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Stability of a Ricker-type competition model and the competitive exclusion principle

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Our main objective is to study a Ricker-type competition model of two species. We give a complete analysis of stability and bifurcation and determine the centre manifolds, as well as stable and unstable manifolds. It is shown that the autonomous Ricker competition model exhibits subcritical bifurcation, bubbles, period-doubling bifurcation, but no Neimark–Sacker bifurcations. We exhibit the region in the parameter space where the competition exclusion principle applies.

Keywords: Ricker competition model; periodic cycles; stability; centre manifold; stable and unstable manifolds; bifurcation; exclusion principle

1. Introduction

Discrete models of single species were popularized by the influential paper of May [35] which was published in Nature more than 30 years ago. Twenty years earlier, two significant papers, that marked the beginning of discrete modelling, were published, one by Beverton and Holt [3] and the other by Ricker [39].

Let x_t be the population density of species x at time t. Then the ratio $f(x_t) = x_{t+1}/x_t$ is called the fitness function of population x. The intraspecific competition among individuals of species x is classified as either scramble or contest competition [21]. For scramble competition f increases until it reaches a maximum after which f decreases monotonically. This scenario is caused by a phenomenon of over-compensatory in which a large population decreases due to fierce competition on resources and habitat. The Ricker model is an example of a scramble intraspecific competition. For the contest competition f is non-decreasing due to increasing utilization of resources [7]. The Beverton–Holt model is an example of the contest competition.

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In the 1970s, Hassell [21] and Maynard-Smith and Slatkin [36] integrated both scramble and contest competitions in their models. A readable account on discrete modelling of single species may be found in the paper by Brannstrom and Sumpter [7], where the authors presented the development of several models.

One of the simplest and the most popular competition model was proposed by Lotka [33, p. 122] and Volterra [44] in the 1920s. Though many consider the model of limited practical utility in many complex organisms, it is generally accepted among researchers that the model gave the impetus to theoretical ecology. By now we have a plethora of continuous (differential equations) competition models that were spawned in the 20th century. However, the discrete counterpart is still lagging behind. Lindstrom [31] has discussed the advantages and disadvantages of utilization discrete models in population dynamics. Though they are simpler than their continuous counterpart to derive, discrete models are much more intractable and less studied.

There are two methods of developing discrete models. The first method is based on a discretization of differential equations, using either a classical numerical scheme such as Euler and Runga–Kutta methods or a nonstandard method such as Mickens [38] scheme. In the latter method, one would derive discrete models from scratch using the underlying biological properties of species. The Leslie–Gower [30] model may be considered as the discrete analogue of the Lotka–Volterra model. A variation of this model was also obtained by Liu and Elaydi [32] via Micken's nonstandard discretization scheme.

Numerous papers on discrete competition models have appeared recently and we will mention a few of them here: Cushing *et al.* [12–14], Edmunds *et al.* [16], Franke and Yakubu [19], Guzowska *et al.* [20], McGehee and Armstrong [37], Clark *et al.* [10], Kulenovic and Nurkanovic [29], Blayneh *et al.* [6], Desharnais *et al.* [15], Jang [25], Roeger [40], Elaydi and Yakubu [18], Blayneh [5], Allen *et al.* [1], Smith [42], Jang and Cushing [26], Yakubu [46], Hirsch [22], Iwata and Takeuchi [24], and AlSharawi and Rhouma [2].

It is noteworthy to mention that in a recent paper, Hone *et al.* [23] utilized a Ricker-type model in the study of a predator–prey system.

In this paper, we adopt the latter approach and focus on an autonomous Ricker-type competition model. In Section 2, we present the theory associated with the invariant manifolds, namely the centre manifolds, the stable manifolds and the unstable manifolds.

In Section 3, we focus on the study of the stability of the exclusion fixed points and the coexistence fixed point of the autonomous Ricker-type competition model. In Section 4, we study the properties of the stable and the unstable manifolds of the fixed points of this model.

In Section 5, a bifurcation scenario is presented in which we develop a bifurcation diagram in the parameter space. We show the presence of both, period-doubling bifurcation and transcritical bifurcation. Moreover, we found bubbles and subcritical bifurcation. Furthermore, the model under analysis does not have a Neimark–Sacker bifurcation.

2. Invariant manifolds

Let $F : \mathbb{R}^k \to \mathbb{R}^k$ be a map such that $F \in C^2$ and $F(0) = 0$. Then one may write F as a perturbation of a linear map L,

$$F(X) = LX + R(X), \tag{1}$$

where L is a $k \times k$ matrix defined by $L = D(F(0))$, $R(0) = 0$ and $DR(0) = 0$, where D denotes the Jacobian matrix. Now we will introduce special subspaces of $\mathbb{R}^k$, called invariant manifolds [45, p. 14], that will play a central role in our study of stability and bifurcation.

An invariant manifold is a manifold embedded in its phase space with the property that it is invariant under the dynamical system generated by F. A subspace M of $\mathbb{R}^k$ is an invariant manifold if whenever $X \in M$, then $F^n(X) \in M$, for all $n \in \mathbb{Z}^+$. For the linear map L, one may split its spectrum $\sigma(L)$ into three sets σ_s, σ_u, and σ_c, for which $\lambda \in \sigma_s$ if $|\lambda| < 1$, $\lambda \in \sigma_u$ if $|\lambda| > 1$, and $\lambda \in \sigma_c$ if $|\lambda| = 1$.

Corresponding to these sets, we have three invariant manifolds (linear subspaces) E^s, E^u, and E^c which are the generalized eigenspaces corresponding to σ_s, σ_u, and σ_c, respectively. It should be noted that some of these subspaces may be trivial.

The main question here is how to extend this linear theory to nonlinear maps. Corresponding to the linear subspaces E^s, E^u, and E^c, we will have the invariant manifolds the stable manifold W^s, the unstable manifold W^u, and the centre manifolds W^c.

The centre manifold theory [8,9,28,34,43,45] is interesting only if $W^u = \{0\}$. For in this case, the dynamics on the centre manifold W^c determines the dynamics of the system. The other interesting case is when $W^c = \{0\}$ and we have a saddle.

Let $E^s \subset \mathbb{R}^s$, $E^u \subset \mathbb{R}^u$, and $E^c \subset \mathbb{R}^t$, with $s+u+t=k$. Then one may formally define the above-mentioned invariant manifolds as follows:

$$W^s(0) = \{x \in \mathbb{R}^k | F^n(x) \longrightarrow 0, n \longrightarrow \infty\}$$

and

$$W^u(0) = \{x \in \mathbb{R}^k | \exists \{q_n\}_{n=0}^{\infty}, q_0 = x, \text{ and } F(q_{k+1}) = q_k, q_n \longrightarrow 0, n \longrightarrow \infty\}.$$

It is noteworthy to mention that the centre manifold is not unique, while the stable and unstable manifolds are unique.

The next result summarizes the basic invariant manifolds theory

THEOREM 2.1 (Invariant manifold theorem) [27,34] *Suppose that $F \in C^2$. Then there exist C^2 stable W^s and unstable W^u manifolds tangent to E^s and E^u, respectively, at $X=0$ and C^1 centre manifold W^c tangent to E^c at $X=0$. Moreover, the manifolds W^c, W^s and W^u are all invariant.*

In Appendix 1, we present the necessary techniques to compute the centre manifolds and the stable and unstable manifolds for nonlinear maps. We apply these techniques throughout the paper to a Ricker-type competition model.

3. The Ricker competition model

The classical Ricker competition model is given by

$$\begin{aligned} u_{n+1} &= u_n \exp(K - c_{11}u_n - c_{12}v_n) \\ v_{n+1} &= v_n \exp(L - c_{21}u_n - c_{22}v_n), \end{aligned}$$

where the parameters K and L are assumed to be positive real numbers and $c_{ij} \in (0,1)$, $1 \le i,j \le 2$.

Letting $c_{11}u_n = x_n$ and $c_{22}v_n = y_n$ yields the system

$$\begin{aligned} x_{n+1} &= x_n \exp(K - x_n - ay_n) \\ y_{n+1} &= y_n \exp(L - y - bx_n), \end{aligned} \tag{2}$$

where $a = c_{12}/c_{22}$ and $b = c_{21}/c_{11}$. Thus $a, b > 0$. In the language of population dynamics, the parameters K and L are known as the carrying capacities of species x and y, respectively, while the parameters a and b are the competition parameters. Equation (2) may be represented by the map

$$F(x, y) = (x\mathrm{e}^{K-x-ay}, y\mathrm{e}^{L-y-bx}).$$

Equation (2) has three fixed points, one extinction fixed point $(0, 0)$, and two exclusion fixed points on the axes $(K, 0)$ and $(0, L)$. A possible fourth positive coexistence fixed point (x^*, y^*) may be present.

Let us write the map $F=(f, g)$. Then the isoclines are defined as $f(x, y)=x$ and $g(x, y)=y$. These are the lines $ay+x=K$ denoted by s_1 and $y+bx=L$ denoted by s_2 (Figure 1(a) and (b)). Moreover, the map F takes a point $(x, y) \in \mathbb{R}_+^2$ lying above (below) s_1 to a point with a smaller (larger) x-coordinate. Similarly, the map F takes a point $(x, y) \in \mathbb{R}_+^2$ lying above (below) s_2 to a point with a smaller (larger) y-coordinate.

Note that on the isocline s_1, the population x has no growth, that is $x_{n+1}=x_n$ and on the isocline s_2 the population y has no growth, that is $y_{n+1}=y_n$.

If the two isoclines s_1 and s_2 intersect in the positive quadrant, we will have the positive fixed point

$$(x^*, y^*) = \left(\frac{K-aL}{1-ab}, \frac{L-bK}{1-ab}\right).$$

There are two cases to consider here: (i) $ab<1$ and (ii) $ab>1$ (Figure 2(a) and (b)). The case $ab=1$ will be discarded since in this case the two isoclines are parallel and no coexistence fixed point is present.

The Jacobian of Equation (2) is given by

$$JF(x, y) = \begin{bmatrix} (1-x)\mathrm{e}^{K-x-ay} & -ax\mathrm{e}^{K-x-ay} \\ -by\mathrm{e}^{L-y-bx} & (1-y)\mathrm{e}^{L-y-bx} \end{bmatrix}.$$

The Jacobians evaluated at the fixed points are

$$J_0 = JF(0, 0) = \begin{bmatrix} \mathrm{e}^K & 0 \\ 0 & \mathrm{e}^L \end{bmatrix},$$

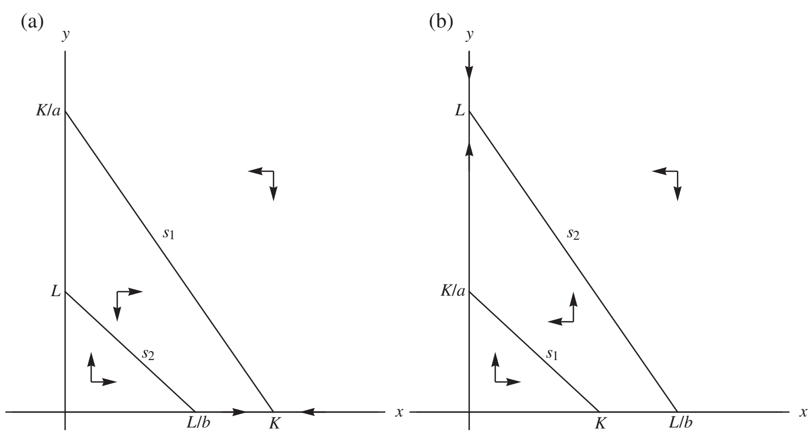

Figure 1. The stability of the exclusion fixed point and the validity of the competition exclusion principle. (i) If $0<K\leq 2$ and $L<bK$, then $(K, 0)$ is locally asymptotically stable and species y goes extinct. (ii) If $0<L\leq 2$ and $L>K/a$, then $(0, L)$ is locally asymptotically stable and species x goes extinct.

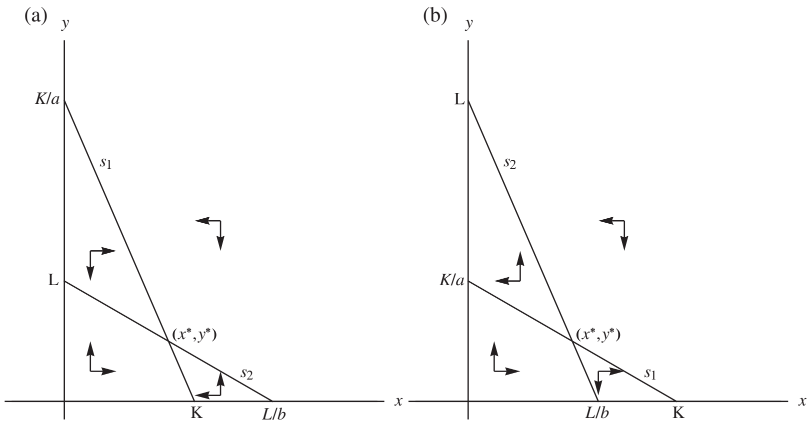

Figure 2. Isoclines: (a) The coexistence fixed point of Equation (2) exists if $bK < L < K/a$ and $ab < 1$. (b) The coexistence fixed point of Equation (2) exists if $K/a < L < bK$ and $ab > 1$. In this scenario, this equilibrium is a saddle.

$$J_K = JF(K,0) = \begin{bmatrix} 1-K & -aK \\ 0 & \mathrm{e}^{L-bK} \end{bmatrix},$$

$$J_L = JF(0,L) = \begin{bmatrix} \mathrm{e}^{K-aL} & 0 \\ -bL & 1-L \end{bmatrix}$$

and

$$J^* = JF(x^*, y^*) = \begin{bmatrix} 1-x^* & -ax^* \\ -by^* & 1-y^* \end{bmatrix}.$$

Before we present the stability of these fixed points, we should mention that Smith [42] has been using monotonicity to prove the global stability of the fixed points of the system

$$\begin{aligned} u_{n+1} &= u_n \exp(r(1-u_n - Bv_n)) \\ v_{n+1} &= v_n \exp(s(1 - Cu_n - v_n)), \end{aligned} \tag{3}$$

when $r, s \leq 1$ in which the invariant set is $[0, r^{-1}] \times [0, s^{-1}]$. Notice that by the changes of variables $ru = x$ and $sv = y$ system (3) is equivalent to

$$\begin{aligned} x_{n+1} &= x_n \exp\left(r - x_n - \frac{Br}{s} y_n\right) \\ y_{n+1} &= y_n \exp\left(s - y_n - \frac{Cs}{r} x_n\right). \end{aligned}$$

Consequently, $K = r$, $L = s$, $a = Br/s$ and $b = Cs/r$. Hence, his global results cover our local analysis when we take the carrying capacities in the unit interval.

In the sequel, we study the stability of these fixed points.

3.1. *Stability of the extinction and exclusion equilibria*

The eigenvalues of J_0 are $\mathrm{e}^K > 1$ and $\mathrm{e}^L > 1$ since $K, L > 0$. Thus $(0,0)$ is unstable for all $K, L > 0$.

The eigenvalues of J_K are $1-K$ and e^{L-bK}. Thus $\rho(J_K) < 1$[1] if and only if $0 < K < 2$ and $L < bK$. Thus $(K, 0)$ is locally asymptotically stable if $0 < K < 2$ and $L < bK$. In the parameter space, we call this region R_1 (Figure 3). Below we will prove that when $K = 2$, this exclusion

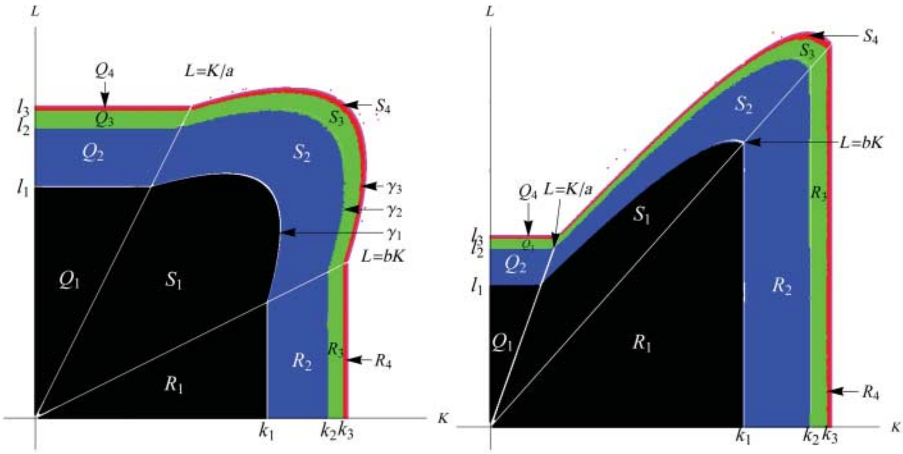

Figure 3. The stability regions in the parameter space of the solution of the Ricker competition equation (2) when $a > 0$ and $b > 0$ such that $ab < 1$. In the plot on the left, the values of the competition parameters are $a = b = 0.5$ while in the plot on the right $a = 0.2$ and $b = 2$.

fixed point is locally asymptotically stable and when $L = bK$ it is unstable. Thus one may define the region R_1 as

$$R_1 = \{(K, L) \in \mathbb{R}^2 : 0 < K \leq 2 \wedge L < bK\}.$$

Note that from the inequality $K > L/b$, we obtain $K/a > L/ab$ and consequently $L < L/ab < K/a$. In Figure 1(a), we represent the orientation of the isoclines in the phase-space diagram. Similarly, $(0, L)$ is locally asymptotically stable if $0 < L \leq 2$ and $L > K/a$. The region of stability of $(0, L)$ in the parameter space $K - L$ is denoted by Q_1 (Figure 3) and is given by

$$Q_1 = \left\{(K, L) \in \mathbb{R}^2 : 0 < L \leq 2 \wedge L > \frac{K}{a}\right\}.$$

Note that from the inequality $K/a < L$ it follows that $K < K/ab < L/b$. In Figure 1(b), we show the orientation of the isoclines in the phase-space diagram.

We now study the stability of the fixed point $(K, 0)$ when $|\rho(J_K)| = 1$. This occurs in two cases, the first is when $K = 2$ and $L < bK$, in which the eigenvalues are $\lambda_1 = -1$ and $\lambda_2 < 1$. The second case is when $0 < K < 2$ and $L = bK$, in which $|\lambda_1| < 1$ and $\lambda_2 = 1$. (The case when $K = 2$ and $L = bK$ at which $\lambda_1 = -1$ and $\lambda_2 = 1$ will not be investigated in this paper due to the lack of the required techniques). To investigate these cases, we need to use the centre manifold theory developed in Appendix 1.

Making the changes of variable $u = x - K$ and $v = y$ in Equation (2), we shift the fixed point $(K, 0)$ to $(0, 0)$. Then the new system is given by

$$\begin{aligned} u_{n+1} &= (u_n + K)\mathrm{e}^{-u_n - av_n} - K \\ v_{n+1} &= v_n \mathrm{e}^{L - v_n - b(u_n + K)}. \end{aligned} \tag{4}$$

Let us now consider the first case, i.e. $K = 2$ and $L < bK$. The Jacobian at $(0, 0)$ is now given by

$$\tilde{J}_0 = \begin{bmatrix} -1 & -2a \\ 0 & -\mathrm{e}^{L-2b} \end{bmatrix}.$$

Consequently, one may write Equation (4) as

$$\begin{bmatrix} u_{n+1} \\ v_{n+1} \end{bmatrix} = \begin{bmatrix} -1 & -2a \\ 0 & -\mathrm{e}^{L-2b} \end{bmatrix} \begin{bmatrix} u_n \\ v_n \end{bmatrix} + \begin{bmatrix} \tilde{f}(u_n, v_n) \\ \tilde{g}(u_n, v_n) \end{bmatrix}, \tag{5}$$

where

$$\tilde{f}(u,v) = (u+2)\mathrm{e}^{-u-av} - 2 + u + 2av$$

and

$$\tilde{g}(u,v) = v\mathrm{e}^{L-v-b(u+2)} + \mathrm{e}^{L-2b}v.$$

Let $v = h(u)$ with $h(u) = \alpha u^2 + \beta u^3 + O(|u^4|), \alpha, \beta \in \mathbb{R}$. The map h must satisfy the centre manifold equation

$$h(-u - 2ah(u) + \tilde{f}(u, h(u))) + \mathrm{e}^{L-2b}h(u) - \tilde{g}(u, h(u)) = 0.$$

By Taylor's series this equation is equivalent to

$$(\alpha - \mathrm{e}^{-2b+L}\alpha)u^2 + (b\mathrm{e}^{-2b+L}\alpha + 4a\alpha^2 - \beta - \mathrm{e}^{-2b+L}\beta)u^3 + O[u]^4 = 0.$$

Solving the system $\alpha - \mathrm{e}^{-2b+L}\alpha = 0$ and $b\mathrm{e}^{-2b+L}\alpha + 4a\alpha^2 - \beta - \mathrm{e}^{-2b+L}\beta = 0$ yields the unique solution $\alpha = 0$ and $\beta = 0$. Hence $h(u) = 0$. Consequently, on the centre manifold $v = 0$, the new map $\hat{f}$ is given by

$$\hat{f}(u) = -u - 2ah(u) + \tilde{f}(u, h(u)) = -2 + \mathrm{e}^{-u}(2+u).$$

Simple computations show that the Schwarzian derivative of this map at $u = 0$ is -1. Hence, by Elaydi [17, p. 30] the exclusion fixed point $(2, 0)$ is asymptotically stable.

We now consider the second case, i.e. $0 < K < 2$ and $L = bK$. After computing the new Jacobian at $(0, 0)$, Equation (4) may be written as

$$\begin{bmatrix} u_{n+1} \\ v_{n+1} \end{bmatrix} = \begin{bmatrix} 1-K & -aK \\ 0 & 1 \end{bmatrix} \begin{bmatrix} u_n \\ v_n \end{bmatrix} + \begin{bmatrix} \tilde{\tilde{f}}(u_n, v_n) \\ \tilde{\tilde{g}}(u_n, v_n) \end{bmatrix}, \tag{6}$$

where

$$\tilde{\tilde{f}}(u,v) = (u+K)\mathrm{e}^{-u-av} - (1-K)u + (av-1)K$$

and

$$\tilde{\tilde{g}}(u,v) = v\mathrm{e}^{-v-bu} - v.$$

In this case, computations show that the centre manifold is given by

$$h(v) = -av - \frac{(1-ab)av^2}{K} + \left(\frac{a(-1+ab)(4 + a(2 + b(-6+K)) - K)}{2K^2} \right) v^3. \tag{7}$$

Thus the new map on the centre manifold is now

$$\hat{\hat{f}}(v) = v\mathrm{e}^{-v-bh(v)}. \tag{8}$$

Computations show that $(\hat{\hat{f}}(v))'_{v=0} = 1$ and $(\hat{\hat{f}}(v))''_{v=0} = 2(-1+ab)$. Thus by Elaydi [17, p. 28], the exclusion fixed point on the centre manifold $u = h(v)$ is unstable. More precisely, it is a semi-stable fixed point from the right since $2(-1+ab) < 0$ (see [17, p. 31]).

We now summarize these remarks in the following result.

THEOREM 3.1 *For the autonomous Ricker equation* (2), *the following statements hold true:*

(1) $(0,0)$ *is unstable.*
(2) $(K,0)$ *is asymptotically stable if* $0 < K \leq 2$ *and* $L < bK$,
(3) $(0,L)$ *is asymptotically stable if* $0 < L \leq 2$ *and* $L > K/a$.

3.2. *Stability of the coexistence fixed point: The case ab < 1*

Recall that $(x^*, y^*) = ((K - aL)/(1 - ab), (L - bK)/(1 - ab))$ is a coexistence fixed point if

$$bK < L < \frac{K}{a} \quad \text{and} \quad ab < 1. \tag{9}$$

In this situation, the lines segments s_1 and s_2 intersect as is shown in Figure 2(a). In order to find the stability region of (x^*, y^*), we need to find the region where

$$|\mathrm{tr}(J^*)| - 1 < \det(J^*) < 1.$$

(Fore more details about this point, see [17, p. 200]). This is equivalent to

$$\det(J^*) < 1 \wedge \det(J^*) > \mathrm{tr}(J^*) - 1 \wedge \det(J^*) > -\mathrm{tr}(J^*) - 1.$$

If at least one of these inequalities is reversed, then (x^*, y^*) is unstable. Now

$$\det(J^*) = \frac{ab - 1 + (1-a)L + (1-b)K - (aL - K)(bK - L)}{ab - 1}$$

and

$$\mathrm{tr}(J^*) = \frac{2(ab-1) + (1-a)L + (1-b)K}{ab - 1}.$$

Consequently, $\det(J^*) < 1$ iff

$$(aL - K)(bK - L) < (1-a)L + (1-b)K, \tag{10}$$

$\det(J^*) > \mathrm{tr}(J^*) - 1$ iff

$$(aL - K)(bK - L) > 0, \tag{11}$$

and finally $\det(J^*) > -\mathrm{tr}(J^*) - 1$ iff

$$(aL - K)(bK - L) > 4(ab - 1) + 2(1-a)L + 2(1-b)K. \tag{12}$$

Notice that inequality (11) is automatically satisfied by Equation (9).

Thus, (x^*, y^*) is locally asymptotically stable if for any fixed $a > 0$ and $b > 0$ with $ab < 1$, the following inequalities hold

$$\begin{aligned}(aL - K)(bK - L) &< (1-a)L + (1-b)K \\ (aL - K)(bK - L) &> 4(ab - 1) + 2(1-a)L + 2(1-b)K.\end{aligned} \tag{13}$$

The solution of this system leads to the interior of the region identified by the letter S_1 in the (K, L)-plane (Figure 3). The region S_1 is bounded by the lines $L = K/a$ and $L = bK$ and the curve γ_1 (Points on this curve may be included as shown below). In Appendix 2, we will show that γ_1 is part of the left branch of the hyperbola defined by the equation

$$(aL - K)(bK - L) = 4(ab - 1) + 2(1-a)L + 2(1-b)K.$$

In the sequel, we will show that when K and L are on γ_1 the coexistence fixed point is asymptotically stable. This happens when $|\rho(J^*)| = 1$, i.e. $\lambda_1 = -1$ and $\lambda_2 < 1$. Note that on the curve

γ_1 one has

$$L = \frac{2(a-1)+(1+ab)K}{2a} \pm \frac{\sqrt{(2(a-1)+(1+ab)K)^2+4a(4(1-ab)+2(b-1)K-bK^2)}}{2a}. \tag{14}$$

Making the change of variables $u_n = x_n - x^*$ and $v_n = y_n - y^*$ in Equation (2), we shift the positive fixed point to the origin. Equation (2) is now equivalent to

$$\begin{bmatrix} u_{n+1} \\ v_{n+1} \end{bmatrix} = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix} \begin{bmatrix} u_n \\ v_n \end{bmatrix} + \begin{bmatrix} \tilde{f}(u_n, v_n) \\ \tilde{g}(u_n, v_n) \end{bmatrix}. \tag{15}$$

where

$$\tilde{f}(u,v) = (u+x^*)\mathrm{e}^{K-(u+x^*)-a(v+y^*)} - x^* - J_{11}u - J_{12}v,$$
$$\tilde{g}(u,v) = (v+y^*)\mathrm{e}^{L-(v+y^*)-b(u+x^*)} - y^* - J_{21}u - J_{22}v,$$

and the Jacobian at $(0,0)$ is given by

$$\begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix} = \begin{bmatrix} \dfrac{-1+K-a(-b+L)}{-1+ab} & -\dfrac{a(-K+aL)}{-1+ab} \\ -\dfrac{b(bK-L)}{-1+ab} & \dfrac{-1+ab-bK+L}{-1+ab} \end{bmatrix}.$$

Now we need to diagonalize this matrix. Let us write the diagonal matrix as

$$\begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix} = \begin{bmatrix} S_{11} & S_{12} \\ 1 & 1 \end{bmatrix} \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix} \begin{bmatrix} \tilde{S}_{11} & \tilde{S}_{12} \\ \tilde{S}_{21} & \tilde{S}_{22} \end{bmatrix},$$

where

$$S_{11} = \frac{-(1+b)K+(1+a)L+\nabla}{2b(bK-L)}, \quad S_{12} = \frac{-(1+b)K+(1+a)L-\nabla}{2b(bK-L)},$$
$$\lambda_1 = \frac{2(ab-1)+(1-b)K+(1-a)L-\nabla}{2(ab-1)}, \quad \lambda_2 = \frac{2(ab-1)+(1-b)K+(1-a)L+\nabla}{2(ab-1)}$$
$$\tilde{S}_{11} = \frac{b(bK-L)}{\nabla}, \quad \tilde{S}_{12} = \frac{(1+b)K-(1+a)L+\nabla}{2\nabla},$$
$$\tilde{S}_{21} = \frac{b(-bK+L)}{\nabla}, \quad \tilde{S}_{22} = \frac{-(1+b)K+(1+a)L+\nabla}{2\nabla},$$

with

$$\nabla = \sqrt{\begin{matrix}(1+2b+(1-4a)b^2)K^2+2(a(b-1)-b-1+2a^2b^2) \\ KL+(1+2a+a^2(1-4b))L^2\end{matrix}}.$$

Using again a new change of variables $u = S_{11}z + S_{12}w$ and $v = z + w$, yields the following system:

$$\begin{bmatrix} z_{n+1} \\ w_{n+1} \end{bmatrix} = \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix} \begin{bmatrix} z_n \\ w_n \end{bmatrix} + \begin{bmatrix} \tilde{\tilde{f}}(z_n, w_n) \\ \tilde{\tilde{g}}(z_n, w_n) \end{bmatrix}, \tag{16}$$

where

$$\begin{bmatrix} \tilde{\tilde{f}}(z_n, w_n) \\ \tilde{\tilde{g}}(z_n, w_n) \end{bmatrix} = \begin{bmatrix} \tilde{S}_{11} & \tilde{S}_{12} \\ \tilde{S}_{21} & \tilde{S}_{22} \end{bmatrix} \begin{bmatrix} \tilde{f}(u_n, v_n) \\ \tilde{g}(u_n, v_n) \end{bmatrix}.$$

Let $z = h(w)$, where $h(w) = \alpha w^2 + \beta w^3 + O(w^4)$. The function h must satisfy the following equation:

$$h(\lambda_2 w + \tilde{\tilde{g}}(h(w), w)) - \lambda_1 h(w) - \tilde{\tilde{f}}(h(w), w) = 0. \quad (17)$$

After simplifying this equation, we write the Taylor expansion and then find the values of the constant α and β. Since the computations here are long, we cannot find the exact values of α and β. However, we are able to find it numerically. Notice that, the maximum value of the carrying capacity K is given by the biggest value on the left branch of hyperbola (A15), namely

$$K_{\max} = \frac{2(1 + a - a\sqrt{b})}{1 - ab}.$$

Notice that depending on the choice of a and b, $K_{\max}$ can be a very large number namely when $ab \approx 1$.

We reduce our analysis when the competition parameters belongs to the interval $(0, 2]$. Taking randomly the values of a and b in the interval $(0, 2]$ such that $ab < 1$ and using the value of carrying capacity L given in Equation (14), we vary the carrying capacity K in the interval $(0, 3]$ and find numerically the values of α and β. After we do this, we compute the value of the Schwarzian derivative of map

$$H(w) = -w + \tilde{\tilde{g}}(h(w), w).$$

From our simulations, we conclude that the Schwarzian derivative $SH(0) < 0$, as it is shown in Figure 4. Note that this simulations can be done for much more larger values of a and b.

By numerical calculations, one may conclude that on the curve γ_1 the coexistence fixed point of Equation (2) must be asymptotically stable. Similar conclusions may be made if we consider the centre manifold $w = h(z)$.

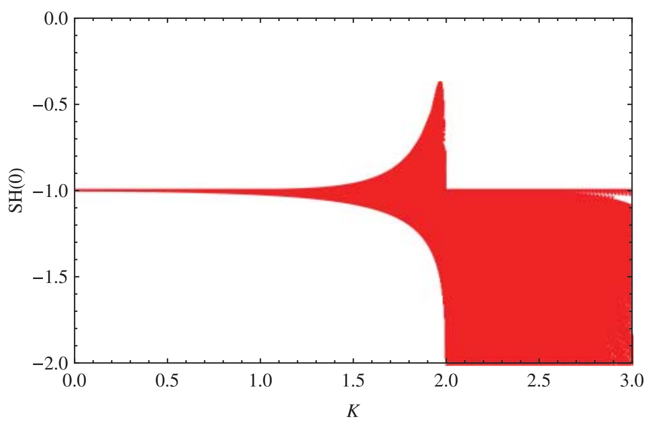

Figure 4. Part of the values of the Schwarzian derivative of the new map on the centre manifold for the coexistence fixed point. In this simulation, we use values of the carrying capacity K in the interval $(0, 3]$ and the competition parameters are in the interval $(0, 2]$ such that $ab < 1$.

We now summarize these conclusions in the following theorem.

THEOREM 3.2 *Suppose that $ab < 1$ and let $\hat{S} = Int(S_1) \cup \gamma_1$, where* $\mathrm{Int}(S_1)$ *denotes the interior of S_1. Then the coexistence fixed point*

$$(x^*, y^*) = \left(\frac{aL - K}{ab - 1}, \frac{bK - L}{ab - 1}\right)$$

of the Ricker equation (2) *is asymptotically stable if*

$$4(ab - 1) + 2(1 - a)L + 2(1 - b)K \leq (aL - K)(bK - L) < (1 - a)L + (1 - b)K.$$

Equivalently, the coexistence fixed point is asymptotically stable if $(K, L) \in \hat{S}$.

4. The stable and unstable manifolds

In this section, we study (via numerical computations) a celebrated scenario in classic competition theory, the saddle exclusion case (or equivalently, a stable and unstable manifolds).

A general two-dimensional map has a stable and an unstable manifolds when the following conditions, in the Trace-Determinant plane, are satisfied

$$\begin{cases} \det(J^*) < \mathrm{tr}(J^*) - 1 \\ \det(J^*) > -\mathrm{tr}(J^*) - 1 \end{cases} \vee \begin{cases} \det(J^*) > \mathrm{tr}(J^*) - 1 \\ \det(J^*) < -\mathrm{tr}(J^*) - 1 \end{cases} \vee$$
$$\begin{cases} \det(J^*) < \dfrac{(\mathrm{tr}(J^*))^2}{4} \\ \det(J^*) > 1 \\ \det(J^*) > -\mathrm{tr}(J^*) - 1 \end{cases} \vee \begin{cases} \det(J^*) < \dfrac{(\mathrm{tr}(J^*))^2}{4} \\ \det(J^*) > \mathrm{tr}(J^*) - 1 \\ \det(J^*) > 1 \end{cases}. \tag{18}$$

For more details about these conditions, see [17, p. 205]. Hence we have two scenarios to consider: (i) $ab > 1$ in which the winner depends on initial conditions and (ii) $ab < 1$, where we have the presence of both locally asymptotically stable cycles and unstable fixed points.

4.1. *Case (4i): ab > 1*

In model (2), the saddle scenario occurs when one has a coexistence equilibrium such that

$$aL > K \quad \text{and} \quad bK > L, \tag{19}$$

which implies that

$$ab > 1. \tag{20}$$

We now determine, in the parameter space, the region where relation (18) is satisfied. Direct computations show that $\det(J^*) > \mathrm{tr}(J^*) - 1$ is equivalent to

$$(aL - K)(bK - L) < 0,$$

which is impossible by Equation (19). Hence there are two systems in Equation (18) that leads to an empty region. Analogously, $\det(J^*) < \mathrm{tr}(J^*) - 1$ is the region in the (K, L)-plane between the two lines $L = K/a$ and $L = bK$, i.e. assumption (19). Notice that by Equation (20), one has $b > 1/a$, and consequently $bK > K/a$.

The inequality $\det(J^*) > -\mathrm{tr}(J^*) - 1$ leads to

$$2(1-a)L + 2(1-b)K - (aL-K)(bK-L) + 4(ab-1) > 0.$$

Notice that by Equation (A15), the second degree equation

$$2(1-a)L + 2(1-b)K - (aL-K)(bK-L) + 4(ab-1) = 0 \tag{21}$$

represents a hyperbola in (K, L)-plane (for more details about this hyperbola, see Appendix 2). Hence the system

$$\begin{aligned}\det(J^*) &< \mathrm{tr}(J^*) - 1\\ \det(J^*) &> -\mathrm{tr}(J^*) - 1\end{aligned} \tag{22}$$

is satisfied whenever K and L are between the lines $L = K/a$ and $L = bK$ and the right branch of hyperbola (21).

Relation $\det(J^*) > 1$ is equivalent to

$$(1-a)L + (1-b)K - (aL-K)(bK-L) > 0.$$

This is the region in the first quadrant outside the right branch of the hyperbola

$$(1-a)L + (1-b)K - (aL-K)(bK-L) = 0 \tag{23}$$

which passes through the origin.

The inequality $\det(J^*) < (\mathrm{tr}(J^*))^2/4$ leads to the following relation:

$$(4a^2b-(a+1)^2)L^2 + 2(1+a+b-ab-2(ab)^2)KL + (4ab^2-(b+1)^2)K^2 < 0. \tag{24}$$

Notice that the second-degree equation

$$(4a^2b-(a+1)^2)L^2 + 2(1+a+b-ab-2(ab)^2)KL + (4ab^2-(b+1)^2)K^2 = 0$$

represents a conic, in the (K, L)-plane, known as a pair of imaginary lines intersecting in a real point (see for instance [4]), provided that the test condition are

$$\left|\begin{pmatrix} 4ab^2-(b+1)^2 & 1+a+b-ab-2(ab)^2 & 0\\ 1+a+b-ab-2(ab)^2 & 4a^2b-(a+1)^2 & 0\\ 0 & 0 & 0\end{pmatrix}\right| = 0$$

and

$$\left|\begin{pmatrix} 4ab^2-(b+1)^2 & 1+a+b-ab-2(ab)^2\\ 1+a+b-ab-2(ab)^2 & 4a^2b-(a+1)^2\end{pmatrix}\right| = -4ab(-1+ab)^3 < 0$$

This point is precisely the origin because the equations of these two lines are $L = m_\pm K$, where

$$m_\pm = \frac{1+a+b-ab-2a^2b^2 \pm 2\sqrt{ab(-1+ab)^3}}{((1+a)^2-4a^2b)}.$$

Hence, the system

$$\begin{aligned}\det(J^*) &< \frac{(\mathrm{tr}(J^*))^2}{4}\\ \det(J^*) &> 1\\ \det(J^*) &> -\mathrm{tr}(J^*) - 1\end{aligned} \tag{25}$$

represents the region in the (K, L)-plane outside both hyperbolas (21) and (23) and between the two lines $L = m_\pm K$.

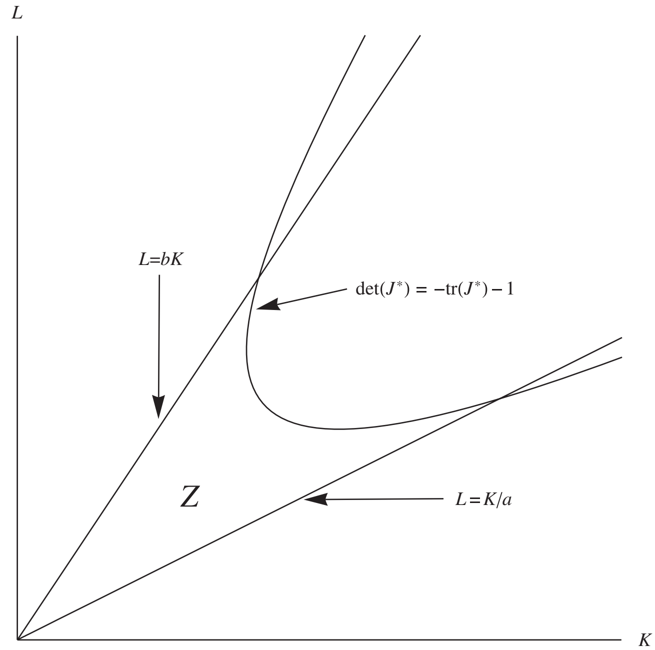

Figure 5. The saddle region Z, in the parameter space K and L, when $a = 2$ and $b = 1.5$.

Numerical computations show that when $a > 1$ and $b > 1$ (which implies $ab > 1$) one has

$$m_+ > b > 1/a > m_-.$$

So assuming this restriction on the competition parameters and under hypothesis (19), system (25) has an empty solution. Consequently, if $a > 1$ and $b > 1$ relation (18) is equivalent to system (22). Hence, the saddle region is enclosed by the two lines $L = K/a$ and $L = bK$ and the right branch of hyperbola (21). In Figure 5 as depicted in the parameter space (K, L) this region when $a = 2$ and $b = 1.5$.

Notice that if we assume that either $a < 1$ or $b < 1$ such that $ab > 1$, then the saddle region is more involved, namely it contains the solution of both systems (22) and (25).

Now let us take $a > 1$ and $b > 1$ such that $(K, L) \in S$. Following the same techniques as in Section (3.2) we find that, locally, the stable manifold of the coexistence fixed point is given by

$$W^s = \{(z, w) \in \mathbb{R}^2 : w = \alpha_1 z^2 + \beta_1 z^3, \alpha_1, \beta_1 \in \mathbb{R}\},$$

and the unstable manifold is

$$W^u = \{(z, w) \in \mathbb{R}^2 : z = \beta_2 w^2, \beta_2 \in \mathbb{R}\}.p$$

Due the big size of the formulas for the constants α_1, β_1 and β_2, we omit them here. In the original coordinates, the values of z and w are given by

$$z = \frac{S_{22}(x - x^*) - S_{12}(y - y^*)}{S_{11}S_{22} - S_{21}S_{12}} \quad \text{and} \quad w = \frac{S_{11}(y - y^*) - S_{21}(x - x^*)}{S_{11}S_{22} - S_{21}S_{12}},$$

where S_{ij} are the entries of the matrix S determined in the previous section.

4.2. *Case (ii):ab < 1*

By Equation (9), it follows that $det(J^*) < \mathrm{tr}(J^*) - 1$ is impossible. Hence the first system in Equation (18) leads to an empty region. In the previous subsection, we determine the inequality

$$\det(J^*) < \frac{(\mathrm{tr}(J^*))^2}{4},$$

which leads to relation (24). We claim that when $ab < 1$, the first member of Equation (24) is negative. In order to show that, let us assume temporally that $L = mK$ for some $m > 0$. Hence, relation (24) is equivalent to $K^2u(m) < 0$, where

$$u(m) = (4a^2b - (a+1)^2)m^2 + 2(1 + a + b - ab - 2(ab)^2)m + 4ab^2 - (b+1)^2.$$

Solving the equation $u(m) = 0$ one has the following two values:

$$m = \frac{(1 + a + b - ab - 2(ab)^2) \pm 2\sqrt{ab(1-ab)^3}i}{(1+a)^2 + 4a^2b}, i = \sqrt{-1}.$$

Now we show that the coefficient of m^2 is a negative number. So

$$4a^2b - (a+1)^2 = 4aab - (a+1)^2 < 4a - (a+1)^1 = -(a-1)^2 < 0$$

(since $ab < 1$). Hence, the function u is a parabola, concave down, with no real zeros. Consequently, relation (24) is satisfied.

Because $\det(J^*) > \mathrm{tr}(J^*) - 1$ is automatically verified and by the fact that $\det(J^*) < (\mathrm{tr}(J^*))^2/4$ is always true, it follows that the system

$$\begin{aligned} \det(J^*) &< \frac{(\mathrm{tr}(J^*))^2}{4} \\ \det(J^*) &> \mathrm{tr}(J^*) - 1 \\ \det(J^*) &> 1 \end{aligned}$$

leads to the same region in the parameter space, then

$$\begin{aligned} \det(J^*) &< \frac{(\mathrm{tr}(J^*))^2}{4} \\ \det(J^*) &> -\mathrm{tr}(J^*) - 1 \\ \det(J^*) &> 1. \end{aligned}$$

Therefore, relation (18) leads to

$$\begin{cases} \det(J^*) > \mathrm{tr}(J^*) - 1 \\ \det(J^*) < -\mathrm{tr}(J^*) - 1 \end{cases} \vee \begin{cases} \det(J^*) > -\mathrm{tr}(J^*) - 1 \\ \det(J^*) > 1 \end{cases}.$$

This leads to the region Z identified in Figure 6. Note that $Z = \cup_{i\geq 2} S_i$ (in Section 5 we will give more details about the regions S_i, $i \geq 2$).

Before we end this subsection we remark that the determination of the saddle and unstable manifolds follows the guidelines as above.

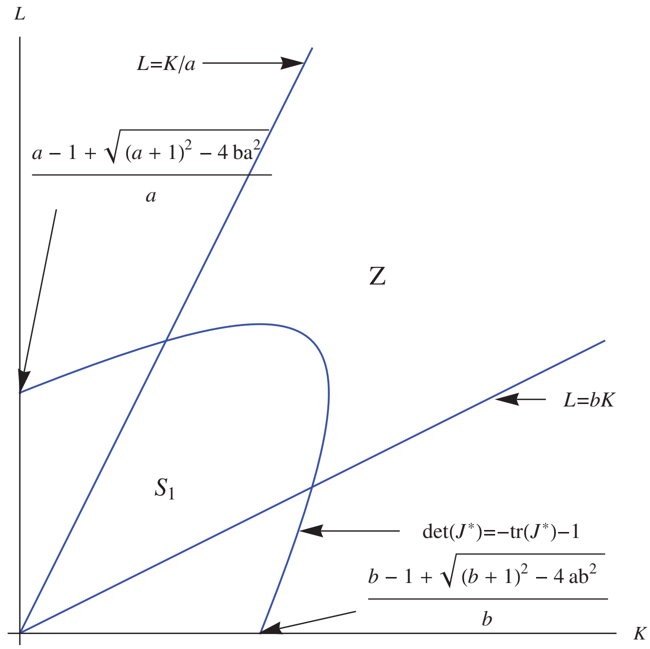

Figure 6. The saddle region Z, in the parameter space K and L, when $a = b = 0.5$.

4.3. *The exclusion fixed point*

We now determine the region, in the parameter space, where the exclusion fixed point $(K, 0)$ of Equation (2) has stable and unstable manifolds. This set is given by

$$Z_K = \{(K, L) \in \mathbb{R}^2 : K > 2 \wedge L < bK\}.$$

Let $(K, L) \in Z_K$. Then similar techniques as before lead us to find locally the stable manifold

$$W_K^s = \{(x, y) \in \mathbb{R}^2 : y = 0\}$$

and the unstable manifold

$$W_K^u = \{(x, y) \in \mathbb{R}^2 : x = K\}$$

of the exclusion fixed point $(K, 0)$.

Similarly, in the set

$$Z_L = \left\{(K, L) \in \mathbb{R}^2 : K > 0 \wedge L > 2 \wedge L > \frac{K}{a}\right\}$$

the exclusion fixed point $(0, L)$ has the stable manifold (locally)

$$W_L^s = \{(x, y) \in \mathbb{R}^2 : x = 0\}$$

and the unstable manifold (locally)

$$W_L^u = \{(x, y) \in \mathbb{R}^2 : y = L\}.$$

5. Bifurcation scenarios

In the absence of species 'y' the dynamics of species 'x' is governed by the one-dimensional Ricker equation

$$x_{n+1} = x_n \mathrm{e}^{K-x_n}, n \in \mathbb{Z}^+. \tag{26}$$

Equation (26) has a globally asymptotically stable fixed point when $0 < K < 2$. At $K = k_1 = 2$, a period-doubling bifurcations occurs. At the bifurcation point $k_1 = 2$, an asymptotically stable 2-periodic cycle $\{\bar{x}_0, \bar{x}_1\}$ is born. The two points $\bar{x}_0, \bar{x}_1$ satisfy the equations $\bar{x}_1 = \bar{x}_0 \mathrm{e}^{K-\bar{x}_0}$ and $\bar{x}_0 = \bar{x}_1 \mathrm{e}^{K-\bar{x}_1}$. By the linearization principle, the stability of this 2-periodic cycle can be seen from the product of the derivatives of the map (26) evaluated at $\bar{x}_0$ and $\bar{x}_1$. This product is less than one in absolute value, i.e. $\prod_{i=0}^{1} |1 - \bar{x}_i| < 1$ if $k_1 < K < k_2$, where $k_2 \approx 2.5265$. At $K = k_2$, a new period-doubling bifurcation occurs. Then there exists k_3 greater than but near k_2 such that a new 4-periodic cycle is asymptotically stable if $k_2 < K < k_3$. This period-doubling scenario continues. So there exist two bifurcations points k_j and k_{j+1} for a specific integer j such that the r-periodic cycle $\{\bar{x}_0, \ldots, \bar{x}_{r-1}\}$, where $r = 2^j$, satisfies the relation

$$\prod_{i=0}^{r-1} |1 - \bar{x}_i| < 1. \tag{27}$$

The r-periodic cycle $\{\bar{x}_0, \ldots, \bar{x}_{r-1}\}$ yields an exclusion r-periodic cycle

$$C_r^x = \{(\bar{x}_0, 0), (\bar{x}_1, 0), \ldots, (\bar{x}_{r-1}, 0)\} \tag{28}$$

of the competition Ricker model (2).

The Jacobian of C_r^x evaluated along the periodic orbit is given by the following 2×2 matrix:

$$\prod_{r-1}^{0} JF(\bar{x}_i, 0) = \begin{pmatrix} \prod_{i=0}^{r-1}(1 - \bar{x}_i) & J_{12} \\ 0 & \mathrm{e}^{rL - b\sum_{i=0}^{r-1} \bar{x}_i} \end{pmatrix}.$$

Its eigenvalues are $\lambda_1 = \prod_{i=0}^{r-1}(1 - \bar{x}_i)$ and $\lambda_2 = \mathrm{e}^{rL - b\sum_{i=0}^{r-1} \bar{x}_i} = \mathrm{e}^{r(L-bK)}$. Using the hypothesis $L < bK$ yields $|\lambda_2| = \lambda_2 < 1$ and from Equation (27) it follows $|\lambda_1| < 1$. Thus C_r^x is asymptotically stable.

Note that if $L = 0$ one has $\lambda_2 < 1$. This implies that the sequence of parameters $\{k_j\}$ on the K-axis follows the one-dimensional case. That is $k_1 = 2$, $k_2 \approx 2.52647$, $k_3 \approx 2.6562$, etc.

We now summarize the above discussion

Theorem 5.1 *Let $0 < L < bK$. Then the cycle C_r^x, defined in Equation* (28), *of Equation* (2), *is asymptotically stable.*

In [17, p. 241] the author presents a complete study of the main types of bifurcations, for two-dimensional systems. When the Jacobian has an eigenvalue equal to one, either the saddle-node bifurcation, the pitchfork bifurcation or the transcritical bifurcation can occur. In the Trace-Determinant plane (T-D), this is equivalent to saying that we cross the line $\det(J^*) = \mathrm{tr}(J^*) - 1$ from the stability region. The period-doubling bifurcation occurs when the Jacobian has an eigenvalue equal to -1. In the T-D plane, this occurs as we cross the line $\det(J^*) = -\mathrm{tr}(J^*) - 1$ from the stability region. When the Jacobian has a pair of complex conjugate eigenvalues of modulus 1, we have the Neimark–Sacker bifurcation. This happens in the T-D plane when $\det(J^*) = 1$ and $-2 < \mathrm{tr}(J^*) < 2$. For details on bifurcation in the higher dimension, see for example [45, p. 357].

Now we are in a position to provide a deeper explanation of Figure 3. Note that the coexistence fixed point (x^*, y^*) is asymptotically stable if $(K, L) \in \hat{S}$. When $L = bK$, the Jacobian of Equation (2) has an eigenvalue equal to one. For the map $\hat{\hat{f}}$ defined in Equation (8) one has

$$\frac{\partial \hat{\hat{f}}}{\partial x}(0) = 1, \ \frac{\partial \hat{\hat{f}}}{\partial K}(0) = 0 \quad \text{and} \quad \frac{\partial^2 \hat{\hat{f}}}{\partial x^2}(0) \neq 0.$$

Hence a transcritical bifurcation occurs when $L = bK$, where the coexistence fixed point $(x^*, y^*) = (K, 0)$, the exclusion fixed point on the x-axis. When (K, L) crosses the line $L = bK$ to region R_1, the branch of equilibria (x^*, y^*) transcritically bifurcates with the branch of exclusion equilibria $(K, 0)$, while (x^*, y^*) moves from the first quadrant into the fourth (or second) quadrant, where it becomes ecologically irrelevant. Moreover, stability exchanges from one branch to the other. Similarly, if $L = K/a$, the coexistence fixed point undergoes a transcritical bifurcation.

Equation (2) has a period-doubling bifurcation when we have equality in relation (12). This is represented by the curve γ_1 in Figure 3. Consequently, as K and L passes the curve γ_1 the coexistence fixed point undergoes a period-doubling bifurcation into a coexistence 2-periodic cycle. Thus in region S_2 Equation (2) has one unstable fixed point and one asymptotically stable coexistence 2-periodic cycle.

When K and L passes the line $L = bK$ from region S_2 to region R_2, the coexistence 2-periodic cycle bifurcates (transcritical). Computations shows that this new 2-periodic cycle is an exclusion cycle on the x-axis. If, however, we move K and L from R_2 to S_2, then the exclusion 2-periodic cycle undergoes a transcritical bifurcation into a coexistence 2-periodic cycle. Another period-doubling bifurcation appears in the exclusion fixed point if the parameters K and L move from region R_1 to region R_2. Thus if the parameters K and L are in region R_2, Equation (2) possesses an asymptotically stable exclusion 2-periodic cycle on the x-axis. Similar analysis can be taken if the parameters are in region Q_2.

The coexistence 2-periodic cycle undergoes a period-doubling bifurcation when the parameters pass the curve γ_2. Thus in region S_3, this coexistence 2-periodic cycle becomes unstable and a new asymptotically stable 4-periodic cycle is born. This new cycle undergoes a transcritical bifurcation to an asymptotically stable exclusion 4-periodic cycle on the x-axis whenever the parameters move from region S_3 to region R_3. We also have a period-doubling bifurcation in the exclusion 2-periodic cycle if we change the parameters from region R_2 to region R_3. Thus in region R_3, Equation (2) has an asymptotically stable exclusion 4-periodic cycle. The same happens in the y-axis if the parameters change from region S_3 to region Q_3. This period-doubling bifurcation route to chaos is reminiscent of the dynamics exhibited by the one-dimensional Ricker-map.

A different scenario appears if the relation between L and K obey the rule $L = \alpha_1 K + \alpha_2, \alpha_2 > 0$ and $-\varepsilon < \alpha_1 < \varepsilon$, for a small $\varepsilon > 0$. We call this scenario the 'bubble scenario'. This occurs if one passes from zone S_{i+1} to the stability region S_i and enter again in the stability region S_{i+1}. In this scenario, if we draw the bifurcation diagram in the (K, x)-plane we find bubbles. In Figure 7, we present two scenarios. In cases A and B, we vary K and fix $L = 2.1$, and let $a = b = 0.5$. This results in the presence of one bubble in plot A. This phenomenon happens because for values of $K \lesssim 1.05$, Equation (2) has one attracting 2-periodic cycles on the y-axis (see plot B) . Thus $x_n = 0$ and y_n oscillates between 1.32152 and 2.87848 as n goes to infinity. At $K \approx 1.05$, the exclusion cycle on the y-axis bifurcates (transcritical) and the fixed point 0 bifurcates (period-doubling). This implies that the coexistence of 2-periodic cycle in the x-axis is born. Here we see the bubble in plot A and a 2-periodic cycle in plot B. For values $1.45 \lesssim K \lesssim 1.78$, Equation (2) has a coexistence fixed point. This observation implies that at $K \approx 1.45$, the 2-periodic cycle in turn will undergo a bifurcation and return to a stable equilibrium.[2] At $K \approx 1.78$ a new period-doubling bifurcation occurs, and then the coexistence fixed point bifurcates into a coexistence 2-periodic cycle. This is clearly shown in plot A and plot B. In cases C and D, we fix $L = 2.6$. For values of $K \approx 1.3$

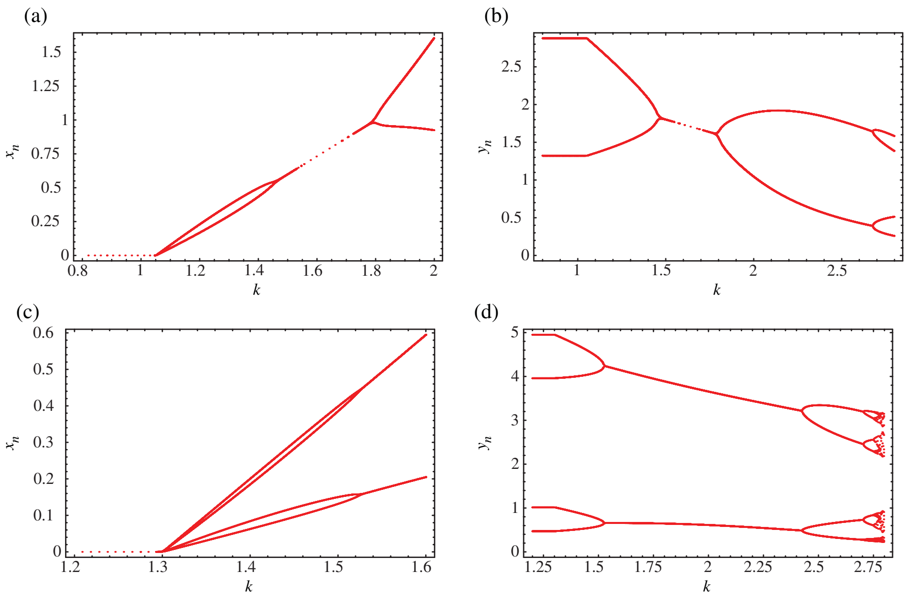

Figure 7. The presence of subcritical bifurcation in the autonomous Ricker type competition model (2)

the equation has an exclusion 4-periodic cycle on the y-axis. As K increases, we enter into the zone where we have a coexistence 4-periodic cycle. Here we see two bubbles in plot C and a coexistence 4-periodic cycle in plot D. Both cases lead to a 2-periodic cycle.

The Neimark–Sacker bifurcation starts when $\det(JF(x^*, y^*)) = 1$ and $-2 < \mathrm{tr}(JF(x^*, y^*)) < 2$, i.e. when

$$(1-a)L + (1-b)K = (aL - K)(bK - L) \tag{29}$$

and

$$0 < (1-a)L + (1-b)K < 4(1-ab). \tag{30}$$

Inequalities (30) are satisfied whenever K and L belong to the region enclosed by the positive axes and the line $(1-a)L = -(1-b)K + 4(1-ab)$. Direct computations show that this line does not intersect the hyperbola (29). On the other hand, the vertices $(0, 0)$ and $(2(1+a)/(1-ab), 2(1+b)/(1-ab))$ of hyperbola (29) are outside this triangle. Hence Equation (2) has no Neimark–Sacker bifurcation.

6. Discussion

Competition models have been investigated by many authors and we listed a few in the references. Here we consider a mathematical model (2) in which the intra-specific competition parameters are scaled to 1. This in effect reduces the number of parameters by two and we only have four parameters.

The main contribution in this paper is to analyse in depth the bifurcation scenario of the main parameters K and L, the carrying capacities of species x and y, respectively. So Figure 3 shows that our model exhibits period-doubling bifurcation of the coexistence equilibrium point in regions S_i, $i = 1, 2, 3, \ldots$.

The regions S_i, $i = 1, 2, 3, \ldots$ are bounded by the lines $L = bK$, and $L = K/a$ and the curve γ_i. Each curve γ_i is a segment of a hyperbola, which we determine explicitly for $i = 1$. Hence, we conclude that the coexistence of two species is possible only iff $(K, L) \in S_i$, $i = 1, 2, 3, \ldots$. The two species may coexist in a variety of forms: an equilibrium state, oscillatory periodic cycles of period 2^n, and eventually chaotic.

The regions R_i and Q_i, $i = 1, 2, 3, \ldots$ in the parameter space $K - L$ are regions where the competition exclusion principle is valid. In regions R_i, species y goes to extinction while species x tends to its carrying capacity K or oscillate periodically with periods 2^n and eventually enters a chaotic region. Similar conclusions may be stated for regions Q_i, in which species x goes to extinction while species y survives.

Finally, our analysis here of the period-doubling bifurcation scenario and identification of the regions in which the competition exclusion principle is valid may be extended to other competition models. In particular, we believe that our analysis here may be applied to many population models with rich dynamics such as the logistic competition model in [20].

Notes

1. ρ denotes the spectral radius.
2. Actually this phenomenon is not a reverse period doubling bifurcation. It is a subcritical bifurcation. For more details about this phenomenon in population models, see [11, p. 81].

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Appendix 1. Centre manifolds and the stable and unstable manifolds

In this section, we give the appropriate tools that allow us, to compute analytically, the centre manifolds and the stable and unstable manifolds for any nonlinear map. We use the terminology and the notation present in Section 2.

A.1. Centre manifolds

Let us first focus on the case when $\sigma_u = \varnothing$. Hence the eigenvalues of L are either inside the unit disk or on the unit disk. By a suitable change of variables, one may represent the map F as the following system of difference equations

$$\begin{aligned} x_{n+1} &= Ax_n + f(x_n, y_n) \\ y_{n+1} &= By_n + g(x_n, y_n). \end{aligned} \tag{A1}$$

First we assume that all eigenvalues of $A_{t\times t}$ are on the unit circle and all the eigenvalues of $B_{s\times s}$ are inside the unit circle, with $t + s = k$. Moreover,

$$f(0, 0) = 0, \quad g(0, 0) = 0, \quad Df(0, 0) = 0 \quad \text{and} \quad Dg(0, 0) = 0.$$

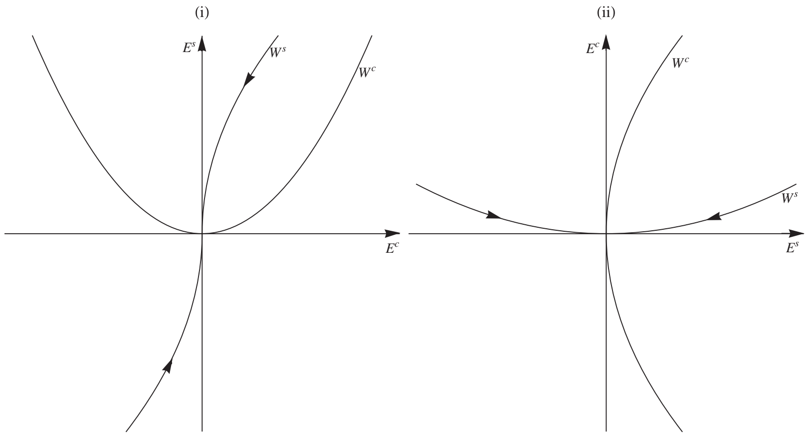

Figure A1. Stable and centre manifolds. In (a) one has $\sigma(A) = \sigma_c$ and $\sigma(B) = \sigma_s$ while in (b), one has $\sigma(A) = \sigma_s$ and $\sigma(B) = \sigma_c$.

Since W^c is tangent to $E^c = \{(x, y) \in \mathbb{R}^t \times \mathbb{R}^s | y = 0\}$, it may be represented locally as the graph of a function $h : \mathbb{R}^t \to \mathbb{R}^t$ such that (Figure A1)

$$W^c = \{(x, y) \in \mathbb{R}^t \times \mathbb{R}^s | y = h(x),\ h(0) = 0,\ Dh(0) = 0,\ |x| < \delta \text{ for a sufficiently small } \delta\}.$$

Furthermore, the dynamics restricted to W^c is given locally by the equation

$$x_{n+1} = Ax_n + f(x_n, h(x_n)), \quad x \in R^t. \tag{A2}$$

The main feature of Equation (A2) is that its dynamics determine the dynamics of Equation (A1). So if $x^* = 0$ is a stable, asymptotically stable, or unstable fixed point of Equation (A2), then the fixed point $(x^*, y^*) = (0, 0)$ of Equation (A1) possesses the corresponding property.

To find the map $y = h(x)$, we substitute for y in Equation (A1) and obtain

$$\begin{aligned} x_{n+1} &= Ax_n + f(x_n, h(x_n)) \\ y_{n+1} &= h(x_{n+1}) = h(Ax_n + f(x_n, h(x_n))). \end{aligned} \tag{A3}$$

But

$$\begin{aligned} y_{n+1} &= By_n + g(x_n, y_n) \\ &= Bh(x_n) + g(x_n, h(x_n)). \end{aligned} \tag{A4}$$

Equating (A3) and (A4) yields the centre manifold equation

$$h[Ax_n + f(x_n, h(x_n))] = Bh(x_n) + g(x_n, h(x_n)). \tag{A5}$$

Analogously if $\sigma(A) = \sigma_s$ and $\sigma(B) = \sigma_c$, one may define the centre manifold W^c, and obtain the equation

$$y_{n+1} = By_n + g(h(y_n), y_n),$$

where $x = h(y)$.

A.2. An upper (lower) triangular system

In working with concrete maps, it is beneficial in certain cases to deal with the system without diagonalization.

Let us now consider the case when L is a block upper triangular matrix

$$\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = \begin{pmatrix} A & C \\ 0 & B \end{pmatrix} \begin{pmatrix} x_n \\ y_n \end{pmatrix} + \begin{pmatrix} f(x_n, y_n) \\ g(x_n, y_n) \end{pmatrix}, \tag{A6}$$

There are two cases to consider:

(1) Assume that $\sigma(A) = \sigma_s$, $\sigma(B) = \sigma_c$, and $\sigma_u = \varnothing$.

The matrix L can be block diagonalizable. Hence there exists, a nonsingular matrix P of the form

$$P = \begin{bmatrix} P_1 & P_3 \\ 0 & P_2 \end{bmatrix}$$

such that

$$\begin{bmatrix} A & B \\ 0 & C \end{bmatrix} = P \begin{bmatrix} A & 0 \\ 0 & B \end{bmatrix} P^{-1}.$$

Let

$$\begin{pmatrix} x \\ y \end{pmatrix} = P \begin{pmatrix} u \\ v \end{pmatrix}. \tag{A7}$$

Then $x = P_1 u + P_3 v$, and $y = P_2 v$. Thus one has

$$\begin{pmatrix} u_{n+1} \\ v_{n+1} \end{pmatrix} = \begin{pmatrix} A & 0 \\ 0 & B \end{pmatrix} \begin{pmatrix} u_n \\ v_n \end{pmatrix} + P^{-1} \begin{pmatrix} f(P_1 u + P_3 v, P_2 v) \\ g(P_1 u + P_3 v, P_2 v) \end{pmatrix}. \tag{A8}$$

Applying the centre manifold theorem to Equation (A8) yields a map $u = \tilde{h}(v)$ with $\tilde{h}(0) = 0 = \tilde{h}'(0)$. Moreover, the dynamics of Equations (A8) is completely determined by the dynamics of the equation

$$v_{n+1} = Bv_n + \tilde{P}_2 g(P_1 \tilde{h}(v_n) + P_3 v_n, P_2 v_n),$$

where $\tilde{P}_1$ and $\tilde{P}_3$ are elements of the matrix

$$P^{-1} = \begin{bmatrix} \tilde{P}_1 & \tilde{P}_3 \\ 0 & \tilde{P}_2 \end{bmatrix}.$$

We now have the relation

$$u = \tilde{P}_1 x - \tilde{P}_2 P_3 \tilde{P}_2 y = \tilde{h}(\tilde{P}_2 y).$$

Hence $x = h(y)$, where h is given by

$$h(y) = P_3 \tilde{P}_2 y + \tilde{P}_1^{-1} \tilde{h}_2(\tilde{P}_2 y).$$

Notice that $Dh(0) = P_3 \tilde{P}_2 I$, where I is the identity matrix.

(2) Assume that $\sigma(A) = \sigma_c$, $\sigma(B) = \sigma_s$, and $\sigma_u = \varnothing$. We start from Equation (A8) and apply the centre manifold theorem to obtain a map $v = \tilde{h}(u)$ with $\tilde{h}(0) = 0 = \tilde{h}'(0)$. The dynamics of Equation (A8) is completely determined by the dynamics of the equation

$$u_{n+1} = Au_n + \tilde{P}_1 f(P_1 u_n + P_3 \tilde{h}(u), P_2 \tilde{h}(u)) + \tilde{P}_3 g(P_1 u_n + P_3 \tilde{h}(u), P_2 \tilde{h}(u)), \tag{A9}$$

where $\tilde{P}_1$, $\tilde{P}_2$, and $\tilde{P}_3$ are entries of the matrix

$$P^{-1} = \begin{pmatrix} \tilde{P}_1 & \tilde{P}_3 \\ 0 & \tilde{P}_2 \end{pmatrix}.$$

From Equation (A7) we have $u = \tilde{P}_1 x - \tilde{P}_1 P_3 \tilde{P}_2 y$ and $v = \tilde{P}_2 y$. Then $v = \tilde{h}(u)$ and thus

$$\tilde{P}_2 y = \tilde{h}(\tilde{P}_1 x - \tilde{P}_1 P_3 \tilde{P}_2 y).$$

Let $Q(x, y) = \tilde{P}_2 y - \tilde{h}(\tilde{P}_1 x - \tilde{P}_1 P_3 \tilde{P}_2 y)$. Then $Q(0, 0) = 0$, $DQ(0, 0)$ is of rank t. Hence by the implicit function theorem [41, p. 223] there exits an open neighbourhood $\Omega \subset \mathbb{R}^k$ of 0 and a unique function $h \in C^1(\Omega)$ such that $h(0) = 0 = Dh(0)$ and $Q(x, h(x)) = 0$, for all $x \in \Omega$.

Hence the curve $y = h(x)$ is the implicit solution of Equation (A9) and is the equation of the centre manifold. To find the map h, we use the centre manifold equation

$$h[Ax + Ch(x) + f(x, h(x))] = Bh(x) + g(x, h(x)).$$

A final remark is in order. If we let $y = h(x)$ in Equation (A9) we obtain

$$h(x) = P_2 \tilde{h}(\tilde{P}_1 x - \tilde{P}_1 P_3 \tilde{P}_2 h(x)).$$

Note that $Dh(0) = 0 = D\tilde{h}(0)$.

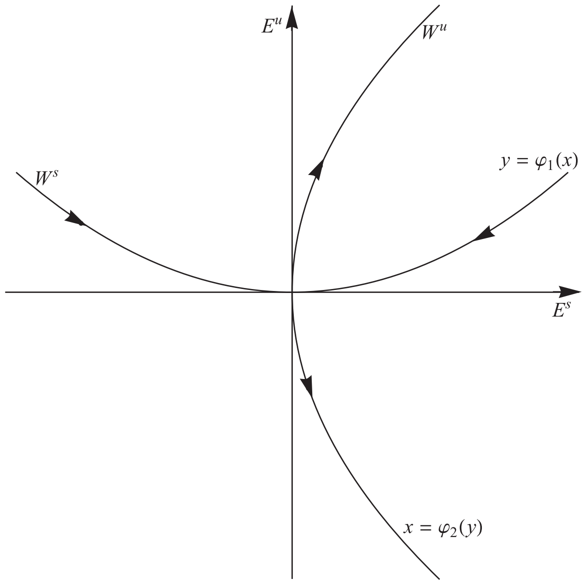

Figure A2. Stable and unstable manifolds.

A.3. Stable and unstable manifolds

Suppose now that the map F is hyperbolic, that is $\sigma_c = \varnothing$. Then by Theorem 2.1, there are two unique invariant manifolds W^s and W^u tangents to E^s and E^u at $X = 0$, which are graphs of the maps (Figure A2)

$$\varphi_1 : E_1 \to E_2 \quad \text{and} \quad \varphi_2 : E_2 \to E_1,$$

such that

$$\varphi_1(0) = \varphi_2(0) = 0 \quad \text{and} \quad D(\varphi_1(0)) = D(\varphi_2(0)) = 0.$$

Letting $y_n = \varphi_1(x_n)$ yields

$$y_{n+1} = \varphi_1(x_{n+1}) = \varphi_1(Ax_n + C\varphi_1(x_n) + f(x_n, \varphi_1(x_n))).$$

But

$$y_{n+1} = B\varphi_1(x_n) + g(x_n, \varphi_1(x_n)).$$

Equating these two equations yields

$$\varphi_1(Ax_n + C\varphi_1(x_n) + f(x_n, \varphi_1(x))) = B\varphi_1(x_n) + g(x_n, \varphi_1(x_n)), \tag{A10}$$

where we can take, without loss of generality, $\varphi_1(x) = \alpha_1 x^2 + \beta_1 x^3 + O(|x|^4)$.

Similarly, letting $x_n = \varphi_2(y_n)$ yields

$$x_{n+1} = \varphi_2(y_{n+1}) = \varphi_2(By_n + g(\varphi_2(y_n), y_n)),$$

where we can take, without loss of generality, $\varphi_2(x) = \alpha_2 x + \beta_2 x^2 + O(|x|^4)$

But

$$x_{n+1} = A\varphi_2(y_n) + Cy_n + f(\varphi_2(y_n), y_n),$$

and hence

$$\varphi_2(By_n + g(\varphi_2(y_n), y_n)) = A\varphi_2(y_n) + Cy_n + f(\varphi_2(y_n), y_n) \tag{A11}$$

Using Equations (A10) and (A11), one can find the stable manifold

$$W^s = \{(x, y) \in \mathbb{R}^t \times \mathbb{R}^s | y = \varphi_1(x)\},$$

and the unstable manifold

$$W^u = \{(x, y) \in \mathbb{R}^t \times \mathbb{R}^s | x = \varphi_2(y)\}.$$

Appendix 2. The stability region S_1

In this section, we study in the (K, L)-plane the region where inequalities (10), (11) and (12) holds.

A simple calculation shows that inequality (10) is equivalent to

$$bK^2 + (1 - b)K - (1 + ab)KL + (1 - a)L + aL^2 > 0, \tag{A12}$$

and inequality (12) is equivalent to

$$bK^2 + 2(1 - b)K - (1 + ab)KL + 2(1 - a)L + aL^2 + 4(ab - 1) < 0. \tag{A13}$$

Before finding the region where the three inequalities are satisfied, we give some notes about the following two equations

$$bK^2 + (1 - b)K - (1 + ab)KL + (1 - a)L + aL^2 = 0, \tag{A14}$$

$$bK^2 + 2(1 - b)K - (1 + ab)KL + 2(1 - a)L + aL^2 + 4(ab - 1) = 0. \tag{A15}$$

It is an elementary exercise to show that these two second-degree equations are hyperbolas in the (K, L)-plane provided that the constants satisfy the determinant condition

$$D = \begin{vmatrix} b & -\dfrac{1+ab}{2} \\ -\dfrac{1+ab}{2} & a \end{vmatrix} = -\frac{1}{4}(1 - ab)^2 < 0.$$

The centre (K_c, L_c) of Equation (A14) is given by $((1 + a)/(1 - ab), (1 + b)/(1 - ab))$ and the centre $(\bar{K}_c, \bar{L}_c)$ of Equation (A15) is given by $(2K_c, 2L_c)$. The angle of the principal axis of each hyperbola and the positive K-axis equals

$$\tan(2\phi) = -\frac{1 + ab}{b - a}.$$

In case of strong symmetry, for example when $a = b = 0.5$, both hyperbolas have the same principal axis, $L = (1 + b)/(1 + a)K$ and the vertices of Equation (A14) are $V_1 = (0, 0)$ and $V_2 = (2K_c, 2L_c)$ and the vertices of Equation (A15) are $\bar{V}_1 = (2K_c(1 - \sqrt{ab}), 2L_c(1 - \sqrt{ab}))$ and $\bar{V}_2 = (2K_c(1 + \sqrt{ab}), 2L_c(1 + \sqrt{ab}))$. It is clear that $V_1 < \bar{V}_1 < V_2 < \bar{V}_2$ since

$$0 < 2K_c(1 - \sqrt{ab}) < 2K_c < 2K_c(1 + \sqrt{ab}),$$

and

$$0 < 2L_c(1 - \sqrt{ab}) < 2L_c < 2L_c(1 + \sqrt{ab}).$$

Knowing these properties and using the implicit function theorem, in Figure A3 is present in the (K, L)-plane the solutions of Equations (A14) and (A15) when $a = b = 0.5$.

In case of strong asymmetry, i.e. when either $a > 1$ or $b > 1$ such that $a.b < 1$, the relative position between these two hyperbolas and the lines is more involved. However, the origin is always a point of Equation (A14) not necessarily a vertex. Furthermore, the left branch of Equation (A14) intersects the two lines at the origin and it enters into the first quadrant but it remains ‘outside’ the two lines.

Now we are going to find the region where inequalities holds. If we pick up a point between each branch of the hyperbola, either the sign is positive or negative. A good candidate for this test is the centre of each hyperbola. A calculation shows that on (K_c, L_c), the value of the first member of Equation (A12) is $1 > 0$. Since $K > 0$ and $L > 0$ inequality (A12) is verified whenever the values of the carrying capacities K and L are between the positive axes and the ‘right’ branch of hyperbola (A14).

Similarly, on $(\bar{K}_c, \bar{L}_c)$ the first member of Equation (A13) is $4ab > 0$. Hence, inequality (A13) is verified whenever the carrying capacities K and L are between the positive axes and the ‘left’ branch of hyperbola (A15) or in the ‘interior’ of the ‘right’ branch of hyperbola (A15).

From Equation (9) it follows that the inequality (11) is verified. This corresponds to the points in the (K, L)-plane between the lines $L = K/a$ and $L = bK$. The stability region S_1 now follows from the intersection of these three regions.

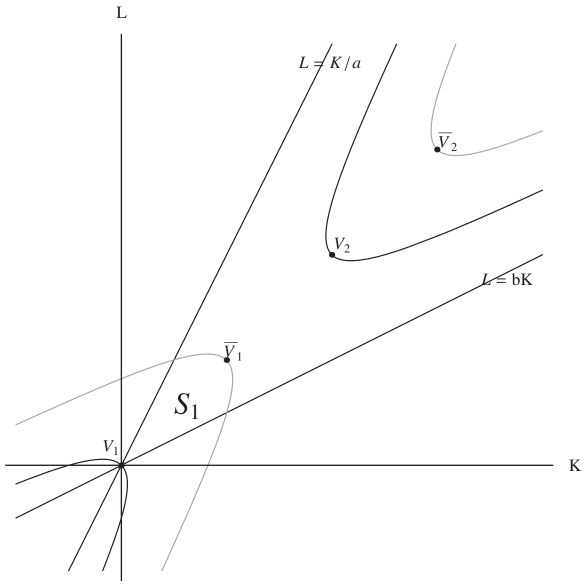

Figure A3. The relative position of the hyperbolas $det(J^*) = 1$ and $\det(J^*) = -\operatorname{tr}(J^*) - 1$ and the lines $L = bK$ and $L = K/a$ when $a = b = 0.5$. The black curves are the implicit solutions of $\det(J^*) = 1$ while the grey curves are the implicit solutions of $\det(J^*) = -\operatorname{tr}(J^*) - 1$. The stability region S_1 is enclosed by the two lines and the left branch of hyperbola $\det(J^*) = -\operatorname{tr}(J^*) - 1$.