

**STABILITY OF EQUILIBRIUMS AND BIFURCATION ANALYSIS  
OF TWO-DIMENSIONAL AUTONOMOUS COMPETITIVE  
LOTKA-VOLTERRA DYNAMICAL SYSTEM**

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ABSTRACT. A detailed analysis of the stability of equilibriums and bifurcations of the two-dimensional autonomous competitive Lotka-Volterra dynamical system is performed. Necessary and sufficient conditions are determined for equilibriums (without the origin) to be asymptotically stable or unstable on  $[0, +\infty)^2$ . Necessary and sufficient conditions are determined so that the observed dynamical system has no equilibriums in  $(0, +\infty)^2$ . All results are presented in five tables and five figures with appropriate ecological interpretation. We also show that four transcritical bifurcations occur in the observed dynamical system if it is analyzed on  $\mathbb{R}^2$ .

1. INTRODUCTION

In this paper, we analyze the stability of equilibriums and bifurcations of a two-dimensional autonomous competitive Lotka-Volterra dynamical system

$$(1.1) \quad \begin{aligned} \dot{x}_1 &= x_1 (b_1 - a_{11}x_1 - a_{12}x_2), \\ \dot{x}_2 &= x_2 (b_2 - a_{21}x_1 - a_{22}x_2), \end{aligned}$$

where  $x_i = x_i(t)$  is the density of species  $i$  at a given time  $t$ ,  $b_i$  is the inherent growth rate of species  $i$ ,  $a_{ij}$  is the effect that species  $j$  has on species  $i$ , for  $i, j \in \{1, 2\}$  and  $i \neq j$ , while for  $i = j$  we have self-interacting terms  $a_{ii}$ ,  $i \in \{1, 2\}$ . In the absence of competition, the observed dynamical system (1.1) consists of two logistic equations (one for each species), with carrying capacity  $b_i/a_{ii}$ , for  $i \in \{1, 2\}$ . Since the dynamical system (1.1) is competitive, we assume that  $a_{ij} > 0$  and  $b_i > 0$ , for every  $i, j \in \{1, 2\}$ .

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The reason for this is the assumed harmfulness of interspecies interactions, which directly implies  $a_{ij} > 0$ , for every  $i, j \in \{1, 2\}$  and  $i \neq j$ . Moreover, the self-regulation of each species implies  $a_{ii} > 0$ , for every  $i \in \{1, 2\}$ . Moreover  $b_i > 0$ , because it is also assumed that the inherent growth rate of species  $i$  is positive in the absence of competition, unless  $x_i$  has the value  $b_i/a_{ii}$  (its carrying capacity), for  $i \in \{1, 2\}$ .

System (1.1) is derived from a model proposed in 1926 by the Italian mathematician Vito Volterra [21] for predator-prey interaction. That model coincides with the two-dimensional system of nonlinear ordinary differential equations that mathematical physicist Alfred Lotka proposed for chemical reactions years before. Hence the name Lotka-Volterra model [14]. In the following year, Volterra extended his model by describing more general two-dimensional systems [22]. In that article, Volterra assumed self-interference between populations [9]. If there is no interaction between species, the system is decoupled, and the populations have independent logistic growth. A more comprehensive study of competition or predation between two populations can be found in [12, 16, 20, 23].

The stability of equilibriums of the autonomous Lotka-Volterra competitive model is analyzed in various literature (see, e.g. [7, 10, 11]). In [13] relationship between the coefficients  $a_{ij}$  and  $b_i$  can be found so that system (1.1), which has no equilibrium in  $(0, +\infty)^2$ , has an asymptotically stable equilibrium on one axis, while an unstable equilibrium lies on the other axes. These conditions are also generalized for the  $n$ -dimensional case of system (1.1) in [13], and [2]. Other papers dealing with suitable conditions for the two-dimensional and  $n$ -dimensional non-autonomous Lotka-Volterra competition model are [1] and [3], respectively.

We note that planar quadratic systems are analyzed in [6, 17, 18, 24], but the most complete analysis of the planar Lotka-Volterra dynamical systems is conducted in [19]. Analysis of the planar Lotka-Volterra dynamical systems conducted in [19] deals with global classification of the planar Lotka-Volterra dynamical systems according to their global geometric properties as reflected in their configurations of invariant straight lines. Motivation for such analysis was full topological classification of Lotka-Volterra dynamical systems. More precisely, in [19] was used the number of distinct straight lines, invariant under the flow of the systems, as well as their multiplicities, as a basic global geometric classifying tool, while we used stability theory for analysis in this paper and we introduced a new notation, suitable for generalization of obtained results for higher dimensions.

There are also some models that represent an extension of the Lotka-Volterra model of competition. For example, Gilpin and Ayala's competition model [8] adds parameter that controls the degree of nonlinearity in intraspecific growth regulation.

The importance of this work lies in the fact that all possible cases concerning the stability of equilibriums of the autonomous Lotka-Volterra competitive model are discussed here in detail, which to our knowledge has not been done anywhere else in the literature in this way. The new results of this paper concern the improvement of several results from [13], specifically the determination of necessary and sufficient

conditions for equilibriums (without the origin) to be asymptotically stable or unstable in  $[0, +\infty)^2$ , as well as the determination of necessary and sufficient conditions for the observed dynamical system to have no equilibriums in  $(0, +\infty)^2$ . Furthermore, we have concluded that four transcritical bifurcations occur in the observed dynamical system if it is analyzed on  $\mathbb{R}^2$ , and we have determined the conditions under which these bifurcations occur. To our knowledge, these are also new results of this paper.

In Section 2 we analyze in detail the stability of equilibriums of system (1.1). We assume that  $x_i \geq 0$  and that the main determinant or the minor determinants of system (1.1) can be zero. This leads to some non-hyperbolic equilibriums and bifurcations. We note that in [15] only the stability of equilibriums of system (1.1) for  $x_i > 0$  and for all non-zero determinants of this system was studied. This analysis can also be found in our paper in Section 2.1.1, but with a new notation that is more suitable for generalization to higher dimensions. In Section 3 we have improved several two-dimensional versions of the theorems from the paper [13], in particular with respect to sufficient and necessary conditions for equilibriums of system (1.1) lying on the axes to be asymptotically stable or an unstable equilibriums. In Section 4 we present a bifurcation analysis of the dynamical system (1.1).

First we introduce the following notation. For the determinant of the matrix of system (1.1) and the corresponding minors, we introduce the following notation

$$(1.2) \quad d_{12} = \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix}, \quad d_{122} = - \begin{vmatrix} b_1 & a_{12} \\ b_2 & a_{22} \end{vmatrix} \quad \text{and} \quad d_{112} = \begin{vmatrix} a_{11} & b_1 \\ a_{21} & b_2 \end{vmatrix}.$$

From (1.2) we can conclude that the number of different indices of the determinant indicates the order of this determinant as well as the elements on its main diagonal. The indices of the determinant  $d_{12}$  of the matrix of system (1.1) show that it is the second-order determinant whose elements on the main diagonal are  $a_{11}$  and  $a_{22}$ . Furthermore, the indices of the minors  $d_{ijk}$ , where  $i, j, k \in \{1, 2\}$  denote the second-order determinant whose elements on the main diagonal are  $a_{ij}$  (position (1, 1)) and  $b_k$  (position (2, 2)). This notation is very useful for calculating the coordinates of the equilibriums of the system and their eigenvalues, as well as for generalizations to higher dimensions.

In [4,5] is analyzed system (1.1), but with assumption that species 1 and 2 are nearly identical and lay claim to the same niche, i.e., the effect that species 1 has on species 2 is the same as the effect that members of species 2 have among themselves, while symmetrical assumption stands for species 1. Those assumptions reflect in  $a_{11} = a_{12}$  and  $a_{21} = a_{22}$ . Also, in [4,5] is assumed that microcosm in which species 1 and 2 live supports more members of species 1 than species 2, which in terms of parameters, using  $a_{11} = a_{12}$  and  $a_{21} = a_{22}$ , means that  $b_1/a_{11} > b_2/a_{21}$  and  $b_1/a_{12} > b_2/a_{22}$ , i.e.  $d_{112} < 0$  and  $d_{122} < 0$ . Therefore, in [4,5] is analyzed only the case  $d_{112} < 0$  and  $d_{122} < 0$  with one ecological interpretation (extinction of one species), while in this paper are analyzed nine different cases regarding to the values of parameters  $d_{12}$ ,  $d_{112}$

and  $d_{122}$ , that have five different phase portraits in the first quadrant which have two different ecological interpretations - extinction of one species and coexistence.

In [9] is proved that for two competing species, if both coordinates of the equilibrium are positive, its local stability implies its global stability. That only deals with the case when the determinant of the system is positive, whereas in this paper we determined conditions for local stability of all hyperbolic equilibriums of system (1.1), for determinant of the system  $d_{12} > 0$ ,  $d_{12} < 0$  and  $d_{12} = 0$ , as well as conditions for global stability of all nonhyperbolic equilibriums that occur if we let  $d_{112} = 0$  or  $d_{122} = 0$ .

The following notation applies to Tables 1–5: U denotes an unstable equilibrium, AS represents an asymptotically stable equilibrium, SS stands for a semi-stable equilibrium and NI stands for a non-isolated equilibrium.

In all figures in our paper, we have colored the points representing unstable equilibriums in yellow, asymptotically stable equilibriums are colored red, semi-stable equilibriums are colored orange and non-isolated equilibriums are colored pink.

## 2. STABILITY ANALYSIS OF THE EQUILIBRIUMS

We consider two cases, depending on whether  $d_{12}$  is zero or not.

**2.1. Case  $d_{12} \neq 0$ .** By (1.2), this condition is equivalent to  $a_{11}a_{22} \neq a_{12}a_{21}$ , which in ecological sense means that the effects of intraspecific competition (competition between members of the same species) are not equal to the effects of interspecific competition (competition between members of different species).

The number of equilibriums and their stability depend on the signs of  $d_{12}$ ,  $d_{112}$  and  $d_{122}$ . We analyze the following cases.

**2.1.1. Case  $d_{112} \neq 0$  and  $d_{122} \neq 0$ .** By (1.2), these conditions are equivalent to  $b_1/a_{11} \neq b_2/a_{21}$  and  $b_2/a_{22} \neq b_1/a_{12}$ . In ecological terms, it means that carrying capacity of the species 1 is not equal to the competitive threshold of the species 2 and that carrying capacity of the species 2 is not equal to the competitive threshold of the species 1. By competitive threshold of the species  $i$ , where  $i \in \{1, 2\}$ , we consider the sufficient number of members of the species  $j$ , for  $j \in \{1, 2\} \setminus \{i\}$ , in order to stop the growth of the species  $i$ .

If  $\text{sgn}(d_{12}) = \text{sgn}(d_{112}) = -\text{sgn}(d_{122})$ , we have four different equilibriums of system (1.1), labelled  $E_0(0, 0)$ ,  $E_1(b_1/a_{11}, 0)$ ,  $E_2(0, b_2/a_{22})$  and  $E_{12}(-d_{122}/d_{12}, d_{112}/d_{12})$ . Otherwise we would have three equilibriums of system (1.1),  $E_0$ ,  $E_1$  and  $E_2$ , since equilibrium  $E_{12}$  would not lie in the first quadrant. We note that the conditions  $d_{112} \neq 0$  and  $d_{122} \neq 0$  ensure that the eigenvalues of the Jacobian matrix in our equilibriums  $E_i$ ,  $i \in \{1, 2, 12\}$  have non-zero real parts, as we will see in the following text. Consequently, our equilibriums are hyperbolic and therefore we can discuss their stability in the framework of the corresponding linearization of the dynamical system (1.1), because the Hartman–Grobman theorem provides us topological equivalence

between a nonlinear dynamical system and its linearization in the neighbourhood of the hyperbolic equilibrium. Now we investigate the stability of all equilibria.

**The equilibrium  $E_0$ .** The eigenvalues of the Jacobian matrix at  $E_0$  are  $\lambda_i = b_i$ , for  $i \in \{1, 2\}$ . Since  $b_i > 0$  for every  $i \in \{1, 2\}$ , we conclude that  $E_0$  is an unstable node (unstable equilibrium).

**The equilibrium  $E_1$ .** The eigenvalues of the Jacobian matrix at  $E_1$  are  $\lambda_1 = -b_1$ ,  $\lambda_1 < 0$  and  $\lambda_2 = d_{112}/a_{11}$ . If  $d_{112} < 0$ , then  $E_1$  is a stable node (asymptotically stable equilibrium). Otherwise, i.e., if  $d_{112} > 0$ ,  $E_1$  is therefore a saddle (unstable equilibrium).

**The equilibrium  $E_2$ .** We note that the eigenvalues of the Jacobian matrix for  $E_2$  are  $\lambda_1 = -d_{122}/a_{22}$  and  $\lambda_2 = -b_2$ ,  $\lambda_2 < 0$ . We conclude that  $E_2$  is a stable node (asymptotically stable equilibrium) if  $d_{122} > 0$ . If  $d_{122} < 0$ , then  $E_2$  is a saddle point (unstable equilibrium).

**The equilibrium  $E_{12}$ .** The situation is a little complicated in this case. As we have already mentioned, the coordinates of  $E_{12}$  ( $-d_{122}/d_{12}, d_{112}/d_{12}$ ) must be positive in order to  $E_{12}$  lie in the first quadrant, i.e. it must be  $\text{sgn}(d_{12}) = \text{sgn}(d_{112}) = -\text{sgn}(d_{122})$ . If we denote the coordinates of  $E_{12}$  by  $x_1 := -d_{122}/d_{12}$  and  $x_2 := d_{112}/d_{12}$ , the Jacobian determinant at  $E_{12}$  is

$$\begin{aligned} \det(J(E_{12})) &= \begin{vmatrix} b_1 - 2a_{11}x_1 - a_{12}x_2 & -a_{12}x_1 \\ -a_{21}x_2 & b_2 - a_{21}x_1 - 2a_{22}x_2 \end{vmatrix} \\ (2.1) \qquad &= (-1)^2 x_1 x_2 \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix} = x_1 x_2 d_{12}, \end{aligned}$$

since  $b_1 - 2a_{11}x_1 - a_{12}x_2 = -a_{11}x_1$  and  $b_2 - a_{21}x_1 - 2a_{22}x_2 = -a_{22}x_2$ . Furthermore,

$$\begin{aligned} \lambda_1 \lambda_2 &= \det(J(E_{12})) = x_1 x_2 d_{12}, \\ (2.2) \qquad \lambda_1 + \lambda_2 &= \text{tr}(J(E_{12})) = -(a_{11}x_1 + a_{22}x_2), \end{aligned}$$

from which we obtain that the characteristic polynomial  $P_{12}(\lambda)$  of the matrix  $J(E_{12})$  is  $P_{12}(\lambda) = \lambda^2 + (x_1 a_{11} + x_2 a_{22})\lambda + x_1 x_2 d_{12}$ . From (2.2) we conclude that  $E_{12}$  is a stable node (asymptotically stable equilibrium) if  $d_{12} > 0$  and  $d_{112} > 0$  and  $d_{122} < 0$ . If  $d_{12} < 0$  and  $d_{112} < 0$  and  $d_{122} > 0$ ,  $E_{12}$  is a saddle (unstable equilibrium).

To summarize,  $E_0$  is an unstable node (unstable equilibrium), while the stability of equilibrium  $E_1$  depends solely on the sign of  $d_{112}$ , the stability of equilibrium  $E_2$  depends solely on the sign of  $d_{122}$ , while the existence and stability of equilibrium  $E_{12}$  depend on the signs of  $d_{12}$ ,  $d_{112}$  and  $d_{122}$ . The results are shown in Table 1.

The case from Table 1, in which  $d_{12} > 0$ ,  $d_{112} < 0$ ,  $d_{122} > 0$  is not possible. If this were possible, then we would have

$$(2.3) \qquad a_{11}a_{22} > a_{12}a_{21}, \quad a_{11}b_2 < a_{21}b_1, \quad a_{12}b_2 > a_{22}b_1.$$

If we multiply the first inequality from (2.3) by  $b_2/a_{22}$  and use the third inequality from (2.3), we get  $a_{11}b_2 > a_{12}b_2 a_{21}/a_{22} > a_{21}b_1$ , which contradicts the second inequality from (2.3). The case that  $d_{12} < 0$ ,  $d_{112} > 0$ ,  $d_{122} < 0$  is also not possible.

TABLE 1. Stability analysis of the equilibriums of system (1.1).

$d_{12}$	eq.	$d_{112} > 0$ $d_{122} > 0$	$d_{112} > 0$ $d_{122} < 0$	$d_{112} < 0$ $d_{122} > 0$	$d_{112} < 0$ $d_{122} < 0$
$d_{12} > 0$	$E_0$	U (u. node)	U (u. node)	not possible case	U (u. node)
	$E_1$	U (saddle)	U (saddle)		AS (s. node)
	$E_2$	AS (s. node)	U (saddle)		U (saddle)
	$E_{12}$	not exist	AS (s. node)		not exist
$d_{12} < 0$	$E_0$	U (u. node)	not possible case	U (u. node)	U (u. node)
	$E_1$	U (saddle)		AS (s. node)	AS (s. node)
	$E_2$	AS (s. node)		AS (s. node)	U (saddle)
	$E_{12}$	not exist		U (saddle)	not exist

We conclude from Table 1 that cases with  $d_{12} > 0, d_{112} > 0, d_{122} > 0$  and  $d_{12} < 0, d_{112} > 0, d_{122} > 0$ , have the same qualitative dynamical properties, as well as the cases  $d_{12} > 0, d_{112} < 0, d_{122} < 0$  and  $d_{12} < 0, d_{112} < 0, d_{122} < 0$ . Therefore, in this section we have four qualitatively different phase portraits of system (1.1). They are shown in Figures 1 and 2.

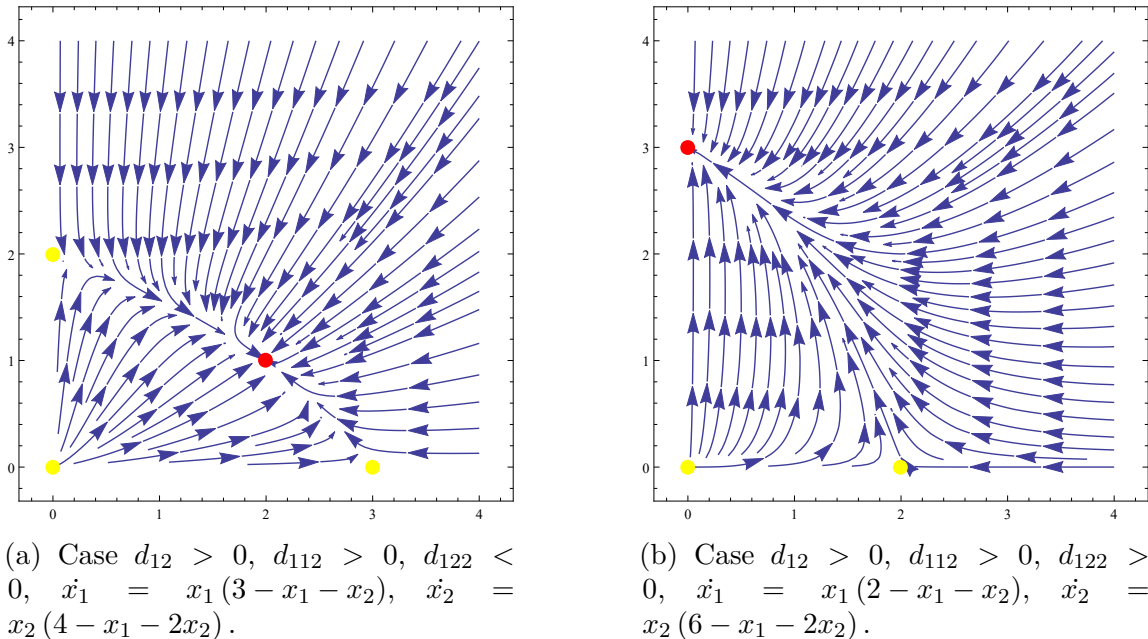


FIGURE 1. Phase portraits for the cases  $d_{12} > 0, d_{112} > 0, d_{122} < 0$  and  $d_{12} > 0, d_{112} > 0, d_{122} > 0$ , respectively.

In Figures 1a and 1b, the equilibrium  $E_0$  at the origin is an unstable node, while the equilibrium  $E_1$  is a saddle. In Figures 1a and 2a, equilibrium  $E_2$  is a saddle, while

in Figures 1b and 2b it is a stable node. Equilibrium  $E_{12}$  in Figure 1a is a stable node, while in Figure 2b is a saddle.

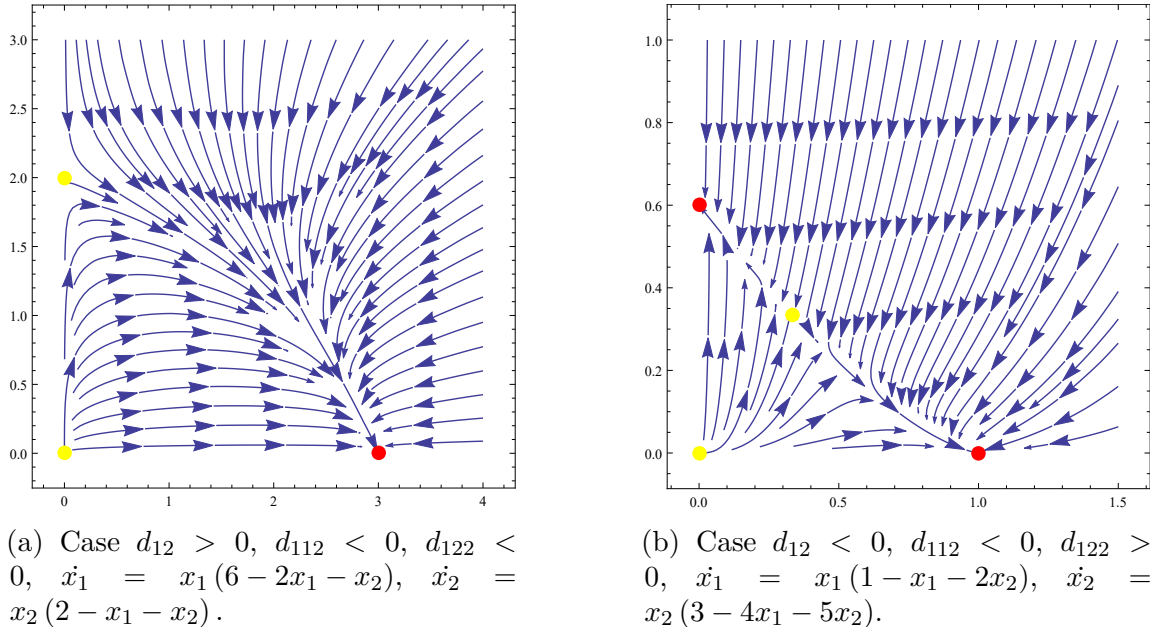


FIGURE 2. Phase portraits for the cases  $d_{12} > 0, d_{112} < 0, d_{122} < 0$  and  $d_{12} < 0, d_{112} < 0, d_{122} > 0$ , respectively.

From Table 1, as well as Figures 1 and 2, we see that in all cases (except one), the struggle for existence between two species results in the extinction of one of the species, which is consistent with [4, 5]. However, for the case  $d_{12} > 0, d_{112} > 0$  and  $d_{122} < 0$  that is depicted in the Figure 1a we have coexistence between two species, since all trajectories converge to the equilibrium in the first quadrant.

**2.1.2. Case  $d_{112} \neq 0$  and  $d_{122} = 0$ .** By (1.2), these conditions are equivalent to  $b_1/a_{11} \neq b_2/a_{21}$  and  $b_2/a_{22} = b_1/a_{12}$ . In ecological sense, it means that carrying capacity of the species 1 is not equal to the competitive threshold of the species 2 and that carrying capacity of the species 2 is equal to the competitive threshold of the species 1.

Since  $d_{122} = 0$ , we directly conclude that the first coordinate of  $E_{12}$  is zero and that  $a_{12} = a_{22}b_1/b_2$ . Substituting  $a_{12} = a_{22}b_1/b_2$  into  $d_{12}$ , we conclude that  $d_{12} = a_{22}d_{112}/b_2$ . Furthermore, the second coordinate of  $E_{12}$  is  $d_{112}/d_{12} = b_2/a_{22}, b_2/a_{22} > 0$ , from which it follows that the equilibrium  $E_{12}$  coincides with  $E_2$  and that  $\text{sgn}(d_{112}) = \text{sgn}(d_{12})$ . The equilibria  $E_0$  and  $E_1$  are hyperbolic and their nature is the same as in Subsection 2.1.1 (see Table 1), considering only the cases where  $\text{sgn}(d_{112}) = \text{sgn}(d_{12})$ . Since the equilibrium  $E_2$  is not hyperbolic ( $\lambda_1 = -d_{122}/a_{22} = 0$ ), we cannot determine its nature using the Hartman-Grobman theorem. Instead, we will determine its

stability by analyzing the phase trajectories around this equilibrium. For this purpose, we first determine the nullclines of system (1.1).

We obtain that  $x_1$ -nullclines are the lines  $x_1 = 0$  and  $x_2 = (b_1 - a_{11}x_1)/a_{12}$ , while  $x_2$ -nullclines are  $x_2 = 0$  and  $x_2 = (b_2 - a_{21}x_1)/a_{22}$ . Note that  $x_1$ -nullcline  $x_1 = 0$  and  $x_2$ -nullcline  $x_2 = 0$  are invariant. The vector field through  $x_1$ -nullcline  $x_1 = 0$  is vertical. If we also substitute  $x_1 = 0$  into the second equation in (1.1), we obtain  $\dot{x}_2 = x_2(b_2 - a_{22}x_2)$ , from which we conclude that the direction of the vector field through the nullcline  $x_1 = 0$  is vertically upwards ( $\uparrow$ ) for  $0 < x_2 < b_2/a_{22}$ , while for  $x_2 > b_2/a_{22}$  the vector field is vertically downwards ( $\downarrow$ ).

The vector field is horizontal through  $x_2$ -nullcline  $x_2 = 0$ . If we insert  $x_2 = 0$  into the first equation of system (1.1), we obtain  $\dot{x}_1 = x_1(b_1 - a_{11}x_1)$ . Consequently, the vector field is directed horizontally to the right ( $\rightarrow$ ) by the nullcline  $x_2 = 0$  for  $0 < x_1 < b_1/a_{11}$ , while for  $x_1 > b_1/a_{11}$  the vector field is directed horizontally to the left ( $\leftarrow$ ).

Using that  $d_{122} = 0$  and  $x_1 > 0$ , we can easily see that the  $x_1$ -nullcline  $x_2 = (b_1 - a_{11}x_1)/a_{12}$  is above the  $x_2$ -nullcline  $x_2 = (b_2 - a_{21}x_1)/a_{22}$  if and only if  $d_{12} < 0$ . We determine that the intersection point of these two nullclines is  $E_2(0, b_2/a_{22})$ . First, we analyze the nature of the equilibrium  $E_2$  when  $d_{12} < 0$ .

Since we conclude that  $\dot{x}_1 = 0$  for  $x_2 = (b_1 - a_{11}x_1)/a_{12}$ , it follows that the vector field through the nullcline  $x_2 = (b_1 - a_{11}x_1)/a_{12}$  is vertical. If we substitute  $x_2 = (b_1 - a_{11}x_1)/a_{12}$  into the second equation in system (1.1) (the substitution only applies to the term  $x_2$  in brackets), we get  $\dot{x}_2 = x_1x_2d_{12}/a_{12}$ . Therefore, using that  $d_{12} < 0$ , the direction of the vector field through the nullcline  $x_2 = (b_1 - a_{11}x_1)/a_{12}$  is vertically downwards ( $\downarrow$ ) if and only if  $x_1x_2 > 0$ , which is the case here, since  $x_1$  and  $x_2$  are positive.

The vector field through the nullcline  $x_2 = (b_2 - a_{21}x_1)/a_{22}$  is horizontal. If we insert  $x_2 = (b_2 - a_{21}x_1)/a_{22}$  into the first equation of system (1.1), we derive  $\dot{x}_1 = -x_1^2d_{12}/a_{22}$ , from which we conclude that the direction of the vector field is directed horizontally to the right ( $\rightarrow$ ) by the nullcline  $x_2 = (b_2 - a_{21}x_1)/a_{22}$ .

The sketch of the direction of the vector field through the nullclines implies that the equilibrium  $E_2$  is unstable, which we will prove.

Consider the subset

$$\mathcal{G}_1 = \{(x_1, x_2) \in \mathbb{R}^2 \mid (b_2 - a_{21}x_1)/a_{22} < x_2 < (b_1 - a_{11}x_1)/a_{12}, x_2 > 0\}.$$

We note that  $\mathcal{G}_1$  is invariant, i.e., any trajectory that starts at some point of  $\mathcal{G}_1$  remains in  $\mathcal{G}_1$ . Let  $M(x_1, x_2)$  be an arbitrary point from the area  $\mathcal{G}_1$ . Therefore,  $x_1 > 0$  and  $b_1 - a_{11}x_1 - a_{12}x_2 > 0$  and from the first equation of system (1.1) we conclude that  $\dot{x}_1 > 0$ , i.e.,  $x_1 = x_1(t)$  increases over time for any point in  $\mathcal{G}_1$ . Consequently, there is a neighbourhood  $\mathcal{O}_{E_2}$  of the equilibrium  $E_2$  such that for every point  $M(x_1, x_2) \in \mathcal{O}_{E_2} \cap \mathcal{G}_1$  the trajectory starting at  $M(x_1, x_2)$  never returns to  $\mathcal{O}_{E_2} \cap \mathcal{G}_1$ . We conclude that  $E_2(0, b_2/a_{22})$  is an unstable equilibrium for  $d_{12} < 0$ .

For  $d_{12} > 0$  we will prove that the equilibrium  $E_2$  is semi-stable. More precisely, we will prove that  $E_2$  is asymptotically stable in  $(0, +\infty)^2$  using Lyapunov stability theorem and that it is unstable in  $(-\infty, 0) \times (0, +\infty)$  by analyzing trajectories around  $E_2$ .

Let suppose that the Lyapunov function has the form

$$(2.4) \quad \begin{aligned} V(x_1, x_2) &= x_1^{a_{22}} x_2^{-a_{12}}, \\ \dot{V}(x_1, x_2) &= -d_{12} x_1^{a_{22}+1} x_2^{-a_{12}}. \end{aligned}$$

From (2.4) we conclude that  $V$  is differentiable on  $(0, +\infty)^2$ ,  $V(E_2) = 0$  and  $V(x_1, x_2) > 0$  for every  $(x_1, x_2) \in (0, +\infty)^2$ . Since  $d_{12} > 0$ , then  $\dot{V}(x_1, x_2) < 0$  for every  $(x_1, x_2) \in (0, +\infty)^2$ . Therefore, the function  $V$  from (2.4) is a Lyapunov function for  $E_2$  and according to the Lyapunov stability theorem,  $E_2$  is an asymptotically stable equilibrium on  $(0, +\infty)^2$ .

Consider the subset

$$\mathcal{G}_2 = \{(x_1, x_2) \in \mathbb{R}^2 \mid (b_2 - a_{21}x_1)/a_{22} < x_2 < (b_1 - a_{11}x_1)/a_{12}\}.$$

We note that, since here  $d_{12} > 0$  and  $x_1 < 0$ , the line  $x_2 = (b_2 - a_{21}x_1)/a_{22}$  is indeed below the line  $x_2 = (b_1 - a_{11}x_1)/a_{12}$ . Moreover, we notice that  $x_2 > b_2/a_{22}$ , where  $b_2/a_{22} = d_{112}/d_{12}$  is exactly the  $x_2$ -coordinate of the equilibrium  $E_2$ .

Similarly to the case  $d_{12} < 0$ , we find that the direction of the vector field of (1.1) by the nullcline  $x_2 = (b_1 - a_{11}x_1)/a_{12}$  is vertically downwards ( $\downarrow$ ) if and only if  $x_1 x_2 < 0$ . The vector field by the nullcline  $x_2 = (b_2 - a_{21}x_1)/a_{22}$  is directed horizontally to the left ( $\leftarrow$ ).

The directions of the vector field through the nullclines suggest that the equilibrium  $E_2$  is unstable in  $\mathcal{G}_2$ , which we will prove.

Let  $M(x_1, x_2)$  be an arbitrary point from the area  $\mathcal{G}_2$ . Therefore,  $x_1 < 0$  and  $x_2 < (b_1 - a_{11}x_1)/a_{12}$ , so we conclude from the first equation of system (1.1) that  $\dot{x}_1 < 0$ , i.e.  $x_1 = x_1(t)$  decreases with time for every point in  $\mathcal{G}_2$ . Consequently, there exists neighbourhood  $\mathcal{O}_{E_2}$  of the equilibrium  $E_2$  such that for every point  $M(x_1, x_2) \in \mathcal{O}_{E_2} \cap \mathcal{G}_2$  a trajectory starting at  $M(x_1, x_2)$  never returns to  $\mathcal{O}_{E_2} \cap \mathcal{G}_2$ . We conclude that  $E_2(0, b_2/a_{22})$  is an unstable equilibrium in  $(-\infty, 0) \times (0, +\infty)$ . Overall,  $E_2$  is a semi-stable equilibrium.

In this section we have two cases that are not possible. The first is for  $d_{12} > 0$ ,  $d_{112} < 0$ ,  $d_{122} = 0$ . If we assume that it is possible, then

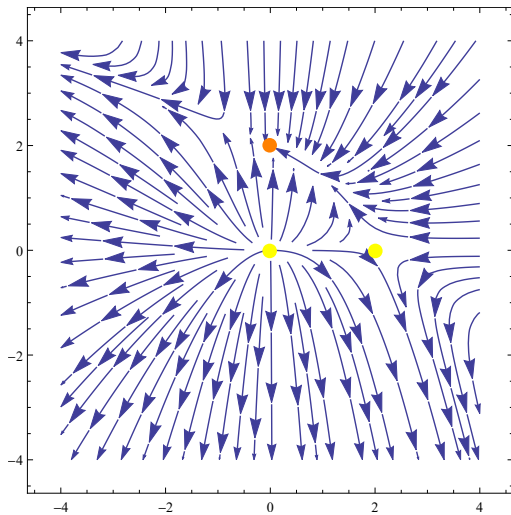
$$(2.5) \quad a_{11}a_{22} > a_{12}a_{21}, \quad a_{11}b_2 < a_{21}b_1, \quad a_{12}b_2 = a_{22}b_1.$$

If we multiply the first inequality from (2.5) by  $b_2/a_{22}$  and apply the third inequality from (2.5), we obtain, as before,  $a_{11}b_2 > a_{12}b_2a_{21}/a_{22} = a_{21}b_1$ , which contradicts the second inequality from (2.5). The case  $d_{12} < 0$ ,  $d_{112} > 0$ ,  $d_{122} = 0$  is also not possible.

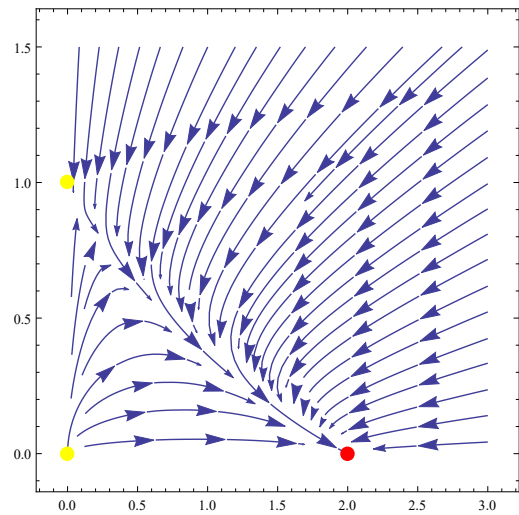
All results are listed in Table 2. To conclude this chapter, we have two different phase portraits of dynamical system (1.1), shown in Figure 3.

TABLE 2. Stability analysis of the equilibriums of system (1.1).

$d_{12}$	eq.	$d_{112} > 0$ and $d_{122} = 0$	$d_{112} < 0$ and $d_{122} = 0$
$d_{12} > 0$	$E_0$	U (u. node)	not possible case
	$E_1$	U (saddle)	
	$E_2$	SS	
$d_{12} < 0$	$E_0$	not possible case	U (u. node)
	$E_1$		AS (s. node)
	$E_2$		U



(a) Case  $d_{12} > 0, d_{112} > 0, d_{122} = 0, \dot{x}_1 = x_1(2 - x_1 - x_2), \dot{x}_2 = x_2(4 - x_1 - 2x_2)$ .



(b) Case  $d_{12} < 0, d_{112} < 0, d_{122} = 0, \dot{x}_1 = x_1(2 - x_1 - 2x_2), \dot{x}_2 = x_2(1 - x_1 - x_2)$ .

FIGURE 3. Phase portraits for the cases  $d_{12} > 0, d_{112} > 0, d_{122} = 0$  and  $d_{12} < 0, d_{112} < 0, d_{122} = 0$ , respectively.

In both figures, the equilibrium  $E_0$  at the origin is an unstable node, while in Figure 3a the equilibrium  $E_1$  is a saddle point and the equilibrium  $E_2$  is a semi-stable, while in Figure 3b the equilibrium  $E_1$  is asymptotically stable and the equilibrium  $E_2$  is an unstable equilibrium.

From Table 2, as well as Figure 3, we see that all trajectories converge to the equilibrium that is on one of the coordinate axes. Therefore, the result in both cases is the extinction of one of the species, which is consistent with [4, 5].

**2.1.3. Case  $d_{112} = 0$  and  $d_{122} \neq 0$ .** By (1.2), these conditions are equivalent to  $b_1/a_{11} = b_2/a_{21}$  and  $b_2/a_{22} \neq b_1/a_{12}$ . In ecological terms, it means that carrying capacity of the species 1 is equal to the competitive treshold of the species 2 and

that carrying capacity of the species 2 is not equal to the competitive treshold of the species 1.

Similarly as in the Subsection 2.1.2, from  $d_{112} = 0$  we conclude that the equilibrium  $E_{12}$  coincides with  $E_1$  and that  $\text{sgn}(d_{122}) = -\text{sgn}(d_{12})$ . The equilibriums  $E_0$  and  $E_2$  are hyperbolic and their nature is the same as in Subsection 2.1.1 (Table 1), considering only the cases when  $\text{sgn}(d_{122}) = -\text{sgn}(d_{12})$ . The equilibrium  $E_1$  is nonhyperbolic ( $\lambda_2 = d_{112}/a_{11} = 0$ ), and we will determine its stability by analyzing the phase trajectories around this equilibrium. However, we will only present the final results here, since the procedure is similar to the one presented in Subsection 2.1.2.

If  $d_{12} < 0$ , then equilibrium  $E_1$  will be unstable (proof of this statement can be obtained using nullclines, similarly as in Subsection 2.1.2). If  $d_{12} > 0$ , then the equilibrium  $E_1$  is semi-stable. The equilibrium  $E_1$  is asymptotically stable on  $(0, +\infty)^2$ . To prove this statement, the reader can use the Lyapunov function  $V(x_1, x_2) = x_1^{-a_{21}}x_2^{a_{11}}$ . The equilibrium  $E_1$  is unstable in  $(0, +\infty) \times (-\infty, 0)$ . To prove this statement, the reader can use nullclines, similar to Subsection 2.1.2. The results are shown in Table 3.

TABLE 3. Stability analysis of the equilibriums of system (1.1).

$d_{12}$	eq.	$d_{112} = 0$ and $d_{122} > 0$	$d_{112} = 0$ and $d_{122} < 0$
$d_{12} > 0$	$E_0$	not possible case	U (u. node)
	$E_1$		SS
	$E_2$		U (saddle)
$d_{12} < 0$	$E_0$	U (u. node)	not possible case
	$E_1$	U	
	$E_2$	AS	

Therefore, in this section we have two different phase portraits of the dynamical system (1.1), which are shown in Figure 4.

In both figures, the equilibrium  $E_0$  at the origin is an unstable node, while in Figure 4a, the equilibrium  $E_1$  is a semi-stable and the equilibrium  $E_2$  is a saddle, while in Figure 4b the equilibrium  $E_1$  is an unstable equilibrium and the equilibrium  $E_2$  is a stable node.

The ecological interpretation of the results from Table 3 as well as Figure 4 is the extinction of one of the species.

**2.1.4. Case  $d_{122} = 0$  and  $d_{112} = 0$ .** These conditions are equivalent to  $b_2/a_{22} = b_1/a_{12}$  and  $b_1/a_{11} = b_2/a_{21}$ . In ecological sense, it means that carrying capacity of the species 2 is equal to the competitive treshold of the species 1 and that carrying capacity of the species 1 is equal to the competitive treshold of the species 2.

This case is not possible. This can be shown in a similar way as in Subsection 2.1.2 (the proof differs if  $d_{12} > 0$  or  $d_{12} < 0$ ).

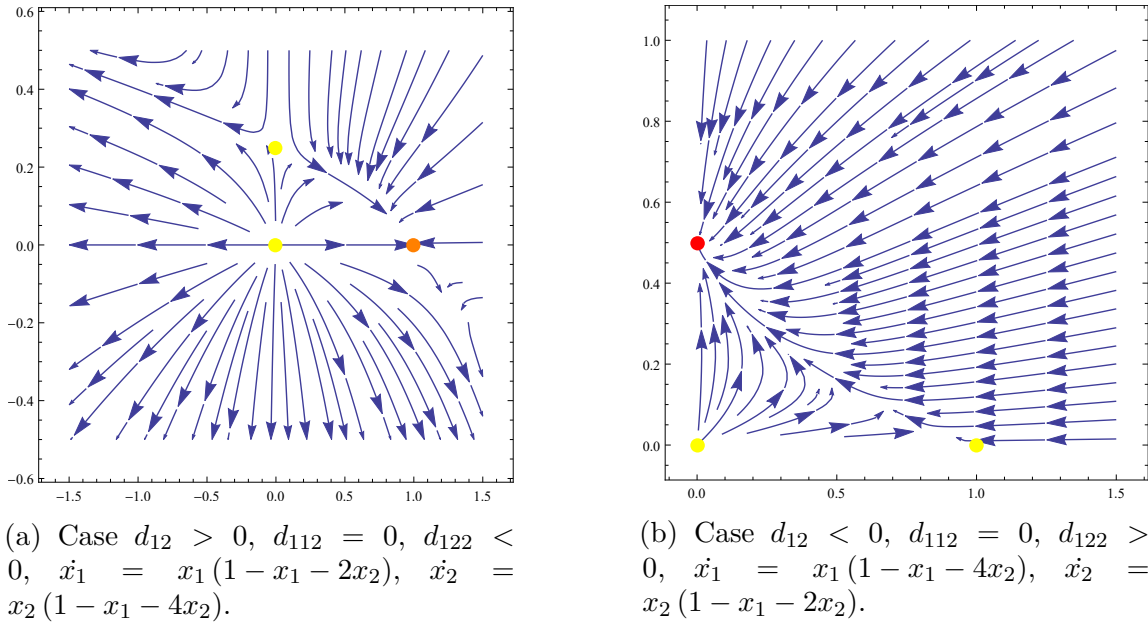


FIGURE 4. Phase portraits for the cases  $d_{12} > 0, d_{112} = 0, d_{122} < 0$  and  $d_{12} < 0, d_{112} = 0, d_{122} > 0$ , respectively.

2.2. **Case  $d_{12} = 0$ .** This condition is equivalent to  $a_{11}a_{22} = a_{12}a_{21}$ , which in ecological sense means that the effects of intraspecific competition are equal to the effects of interspecific competition.

We distinguish between two cases, when at least one minor is not equal to zero and when both minors are equal to zero.

2.2.1. **Case  $d_{122} \neq 0$  or  $d_{112} \neq 0$ .** These conditions are equivalent to  $b_2/a_{22} \neq b_1/a_{12}$  or  $b_1/a_{11} \neq b_2/a_{21}$ . In ecological terms, it means that carrying capacity of the species 2 is not equal to the competitive threshold of the species 1, or that carrying capacity of the species 1 is not equal to the competitive threshold of the species 2.

The equilibrium  $E_{12}$  does not exist in this case, since the system

$$(2.6) \quad \begin{aligned} a_{11}x_1 + a_{12}x_2 &= b_1, \\ a_{21}x_1 + a_{22}x_2 &= b_2, \end{aligned}$$

has no solutions. Accordingly, system (1.1) has three equilibriums,  $E_0, E_1$  and  $E_2$ . If  $d_{122} \neq 0$  and  $d_{112} \neq 0$ , then all three equilibriums are hyperbolic and the conclusions regarding their stability are given in Table 4.

Here the cases for  $d_{12} = 0$  and  $d_{112}d_{122} < 0$  are impossible and the cases for  $d_{12} = 0, d_{112}d_{122} = 0$  and  $d_{112}^2 + d_{122}^2 \neq 0$  are also impossible. The proofs are similar to those in Subsection 2.1.2 and so we omit them here.

We note that this section does not provide us with any qualitatively new phase portraits of the dynamical system (1.1), since we already had these qualitatively equal

TABLE 4. Stability analysis of the equilibriums of system (1.1).

eq.	$d_{12} = 0$ $d_{112} > 0$ $d_{122} > 0$	$d_{12} = 0$ $d_{112} d_{122} < 0$	$d_{12} = 0$ $d_{112} d_{122} = 0$ $d_{112}^2 + d_{122}^2 \neq 0$	$d_{12} = 0$ $d_{112} < 0$ $d_{122} < 0$
$E_0$	U (u. node)	not possible cases	not possible cases	U (u. node)
$E_1$	U (saddle)			AS (s. node)
$E_2$	AS (s. node)			U (saddle)

phase portraits before. For  $d_{12} = 0$ ,  $d_{112} > 0$ ,  $d_{122} > 0$ , we have the same phase portrait as for  $d_{12} > 0$ ,  $d_{112} > 0$ ,  $d_{122} > 0$  and  $d_{12} < 0$ ,  $d_{112} > 0$ ,  $d_{122} > 0$  from Subsection 2.1.1. Furthermore, for  $d_{12} = 0$ ,  $d_{112} < 0$ ,  $d_{122} < 0$ , we have the same phase portrait as for the  $d_{12} > 0$ ,  $d_{112} < 0$ ,  $d_{122} < 0$  and  $d_{12} < 0$ ,  $d_{112} < 0$ ,  $d_{122} < 0$  from Subsection 2.1.1.

Consequently, the ecological interpretation of the results from Table 4 is extinction of one of the species.

**2.2.2. Case  $d_{122} = 0$  and  $d_{112} = 0$ .** These conditions are equivalent to  $b_2/a_{22} = b_1/a_{12}$  and  $b_1/a_{11} = b_2/a_{21}$ . In ecological sense, it means that carrying capacity of the species 2 is equal to the competitive threshold of the species 1 and that carrying capacity of the species 1 is equal to the competitive threshold of the species 2.

If both minors are equal to zero, system (2.6) has infinitely many solutions  $(x_1, x_2) = ((b_1 - a_{12}\alpha)/a_{11}, \alpha)$ , where  $\alpha \geq 0$  and  $b_1 \geq a_{12}\alpha$ . Consequently, system (1.1) has infinitely many equilibriums,  $E_0$  and  $E^\alpha = ((b_1 - a_{12}\alpha)/a_{11}, \alpha)$ , where  $0 \leq \alpha \leq b_1/a_{12}$ . We note that the equilibriums  $E^\alpha$  are non-isolated and that for  $\alpha = 0$  we conclude  $E^0 = E_1$ , while for  $\alpha = b_1/a_{12}$  we obtain  $E^{b_1/a_{12}} = E^{b_2/a_{22}} = E_2$ . Therefore we exclude these values for  $\alpha$  in the following discussion.

The Jacobian matrix calculated for  $E^\alpha$  is given by

$$(2.7) \quad J(E^\alpha) = \begin{bmatrix} -(b_1 - a_{12}\alpha) & -\frac{(b_1 - a_{12}\alpha) a_{12}}{a_{11}} \\ -a_{21}\alpha & \frac{a_{11}(b_2 - 2a_{22}\alpha) - a_{21}(b_1 - a_{12}\alpha)}{a_{11}} \end{bmatrix}.$$

From (2.7), using  $d_{112} = 0$  and  $d_{12} = 0$ , we deduce that

$$(2.8) \quad \begin{aligned} \lambda_1 \lambda_2 &= \det(J(E^\alpha)) = 0, \\ \lambda_1 + \lambda_2 &= \text{tr}(J(E^\alpha)) = a_{12}\alpha - a_{22}\alpha - b_1, \end{aligned}$$

from which we conclude that  $\lambda_2 = -(b_1 - a_{12}\alpha) - a_{22}\alpha$ ,  $\lambda_2 < 0$ ,  $\lambda_1 = 0$ , since  $(b_1 - a_{12}\alpha)/a_{11} = x_1$ ,  $x_1 > 0$  and  $\alpha = x_2$ ,  $x_2 > 0$ . Thus,  $E^\alpha$  is nonhyperbolic equilibrium for every  $0 < \alpha < b_1/a_{12}$ .  $E^\alpha$  is a nonhyperbolic equilibrium for every  $0 \leq \alpha \leq b_1/a_{12}$ , i.e.,  $x_2 = (b_1 - a_{11}x_1)/a_{12}$  is a line of equilibriums.  $E_0$  is a hyperbolic equilibrium, which is an unstable node, just as in the previous sections. The phase portrait is shown in Figure 5.

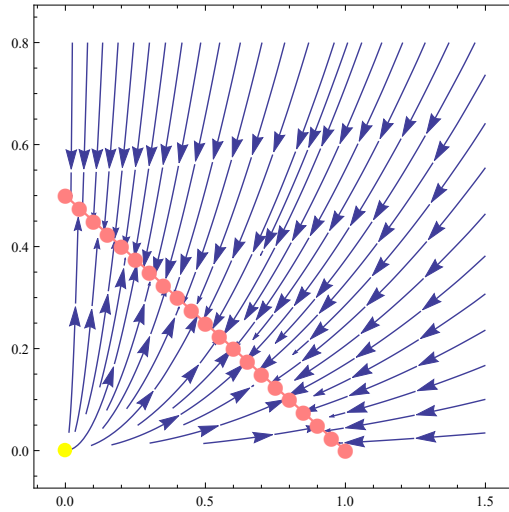


FIGURE 5. Case  $d_{12} = d_{112} = d_{122} = 0$ ,  $\dot{x}_1 = x_1(1 - x_1 - 2x_2)$ ,  $\dot{x}_2 = x_2(2 - 2x_1 - 4x_2)$ .

The equilibrium  $E_0$  at the origin is unstable, while the equilibria  $E^\alpha$ , where  $0 \leq \alpha \leq b_1/a_{12}$ , are non-isolated.

Therefore, this is another example with coexisting species.

### 3. NECESSARY AND SUFFICIENT CONDITIONS FOR STABILITY OF EQUILIBRIUMS

Section 2 shows that there are nine qualitatively different phase portraits of dynamical system (1.1) which are shown in Figures 1–5, when we consider the stability of equilibria of system (1.1) on their full neighbourhoods. The signs of  $d_{12}$ ,  $d_{112}$  and  $d_{122}$  as well as the equilibria of dynamical system (1.1) are shown in Table 5. After

TABLE 5. Stability analysis of equilibria of the dynamical system (1.1).

Serial No.	$d_{12}$	$d_{112}$	$d_{122}$	$E_0$	$E_1$	$E_2$	$E_{12}$	$E_\alpha$
1	$d_{12} > 0$	$d_{112} > 0$	$d_{122} < 0$	U	U	U	AS	/
2	$d_{12} > 0$	$d_{112} > 0$	$d_{122} = 0$	U	U	SS	/	/
3	$d_{12} > 0$	$d_{112} > 0$	$d_{122} > 0$	U	U	AS	/	/
4	$d_{12} > 0$	$d_{112} = 0$	$d_{122} < 0$	U	SS	U	/	/
5	$d_{12} > 0$	$d_{112} < 0$	$d_{122} < 0$	U	AS	U	/	/
6	$d_{12} < 0$	$d_{112} = 0$	$d_{122} > 0$	U	U	AS	/	/
7	$d_{12} < 0$	$d_{112} < 0$	$d_{122} = 0$	U	AS	U	/	/
8	$d_{12} < 0$	$d_{112} < 0$	$d_{122} > 0$	U	AS	AS	U	/
9	$d_{12} = 0$	$d_{112} = 0$	$d_{122} = 0$	U	NI	NI	/	NI

analyzing Figures 1–5 and the data in Table 5, we conclude that the phase portraits

under serial numbers 2, 3 and 6 that are shown in Figures 3a, 1b and 4b have qualitatively the same dynamical properties in  $[0, +\infty)^2$ , i.e., that in  $[0, +\infty)^2$  the equilibrium  $E_1$  is an unstable equilibrium and that the equilibrium  $E_2$  is asymptotically stable.

Moreover, the phase portraits under serial numbers 4, 5 and 7 that are shown in Figures 4a, 2a and 3b have qualitatively the same dynamical properties in  $[0, +\infty)^2$ , i.e. the equilibrium  $E_1$  is asymptotically stable and the equilibrium  $E_2$  is unstable.

In summary, we have nine qualitatively different phase portraits of the dynamical system (1.1) when we consider the stability of equilibriums of system (1.1) on their full neighbourhoods, while we have five qualitatively different phase portraits when we analyze the stability of its equilibriums on  $[0, +\infty)^2$ . We note that it is interesting from mathematical point of view to analyze the stability of the equilibriums of system (1.1) on their full neighbourhoods, although it lacks an appropriate physical interpretation since the density of the species cannot be negative.

To summarize all the results from the Section 2, we formulate the following theorems.

**Theorem 3.1.** *The equilibrium  $E_1(b_1/a_{11}, 0)$  of system (1.1) is asymptotically stable on  $[0, +\infty)^2$  if and only if one of the following conditions is satisfied:*

- (1)  $d_{112} < 0$  and  $d_{122} < 0$  (regardless of the  $\text{sgn}(d_{12})$ );
- (2)  $d_{12} < 0$  and  $d_{112} < 0$  and  $d_{122} = 0$ ;
- (3)  $d_{12} > 0$  and  $d_{112} = 0$  and  $d_{122} < 0$ ;
- (4)  $d_{12} < 0$  and  $d_{112} < 0$  and  $d_{122} > 0$ .

Theorem 3.1 is an extension of Theorem 2.1. from [13] for  $n = 2$ , where it states (with a different notation than the one used here) that if  $d_{122} < 0$  and  $d_{112} < 0$ , then  $E_1(b_1/a_{11}, 0)$  is asymptotically stable on  $(0, +\infty)^2$ .

The ecological interpretation of Theorem 3.1 is domination of the species 1 which results in extinction of the species 2.

Now we formulate a similar theorem for the equilibrium  $E_2$ .

**Theorem 3.2.** *The equilibrium  $E_2(0, b_2/a_{22})$  of system (1.1) is asymptotically stable on  $[0, +\infty)^2$  if and only if one of the following conditions is satisfied:*

- (1)  $d_{112} > 0$  and  $d_{122} > 0$  (regardless of the  $\text{sgn}(d_{12})$ );
- (2)  $d_{12} > 0$  and  $d_{112} > 0$  and  $d_{122} = 0$ ;
- (3)  $d_{12} < 0$  and  $d_{112} = 0$  and  $d_{122} > 0$ ;
- (4)  $d_{12} < 0$  and  $d_{112} < 0$  and  $d_{122} > 0$ .

The ecological interpretation of the Theorem 3.2 is domination of the species 2 which results in extinction of the species 1.

As a consequence of Theorem 3.1 and Theorem 3.2 and the fact that  $E_0$  is an unstable node (unstable equilibrium) regardless of the signs of  $d_{12}$ ,  $d_{112}$  and  $d_{122}$ , we formulate the following two theorems.

**Theorem 3.3.** *The equilibrium  $E_1(b_1/a_{11}, 0)$  of system (1.1) is unstable if and only if one of the conditions (1), (2), (3) from Theorem 3.2 is satisfied, or  $d_{12} > 0$  and  $d_{112} > 0$  and  $d_{122} < 0$  is satisfied.*

**Theorem 3.4.** *The equilibrium  $E_2(0, b_2/a_{22})$  of system (1.1) is unstable if and only if one of the conditions (1), (2), (3) from Theorem 3.1 is satisfied, or  $d_{12} > 0$  and  $d_{112} > 0$  and  $d_{122} < 0$  is satisfied.*

Moreover, the following can be concluded.

**Theorem 3.5.** *System (1.1) has no equilibriums in  $(0, +\infty)^2$  if and only if one of the conditions (1), (2), (3) from Theorem 3.1 or one of the conditions (1), (2), (3) from Theorem 3.2 is satisfied.*

Theorem 3.5 is an extension of Lemma 7.2. from [13] for  $n = 2$ , which states (with a different notation than the one used here) that if system (1.1) satisfies the inequalities  $d_{122} < 0$  and  $d_{112} < 0$ , then there is no equilibrium in  $(0, +\infty)^2$ . The next theorem considers the stability of equilibrium  $E_{12}$ .

**Theorem 3.6.** *The equilibrium  $E_{12}(-d_{122}/d_{12}, d_{112}/d_{12})$  of system (1.1) is:*

- (1) *asymptotically stable on  $(0, +\infty)^2$  if and only if  $d_{12} > 0$  and  $d_{112} > 0$  and  $d_{122} < 0$ ;*
- (2) *unstable if and only if  $d_{12} < 0$  and  $d_{112} < 0$  and  $d_{122} > 0$ .*

Proofs for all theorems can be found in discussions in the Section 2 and so are omitted here. We note that in [15] are considered only the cases when appropriate determinants are non-zero, while here we investigated those cases too.

The ecological interpretation of the Theorem 3.6 (1) is coexistence between two species, while the result of the part (2) is extinction of one of the species, since this case is the same as case (4) in both Theorem 3.1 and Theorem 3.2.

#### 4. BIFURCATION ANALYSIS

As a consequence of Section 2, there are five different phase portraits of system (1.1) in  $[0, +\infty)^2$ , which can be found in Table 5 under serial numbers 1, 2, 4, 8 and 9. They are already shown in Figures 1a, 3a, 4a, 2b and 5 respectively. We note that it is interesting from mathematical point of view to analyze the stability of the equilibriums of system (1.1) on  $\mathbb{R}^2$ , although it lacks an appropriate physical interpretation. In that case, four transcritical bifurcations can occur.

Comparing cases 1, 2 and 3 from Table 5 but with the stability of equilibriums analyzed on  $\mathbb{R}^2$ , we see that for  $d_{122} < 0$  (case 1) all equilibriums are hyperbolic and that  $E_0$ ,  $E_1$  and  $E_2$  are an unstable equilibriums, while  $E_{12}$  is an asymptotically stable equilibrium. For  $d_{122} = 0$  (case 2), nonhyperbolic equilibrium  $E_2$  collides with  $E_{12}$  and becomes a semi-stable equilibrium, while the stability of other two equilibriums remains the same. Furthermore, for  $d_{122} > 0$  (case 3), the equilibrium  $E_{12}$  appears again, but this time as an unstable equilibrium in the second quadrant, while the equilibrium  $E_2$  is now an asymptotically stable equilibrium, i.e. the equilibrium  $E_2$  have swapped stability with the equilibrium  $E_{12}$  at  $d_{122} = 0$ , while the stability of other equilibriums have remained the same.

We notice similar situation when we compare cases 1, 4 and 5 from Table 5, again analyzing system (1.1) on  $\mathbb{R}^2$ . More precisely, the equilibrium  $E_1$  have swapped stability with  $E_{12}$  (which transitioned from the first quadrant to the fourth quadrant) at  $d_{112} = 0$ . Furthermore, when we compare cases 8 and 6 from Table 5 and the case  $d_{12} < 0$ ,  $d_{112} > 0$  and  $d_{122} > 0$  from Table 1 (again on  $\mathbb{R}^2$ ), we easily obtain that the equilibrium  $E_1$  have swapped stability with the equilibrium  $E_{12}$  (which transitioned from the first quadrant to the fourth quadrant) at  $d_{112} = 0$  if  $a_{11}x_1 + a_{22}x_2 > 0$  ( $a_{22}d_{112} < a_{11}d_{122}$ ). Finally, when we compare cases 8 and 7 from Table 5 and the case  $d_{12} < 0$ ,  $d_{112} < 0$  and  $d_{122} < 0$  from Table 1, we derive that the equilibrium  $E_2$  have swapped stability with the equilibrium  $E_{12}$  (which transitioned from the first quadrant to the second quadrant) at  $d_{122} = 0$ , again if  $a_{11}x_1 + a_{22}x_2 > 0$ .

## 5. CONCLUSION

We have analyzed the stability of equilibriums and bifurcations of the dynamical system (1.1) for various signs of the main and minor determinants of this system,  $d_{12}$ ,  $d_{112}$  and  $d_{122}$ . Of the total of twenty-seven different combinations of the signs of the determinants  $d_{12}$ ,  $d_{112}$  and  $d_{122}$ , thirteen were meaningful, while nine of them were different from each other on full neighborhood of the equilibriums and their phase portraits are shown in Figures 1–5. Only five of these nine cases had different phase portraits on  $[0, +\infty)$ , which are shown in Figures 1a, 3a, 4a, 2b and 5. Four of these five phase portraits can also be found in [15], while the last one is new and very specific as it has infinitely many equilibriums. All results are presented in Tables 1-5 and they are discussed in the ecological framework. Concretely, there are two outcomes - extinction of one of the species, or their coexistence. In addition, we have improved several results from [13], mainly in terms of necessary and sufficient conditions for the equilibriums  $E_1$ ,  $E_2$  and  $E_{12}$  to be asymptotically stable or unstable. We noticed four transcritical bifurcations among thirteen meaningful and different phase portraits on  $\mathbb{R}^2$ .

## REFERENCES

- [1] S. Ahmad, *On the nonautonomous Volterra-Lotka competition equations*, Proc. Am. Math. Soc. **117** (1993), 199–204. <https://doi.org/10.2307/2159717>
- [2] S. Ahmad and A. C. Lazer, *On species extinction in an autonomous competition model*, in: *World Congress of Nonlinear Analysts '92. Proceedings of the First World Congress*, Tampa, FL, USA, August 19–26, 1992, 4 volumes, Berlin, de Gruyter, 1996, 359–368. <https://doi.org/10.1515/9783110883237.359>
- [3] S. Ahmad and A. C. Lazer, *Necessary and sufficient average growth in a Lotka-Volterra system*, Nonlinear Anal. **34** (1998), 191–228. [https://doi.org/10.1016/S0362-546X\(97\)00602-0](https://doi.org/10.1016/S0362-546X(97)00602-0)
- [4] M. Braun, *The principle of competitive exclusion in population biology*, in: M. Braun, C. S. Coleman and D. A. Drew (Eds.), *Differential Equation Models*, Springer, New York, 1983. [https://doi.org/10.1007/978-1-4612-5427-0\\_17](https://doi.org/10.1007/978-1-4612-5427-0_17)
- [5] M. Braun, *Differential Equations and Their Applications*, 4th Edition, Texts in Applied Mathematics, Springer, New York, 1993. <https://doi.org/10.1007/978-1-4612-4360-1>

- [6] F. Cao and J. Jiang, *The classification on the global phase portraits of two-dimensional Lotka-Volterra system*, J. Dynam. Differential Equations **20** (2008), 797–830. <https://doi.org/10.1007/s10884-008-9122-5>
- [7] J. D. Murray, *Mathematical Biology*, 2nd Edition, Springer, Berlin, 1993.
- [8] M. Gilpin and F. Ayala, *Global models of growth and competition*, Proc. Nat. Acad. Sci. USA **70** (1973), 3590–3593. <https://doi.org/10.1073/pnas.70.12.3590>
- [9] B.-S. Goh, *Management and Analysis of Biological Populations*, Developments in Agricultural and Managed-forest Ecology, Elsevier Scientific Pub. Co., 1980.
- [10] E. González-Olivares and A. Rojas-Palma, *Stability in Kolmogorov-type quadratic systems describing interactions among two species. A brief revision*, Sel. Mat. **8** (2021), 131–146. <https://doi.org/10.17268/sel.mat.2021.01.13>
- [11] J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems. Mathematical Aspects of Selection*, Cambridge University Press, Cambridge, 1988.
- [12] A. J. Lotka, *Elements of mathematical biology*, (unabridged), Republication of the first edition published under the title: *Elements of Physical Biology*, Dover Publications Inc., New York, 1956, 465 p.
- [13] M. Lou Zeeman, *Extinction in competitive Lotka-Volterra systems*, Proc. Am. Math. Soc. **123** (1995), 87–96. <https://doi.org/10.2307/2160613>
- [14] R. May, *Stability and Complexity in Model Ecosystems*, 2nd Edition, Princeton University Press, 2001.
- [15] F. Munteanu, *A study of a three-dimensional competitive Lotka-Volterra system*, ITM Web Conf. **34** (2020), Article ID 03010. <https://doi.org/10.1051/itmconf/20203403010>
- [16] D. Neal, *Introduction to Population Biology*, Cambridge University Press, 2003. <https://doi.org/10.1017/CB09780511809132>
- [17] J. Reyn, *Phase portraits of a quadratic system of differential equations occurring frequently in applications*, Nieuw Arch. Wisk. **5** (1987), 107–151.
- [18] J. Reyn, *Phase Portraits of Planar Quadratic Systems*, Springer, New York, 2007. <https://doi.org/10.1007/978-0-387-35215-2>
- [19] D. Schlomiuk and N. Vulpe, *Global classification of the planar Lotka-Volterra differential systems according to their configurations of invariant straight lines*, J. Fixed Point Theory Appl. **8** (2010), 177–245. <https://doi.org/10.1007/s11784-010-0031-y>
- [20] F. Scudo and J. Ziegler, *The golden age of theoretical ecology, 1923–1940: A collection of works by Volterra, Kostitzin, Lotka, and Kolmogoroff*, Lecture Notes in Biomathematics, Springer-Verlag, Berlin, 1978.
- [21] V. Volterra, *Fluctuations in the abundance of a species considered mathematically*, Nature **118** (1926), 558–560. <https://doi.org/10.1038/118558a0>
- [22] V. Volterra, *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi*, Memorie del R. Comitato Talassografico Italiano, Mem. CXXXI 1927.
- [23] V. Volterra, *Leçons sur la théorie mathématique de la Lutte pour la vie*, Gauthier-Villars, Paris, 1931.
- [24] A. Wörz-Busekros, *A complete classification of all two-dimensional Lotka-Volterra systems*, Differential Equations Dynam. Systems **1** (1993), 101–118.

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