pmatrix}.$$

By using K_{20}, K_{11} and K_{02} and formula

$$g_{21} = \frac{\partial^3}{\partial z^2 \partial \overline{z}} H\left(\Phi\begin{pmatrix} z \\ \overline{z} \end{pmatrix} + \frac{1}{2}\left(K_{20}z^2 + 2K_{11}z\overline{z} + K_{02}\overline{z}^2\right)\right)\Bigg|_{z=0}$$

we get

$$q_{21} = \begin{pmatrix} m_1 \\ m_2 \end{pmatrix},$$

where

$$\begin{aligned} m_1 = &-\frac{\Delta R^2\left(\beta_0\left(2A_0^2\beta_0^3+5A_0^2\beta_0^2-7A_0^2\beta_0-A_0^2-7A_0\beta_0^2+11A_0\beta_0-4\beta_0+1\right)+(A_0-1)^2\right)}{2A_0\beta_0(A_0-1)(3A\beta_0-A_0+1)} \\ &-\frac{R^2\left(4A_0^2\beta_0^4-5A_0^2\beta_0^3+3A_0^2\beta_0^2-3A_0^2\beta_0+9A_0\beta_0^3-23A_0\beta_0^2+10A_0\beta_0+(A_0-1)^2+4\beta_0^2-7\beta_0\right)}{2A_0\beta_0(3A_0\beta_0-A_0+1)}, \end{aligned}$$

$$m_2 = \frac{R^3\left(A_0^2(\beta_0-1)(\beta(14\beta_0-3)-1)+A_0\left(\beta_0^2(3\Delta-1)-4\beta_0\Delta+\beta_0+\Delta-2\right)+(3\beta_0-1)(\Delta-1)\right)}{A_0(6\beta_0-2)+2}.$$

Finally, we get

$$\begin{aligned} a(\beta_0) &= \frac{1}{2}\mathrm{Re}(\left(\mathbf{p}q_{21}\overline{\lambda}\right)) \\ &= \frac{1}{4}(1-\beta_0)\beta_0 R^2 \\ &= -\frac{(R-1)R^2}{4(R-2)^2}. \end{aligned}$$

If $(\bar{x},\bar{y})$ is fixed point of T, then the invariant curve can be approximated by

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \approx \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} + 2\rho_0 \Re\left(\mathbf{q}e^{i\theta}\right) + \rho_0^2\left(\Re\left(K_{20}e^{2i\theta}\right) + K_{11}\right),$$

where

$$d = \frac{d}{d\beta}\left|\lambda(\beta)\right|\Big|_{\beta=\beta_0}$$

$$\rho_0 = \sqrt{-\frac{d}{a}\eta},\ \theta \in \mathbb{R}.$$

Therefore, we have proved the following result.

Theorem 4.1. *Let $R > 2$, $M > 1$, $A_0 = M^{\beta_0}R^{1-\beta_0}\frac{R-1}{R-2} > 1$, $\beta_0 = \frac{R-1}{R-2}$, and $E_+ = \left(\frac{1}{R}, M^{\beta}R^{1-\beta}\frac{R-1}{R-2} - 1\right)$. Then there is a neighborhood U of the equilibrium point E_+ and $\eta > 0$ such that for $|\beta - \beta_0| < \eta$ and $(x_{-1}, x_0) \in U$, the ω-limit set of the solution of System (1.1), with initial condition (x_{-1}, x_0) is the equilibrium point E_+ if $\beta < \beta_0$ and it belongs to a closed invariant C^1 curve Γ encircling the equilibrium point E_+ if $\beta > \beta_0$. Furthermore, $\Gamma(\beta_0) = 0$ and the invariant curve $\Gamma(\beta) = 0$ can be approximated by*

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \approx \begin{pmatrix} \frac{2\sqrt{2(\beta-\beta_0)}\cos(t)}{R} + \frac{1}{R} \\ \left(\frac{M}{R}\right)^{\beta}\frac{R(R-1)}{R-2} - 1 + \frac{\sqrt{2(\beta-\beta_0)}((1-A_0)\cos(t)+\Lambda\sin(t))}{\beta_0} + \frac{2(A_0\beta_0-1)(\beta-\beta_0)}{\beta_0} \end{pmatrix}$$
$$+ \begin{pmatrix} \frac{\beta-\beta_0}{\beta_0^2 R}\left(\frac{\Lambda\left(2A_0\beta_0^2+3\beta_0-\Upsilon\right)\sin(2t)}{\Upsilon(A_0-1)} + \frac{\left(A_0\left(4\beta_0^2+\beta_0-1\right)+\beta_0+1\right)\cos(2t)}{\Upsilon A_0} + 2\right) \\ \frac{\beta_0-\beta}{\beta_0^2}\left(\frac{(\Lambda(\Upsilon+\beta_0))\sin(2t)}{\Upsilon} + \frac{(A_0(A_0\beta_0(2\beta_0(\beta_0+2)-5)+A_0+2\beta_0(\beta_0+2)-2)+\beta_0+1)\cos(2t)}{\Upsilon}\right) \end{pmatrix},$$

where

$$\Lambda = \sqrt{(A_0-1)(4\beta_0 A_0 - (A_0-1))} \quad \text{and} \quad \Upsilon = A_0(3\beta_0 - 1) + 1.$$

The simulations in the following example confirm our results.

Example 4.1. *For $R = 3$, $M = 2$, we obtain $\beta_0 = 2$, $E_+ = (8/3, 1/3)$, and $a(\beta_0) = -9/2$. Since $a(\beta_0) < 0$, by changing the value of the parameter β from $\beta < \beta_0$ to $\beta > \beta_0$, supercritical Neimark-Sacker bifurcation occurs of the critical value. Figure 3 shows the bifurcation diagrams ((A),(C), and (E)) and the corresponding Lyapunov coefficients ((B),(D), and (F)) for the map T. We compute the numerical calculation of Lyapunov exponents with 1000 iterations and $(x_0, y_0) = (5.4, 3.4)$. If $\beta = 2.01 > \beta_0$ a unique closed invariant curve Γ encircles the equilibrium point (see Figure 8((C),(D)), which is a stable invariant curve (black). This means that the average quality of the individuals and population size at t generation will eventually form a cycle.*

Figure 8(A) shows trajectory with initial value $(x_0, y_0) = (0.33, 1.7)$ (blue) and Figure 8(B) shows the trajectory with initial value $(x_0, y_0) = (0.43, 2.3)$ (red), and

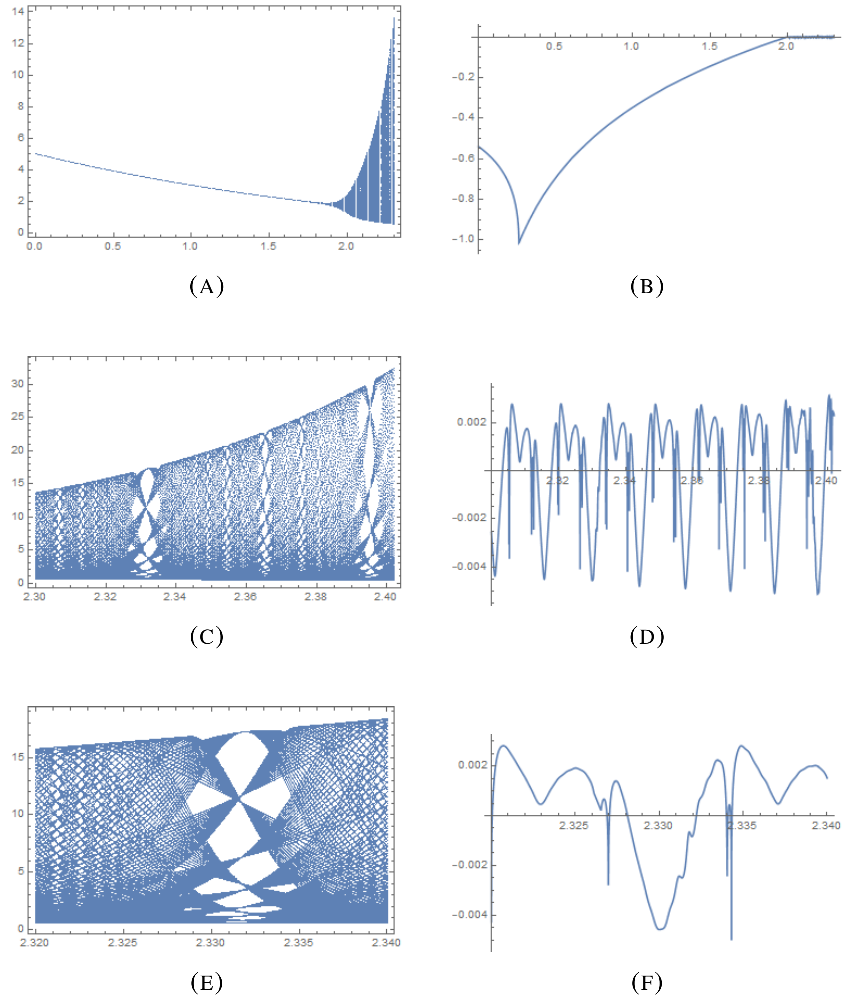


FIGURE 3. Bifurcation diagrams in the (β, x_n)-plane (left) and corresponding Lyapunov coefficients (right) for the map T.

all for $\beta = 2.01 > \beta_0 = 2$. *Figure 8(E) shows the trajectory with initial value* $(x_0, y_0) = (0.4, 1.7)$ *(blue) and* $\beta = 2.4 > \beta_0$*, and Figure 8(E) shows the trajectory with initial value* $(x_0, y_0) = (0.4, 1.7)$ *(green) and* $\beta = 1.95 < \beta_0$. *Figure 4 shows a family of attracting curves for* $\beta \in (2, 2.1)$ *that form a paraboloid.*

The eigenvalues $\lambda_\pm$ *at the fixed point* $(0,0)$ *of the map K are of the form* $\lambda = e^{i\theta}$ *with* $\theta = \arccos \frac{\beta A(R-2)+R+A-2}{2A(R-1)}$ *and* $0 < \theta < \frac{\pi}{2}$. *Thus, in the case $R = 3$ and $M = 2$, the eigenvalues are* $\lambda = e^{i\theta}$ *with* $\theta = \arccos \frac{6(2/3)^\beta(\beta+1)+1}{24(2/3)^\beta}$*, and Figure 5 shows the*

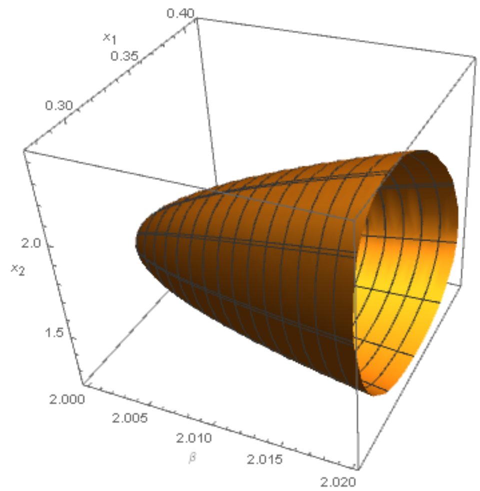


FIGURE 4. Attracting curves for $M = 2$, $R = 3$, and $\beta \in (2.00, 2.02)$.

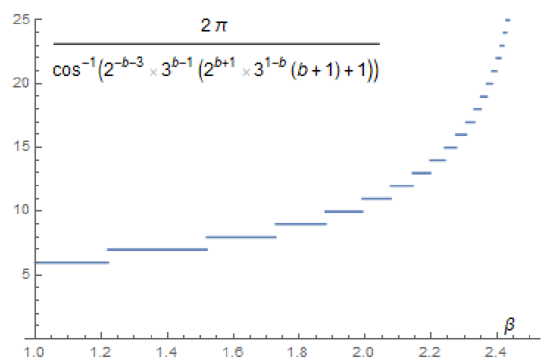
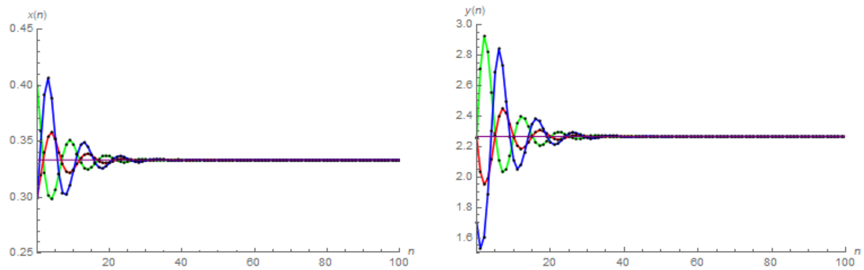


FIGURE 5. Minimal possible period for a periodic orbit in a neighborhood of the fixed point $(0,0)$ for the map K ($R = 3$ and $M = 2$).

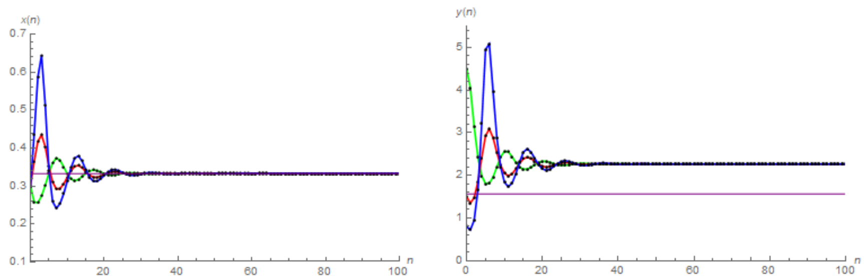
minimal possible period for a periodic orbit in a neighborhood of the fixed point $(0,0)$ *for the map* K *.*

Figures 6 and 7 show the times series plots of the components x_n *and* y_n *for the map* T*.*



(A) (B)

FIGURE 6. Time series plot of the components x_n ((A)) and y_n ((B)) for the map T, when $R = 3$, $M = 2$, $\beta = 1.5$, with initial values $(x_0, y_0) = (0.3, 2.26)$–red, $(x_0, y_0) = (0.4, 2.26)$–green, and $(x_0, y_0) = (0.3, 1.7)$–blue, and eguuilibrium $(x_n, y_n) = (\bar{x}, \bar{y}) = E_+$–purple (sink).



(A) (B)

FIGURE 7. Time series plot of the components x_n ((A)) and y_n ((B)) for the map T, when $R = 3$, $M = 2$, $\beta = 2.1$, with initial values $(x_0, y_0) = (0.3, 1.5)$–red, $(x_0, y_0) = (0.3, 4.5)$–green, and $(x_0, y_0) = (0.3, 0.8)$–blue, and eguuilibrium $(x_n, y_n) = (\bar{x}, \bar{y})) = E_+$–purple (repeller).

5. CONCLUSION

In this paper, our analysis is based on two fundamental assumptions: that the maternal effect is nonlinear and that it has a defined minimum value. The nonlinear maternal effect plays a crucial role in shaping population dynamics, as even small changes within the population can lead to substantial alterations in offspring quality. This non-linearity can also give rise to multiple equilibrium points, which may be either stable or unstable, thereby influencing the overall growth regime of the population and increasing the likelihood of bifurcations.

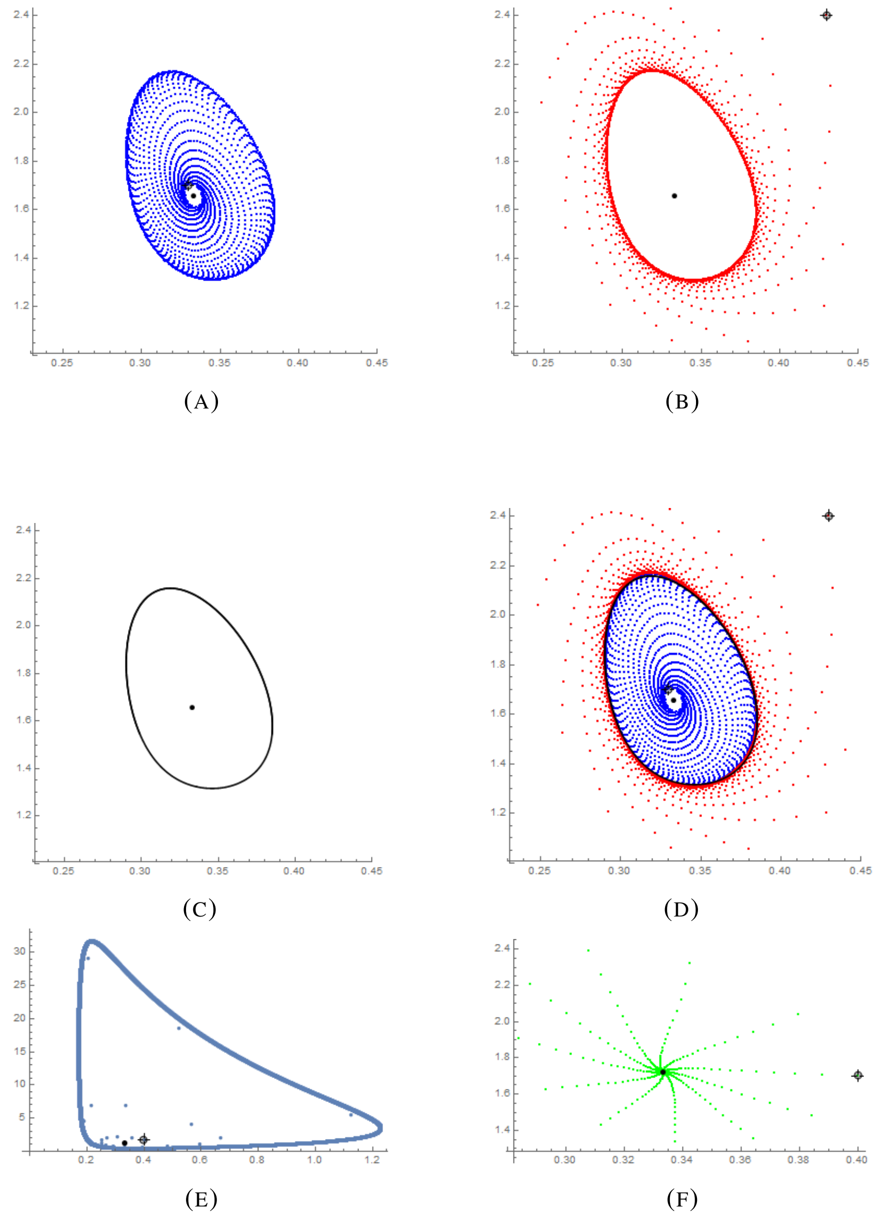


FIGURE 8. Trajectories (a), (b), and (d) for $M = 2$, $R = 3$, and $\beta = 2.01$, with initial values $(x_0, y_0) = (0.33, 1.7)$ (blue), $(x_0, y_0) = (0.43, 2.3)$ (red), and (c) the stable curve Γ. Trajectories for (e) $M = 2$, $R = 3$, and $\beta = 2.4$, with initial value $(x_0, y_0) = (0.4, 1.7)$ (blue), and (f) $M = 2$, $R = 3$, and $\beta = 1.95$, with initial value $(x_0, y_0) = (0.4, 1.7)$ (green).

The minimum quality, in turn, sets a lower bound on offspring quality, ensuring the persistent existence of individuals and reducing the risk of extinction. By preventing extreme values that could drastically alter the system's dynamics, it also influences the occurrence of bifurcations. When combined with the nonlinear maternal effect, the minimum quality contributes to the formation of stable invariant curves, supporting predictable and structured population dynamics. The existence of an invariant curve means that the average quality of the individuals and population size at t generation will eventually form a cycle.

To operationalize this concept within the model, an additional assumption was introduced: the minimum quality k is defined as the quality at the equilibrium point divided by the maximum rate of numerical increase R. This implies that species with higher potential growth rates correspond to a lower minimum quality. Within the model, k is thus replaced by the expression $\frac{1}{R(R-1)}$, a convenient form that facilitates the analysis of bifurcation behavior. Without this assumption, k would need to be introduced as an additional parameter, increasing the complexity of the system and potentially preventing the occurrence of certain bifurcations.

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