An augmented phase plane approach for discrete planar maps: Introducing next-iterate operators

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Abstract

The next-iterate operators and corresponding next-iterate root-sets and root-curves associated with the nullclines of a planar discrete map are introduced. How to augment standard phase portraits that include the nullclines and the direction field, by including the signs of the root-operators associated with their nullclines, thus producing an augmented phase portrait, is described. The sign of a next-iterate operator associated with a nullcline determines whether a point is mapped above or below the corresponding nullcline and can, for example, identify positively invariant regions. Using a Lotka–Volterra type competition model, we demonstrate how to construct the augmented phase portrait. We show that the augmented phase portrait provides an elementary, alternative approach for determining the complete global dynamics of this model. We further explore the limitations and potential of the augmented phase portrait by considering a Ricker competition model, a model involving mutualism, and a predator–prey model.

Keywords: Discrete population models, root-sets, root-curves, positively invariant regions, global analysis, phase portrait

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1 Introduction

Phase plane analysis of planar systems of ordinary differential equations with vector fields defined by continuously differentiable functions has proven very useful for determining both local and global dynamics. We refer to the phase portrait that includes only the nullclines and the direction and bounds on the slope of the orbits in each of the regions bounded by the nullclines, as “standard phase portrait”. For planar differential equations, it can be used to identify invariant and positively invariant regions. This is because, by the Poincaré-Bendixson Theorem (see e.g., [1] [7]), distinct orbits in phase-space cannot intersect and by the continuity of orbits in phase-space, they can only cross nullclines in the direction indicated by the direction field.
A well-known example of the successful application of phase plane analysis in the context of planar systems of ordinary differential equations that has been extensively studied (see e.g., [3, 4, 7, 9, 16]), is the classical two-species competition model:

\[
\begin{align*}
x' &= r_1 x \left(1 - \frac{x}{K_1}\right) - \alpha_1 xy, \\
y' &= r_2 y \left(1 - \frac{y}{K_2}\right) - \alpha_2 xy,
\end{align*}
\]

(1)

where \(r_1, r_2 > 0\) denote the growth rate, \(K_1, K_2 > 0\) the carrying capacities, and \(\alpha_1, \alpha_2 > 0\) the inter-specific competition impact rates, of species \(x\) and \(y\), respectively. System (1) was proposed by Lotka [13] and Volterra [20]. It is assumed that each species grows logistically in the absence of the other and both inter- and intra-specific competition reduces each species numbers. It is possible to determine the invariant and positively invariant regions and hence the local and global stability of the equilibria from the standard phase portraits shown in Fig. 1 (see e.g., [1, 7]). For positive initial conditions, in a) and b) there is competitive exclusion (in a) \(y\) excludes \(x\), in b) \(x\) excludes \(y\)), in c) outcomes are initial condition dependent, and in d) all solutions converge to the coexistence equilibrium.

The standard phase portrait has not been as helpful for analyzing planar discrete maps. Unlike for smooth systems of planar ordinary differential equations for which the standard phase portrait can be used to find all of the invariant and positively invariant regions, for planar discrete maps it is possible for orbits to jump across one or more nullclines in a single iteration. Therefore, the standard phase portrait cannot be used successfully to detect invariant or positively invariant regions. This is demonstrated in Fig. 2, where the standard phase plane is shown for the discrete Ricker competition map:

\[
\begin{align*}
X_{t+1} &= X_t e^{(0.9 - X_t - 0.4Y_t)}, \\
Y_{t+1} &= Y_t e^{(1.6 - 0.3X_t - Y_t)}.
\end{align*}
\]

(2)

Fig. 2 shows the first few iterations of orbits of (2) with the initial conditions indicated by stars. In these phase portrait, as well as in all of the phase portraits, nullclines will be included using dashed curves, with black curves used for the \(X\)-equation and gray curves for the \(Y\)-equation. The line segments with arrows indicate the direction and bounds on the slope of the orbits in each of the regions bounded by the nullclines, and will be referred to simply as the direction field, for convenience.

In Fig. 2a), the orbit jumps across both nullclines and in b) the orbit jumps outside of a region that would be positively invariant if the phase portrait were for a continuous system. This illustrates the main drawbacks with regard to using standard phase portraits to analyze discrete planar models. Such issues even occur in linear planar maps as pointed out in [8] p. 48.

To overcome some of these drawbacks, in Section 2, we introduce next-iterate operators associated with nullclines and the corresponding root-sets and root-curves. The sign of the next-iterate operator associated with its nullcline determines on which side of that nullcline the next iterate lies. Root-sets determine root-curves that are curves along which the next-iterate operator equals zero. Root-curves therefore sub-divide the phase plane into regions in which the sign of the operator is constant.

To show how to augment the standard phase plane by including the signs of the next-iterate operators and then use the augmented phase plane to analyze planar discrete models, all of the figures were produced using Matlab [15].
maps, in Section 3, we illustrate the method on the following discrete version of (1),

\[
\begin{align*}
X_{t+1} &= F(X_t, Y_t) = \frac{1 + r_1}{1 + \frac{r_1}{K_1}X_t + \alpha_1 Y_t}X_t, \\
Y_{t+1} &= G(X_t, Y_t) = \frac{1 + r_2}{1 + \frac{r_2}{K_2}Y_t + \alpha_2 X_t}Y_t,
\end{align*}
\] (3)

with initial conditions \(X_0, Y_0 \geq 0\). The model parameters have the same interpretation as in model (1).

Model (3) is well-known and was first derived by Leslie [11] who described the possible asymptotic outcomes of (3) as the same as for model (1). More recently, (3) was derived in [12], using a Mickens discretization scheme and in [18] by applying a fitness function approach. The local analysis of (3) (see [12, 16]), was extended in [2, 6, 12] using different techniques. For example, in [2], the idea of a carrying simplex was applied while the analysis in [12] relied on the theory of monotone dynamical systems.

Using the augmented phase portrait to analyze model (3), we were able to determine the complete global dynamics using an alternative, more elementary method, compared to the approaches used in [2, 6, 12]. In Section 4, we apply the method to several other
Figure 2: The standard phase portrait for discrete planar system (2), including different positive semi-orbits with the initial point of each indicated by a star. The nullclines are shown as dashed curves using black and gray for the ones related to the $X$ and $Y$-equations, respectively. Unlike for systems of ordinary differential equations, orbits of maps can jump over both nullclines as in a). The orbit in b) leaves the region bounded by the nontrivial nullclines and the $X$-axis in one iteration, a region that would be positively invariant if the phase portrait was for a planar system of ordinary differential equations. For example, the configuration of the nullclines and the direction field is the same as in Fig 1 d).

systems and discuss some limitations.

2 The next-iterate operator and associated root-set and root-curves

Consider the general planar system

$$X_{t+1} = F(X_t, Y_t), \quad Y_{t+1} = G(X_t, Y_t). \tag{4}$$

Let $Y = \ell(X)$ be a nullcline of (4). We introduce the next-iterate operator, root-set, and root-curve associated with this nullcline to augment the standard phase portrait to make it more useful for the analysis of (4).

**Definition 2.1.** The next-iterate operator associated with the nullcline $Y = \ell(X)$ is the function

$$\mathcal{L}_\ell(X, Y) := G(X, Y) - \ell(F(X, Y)).$$

By Definition 2.1 it follows that $\mathcal{L}_\ell(X_t, Y_t) = Y_{t+1} - \ell(X_{t+1})$, so that

- $\mathcal{L}_\ell(X_t, Y_t) > 0 \iff$ next iterate lies above $\quad Y = \ell(X)$,
- $\mathcal{L}_\ell(X_t, Y_t) = 0 \iff$ next iterate lies on $\quad Y = \ell(X)$,
- $\mathcal{L}_\ell(X_t, Y_t) < 0 \iff$ next iterate lies below $\quad Y = \ell(X)$. 

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Since the sign of the next-iterate operator tells us on which side of the associated nullcline the next iterate lies, it is useful to subdivide the phase plane into regions based on the signs of the next-iterate operators associated with the nontrivial nullclines and augment the standard phase portrait by including these signs.

In all of the phase portraits in this manuscript, all curves related to the $X$-equation in (1) will be black and all curves related to the $Y$-equation in (1) will be gray. Besides the dashed curves for the nullclines, we include ’+’ and ’−’ symbols to indicate the sign of the next-iterate operator in various regions using the matching colors. When the root-curves are included, we will use solid curves in the matching colors.

**Remark 2.2.** Definition 2.1 requires that the nullcline can be expressed as a function $Y = \ell(X)$. If this is however not the case, but rather, the nullcline can be expressed as $X = \kappa(Y)$, then the corresponding next-iterate operator would be defined as

$$\hat{\mathcal{L}}_n(X,Y) = F(X,Y) - \kappa(G(X,Y)).$$

In this case, the next-iterate operator identifies next iterates of an orbit to be on the “left” or the “right” of the nullcline $X = \kappa(Y)$ instead of “above” or “below”. In this case, the following Definitions 2.3 and 2.4 of root-set and root-curves would have to be adjusted accordingly.

**Definition 2.3.** The next-iterate root-set (in short: root-set) associated with the nullcline $Y = \ell(X)$ is the set

$$S_\ell := \{(X,Y) \in \mathbb{R}^2 : \mathcal{L}_\ell(X,Y) = 0\}.$$

**Definition 2.4.** The next-iterate root-curves (in short: root-curves) associated with the nullcline $Y = \ell(X)$ are curves $Y = r(X)$ or $X = R(Y)$ that satisfy $\mathcal{L}_\ell(X,r(X)) = 0$ or $\mathcal{L}_\ell(R(Y),Y) = 0$.

**Lemma 2.5.** Let $S_\ell$ be the root-set defined in Definition 2.3 associated with the nullcline $Y = \ell(X)$ of (1). Let $\mathcal{E}_\ell$ denote the subset of equilibria of (1) that lie on $Y = \ell(X)$.

a) If $Y = \ell(X)$ is a nullcline for the $X$-equation, that is $F(X,\ell(X)) = X$, then $S_\ell \cap \{(X,Y) : Y = \ell(X)\} = \mathcal{E}_\ell$.

b) If $Y = \ell(X)$ is a nullcline for the $Y$-equation, that is $G(X,\ell(X)) = \ell(X)$, and $Y = \ell(X)$ is injective, then $S_\ell \cap \{(X,Y) : Y = \ell(X)\} = \mathcal{E}_\ell$.

**Proof.** Assume that $(X,Y) \in \mathcal{E}_\ell$. Then, $Y = \ell(X)$ and $\mathcal{L}_\ell(X,Y) = G(X,Y) - \ell(F(X,Y)) = Y - \ell(X) = 0$. Therefore, $\mathcal{E}_\ell \subseteq S_\ell \cap \{(X,Y) : Y = \ell(X)\}$.

a) Assume $(X,Y) \in S_\ell \cap \{(X,Y) : Y = \ell(X)\}$, where $Y = \ell(X)$ is a nullcline for the $X$-equation so that $F(X,\ell(X)) = X$. Since $(X,Y) \in S_\ell$, $\mathcal{L}_\ell(X,Y) = 0$ and therefore, $G(X,Y) = \ell(F(X,Y))$. Since $Y = \ell(X)$, $G(X,Y) = G(X,\ell(X)) = \ell(F(X,\ell(X))) = \ell(X) = Y$. Thus, $X = F(X,Y)$ and $Y = G(X,Y)$, and therefore $(X,Y) \in \mathcal{E}_\ell$, completing the proof for a).

b) Assume that $Y = \ell(X)$ is injective and is a nullcline for the $Y$-equation so that $Y = G(X,Y)$. If $(X,Y) \in S_\ell \cap \{(X,Y) : Y = \ell(X)\}$, then $0 = \mathcal{L}_\ell(X,Y) = G(X,Y) - \ell(F(X,Y))$, so that $\ell(X) = Y = G(X,Y) = \ell(F(X,Y))$. Since $Y = \ell(X)$ is injective, $F(X,Y) = X$. Therefore, $(X,Y) \in \mathcal{E}_\ell$, completing the proof for b).
Remark 2.6. If $Y = \ell(X)$ is a nullcline for $Y$ where $Y = \ell(X)$ is not injective, and if instead, the nullcline can be expressed as a function $X = \kappa(Y)$, then the result in Lemma 2.5 still holds for the next-iterate operator $\tilde{\mathcal{L}}_{\kappa}(X,Y)$ defined in Remark 2.2, with Definitions 2.3 and 2.4 adjusted accordingly.

Remark 2.7. Let $Y = \ell_1(X)$ and $Y = \ell_2(X)$ be the nullclines associated with the $X$- and $Y$-equations, respectively, i.e., $F(X,\ell_1(X)) = X$ and $G(X,\ell_2(X)) = \ell_2(X)$. Then, $(X,Y) \in S_{\ell_1} \cap S_{\ell_2}$, where $S_{\ell_1}$ and $S_{\ell_2}$ are the corresponding root-sets, if and only if $(X,Y)$ is an equilibrium or is mapped in one iteration to an equilibrium.

3 Analysis of (3) using the Augmented Phase Portrait

For (3), we define the competitive efficiency of species $X_i$ with competitor $X_j$ as

$$C_{ij} := \frac{r_i}{\alpha_i} - K_j, \quad i \neq j; \ i, j \in \{1, 2\}. \quad (5)$$

The relative values of these competitive efficiencies will be shown to determine the asymptotic outcome of the solutions.

Model (3) satisfies the Axiom of Parenthood [7, 10], that is, every new generation must have had a parent generation so that if $X_0 = 0$, then $X_t = 0$ for all $t \geq 0$. Similarly, if $Y_0 = 0$, then $Y_t = 0$, for all $t \geq 0$. Therefore, each axis bounding the first quadrant is invariant. For all $t \geq 0$, if $X_0 > 0$, then $X_t > 0$ and if $Y_0 > 0$, then $Y_t > 0$. Therefore, solutions with positive initial conditions cannot become negative.

In this section, we use model (3) with initial conditions $X_0, Y_0 \geq 0$ to illustrate how to construct the augmented phase portrait and then use it to determine the global dynamics of (3).

3.1 Construction of the Augmented Phase Portrait for (3)

3.1.1 Step I: Nullclines, Equilibria, and Direction Field

First, we obtain the nullclines and determine the direction of component-wise monotonicity in each of the regions separated by the nullclines.

The nullclines for competitor population $X$ are the vertical line $X = 0$ and

$$Y = h(X) = \frac{r_1}{\alpha_1 K_1} (K_1 - X), \quad (6)$$

so that for $X > 0$ and $Y > 0$,

$$F(X,Y) - X = \frac{\alpha_1 X}{1 + \frac{r_1}{K_1} X + \alpha_1 Y} (h(X) - Y) = \begin{cases} < 0, & \text{if } Y > h(X), \\ = 0, & \text{if } Y = h(X), \\ > 0, & \text{if } Y < h(X). \end{cases} \quad (7)$$

The nullclines for competitor population $Y$ are the horizontal line $Y = 0$ and the line

$$Y = k(X) = \frac{K_2}{r_2} (r_2 - \alpha_2 X), \quad (8)$$
so that for $X > 0$ and $Y > 0$,

$$G(X, Y) - Y = \frac{r_2 Y}{1 + \frac{r_2}{K_2} Y + \alpha_2 X} (k(X) - Y) = \begin{cases} < 0, & \text{if } Y > k(X) \\ = 0, & \text{if } Y = k(X) \\ > 0, & \text{if } Y < k(X). \end{cases} \quad (9)$$

The set of biologically relevant equilibria of (3), denoted $\mathcal{E}$, always contains three boundary equilibria:

$$E_0 = (0, 0), \quad E_1 = (K_1, 0), \quad E_2 = (0, K_2).$$

When $C_{12} \cdot C_{21} > 0$, the two nullclines $Y = h(X)$ and $Y = k(X)$ cross in the interior of the first quadrant at a unique coexistence equilibrium, $E^*$, also contained in $\mathcal{E}$, where

$$E^* = (X^*, Y^*) = \left( \frac{r_2 K_1 (\alpha_1 K_2 - r_1)}{(\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2)}, \frac{r_1 K_2 (\alpha_2 K_1 - r_2)}{(\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2) \cdot (\alpha_1 K_2 - r_1)} \right) \in (0, K_1) \times (0, K_2). \quad (10)$$

In the special case when $C_{12} = C_{21} = 0$, and so $h(X) = k(X)$ for all $X$, the entire line

$$\mathcal{E}_X^* = \{(X, Y) : Y = h(X), 0 \leq X \leq K_1\},$$

is contained in $\mathcal{E}$. Note that in this case, $E_1$ and $E_2$ are in $\mathcal{E}_X^*$, and $\mathcal{E} = \{E_0\} \cup \mathcal{E}_X^*$.

It follows that the standard phase portrait for the discrete map (3) looks the same as the phase portrait for the system of differential equations (1) shown in Fig. 4 if the labels $x$ and $y$ on the axes are replaced by $X$ and $Y$, respectively.

### 3.1.2 Step II: Next-iterate operators, Root-Sets, and Root-Curves

By Definition 2.1, the next-iterate operators associated with the positive nullclines for competitors $X$ and $Y$ are given by

$$\mathcal{L}_h(X, Y) := G(X, Y) - h(F(X, Y)) \quad \text{and} \quad \mathcal{L}_k(X, Y) := G(X, Y) - k(F(X, Y)),$$

respectively. Then,

$$\mathcal{L}_h(X, 0) = G(X, 0) - h(F(X, 0)) = 0 - h(F(X, 0)) = -h(F(X, 0)), \quad (11)$$

$$\mathcal{L}_k(X, 0) = G(X, 0) - k(F(X, 0)) = 0 - k(F(X, 0)) = -k(F(X, 0)), \quad (12)$$

$$\mathcal{L}_h(0, Y) = G(0, Y) - h(F(0, Y)) = G(0, Y) - h(0) = G(0, Y) - \frac{r_1}{\alpha_1}, \quad (13)$$

$$\mathcal{L}_k(0, Y) = G(0, Y) - k(F(0, Y)) = G(0, Y) - k(0) = G(0, Y) - K_2. \quad (14)$$

By (11), $\mathcal{L}_h(X, 0) < 0$ for all $X \in [0, K_1]$ and, by (14), $\mathcal{L}_k(0, Y) < 0$ for all $Y \in [0, K_2]$.

**Lemma 3.1.** Assume that $X > 0$ and $Y > 0$.

a) If $h(X) < k(X)$, then $\mathcal{L}_h(X, h(X)) > 0$ for $X \in (0, K_1)$ and $\mathcal{L}_k(X, k(X)) < 0$ for $X \in (0, \frac{r_2}{\alpha_2})$.  

7
Hence, both results in (14) and therefore $F_h$ are similar. Assume therefore that $X \in (0, \frac{a_1}{a_2})$.

Proof. Assume that $X > 0$ and $Y > 0$. We only prove (a), since the argument for (b) is similar. Assume therefore that $h(X) < k(X)$ and first that $X \in (0, K_1)$. Then, $0 < h(X)$. By Definition 2.1, $L_h(X, h(X)) = G(X, h(X)) - h(F(X, h(X))) = G(X, h(X)) - h(X)$.

Since $0 < h(X) < k(X)$, by (9), $G(X, h(X)) - h(X)) > 0$, i.e., $L_k(X, h(X)) > 0$.

Next, assume that $X \in (0, \frac{a_1}{a_2})$. Then $k(X) > \max\{0, h(X)\} \geq 0$. Thus, by (7), $F(X, k(X)) < X$. Since $k(X)$ is a decreasing function of $X$, $k(X) < k(F(X, k(X))$ and therefore $L_k(X, k(X)) = G(X, k(X)) - k(F(X, k(X))) = k(X) - k(F(X, k(X))) < 0$. Hence, both results in (a) follow.

For (3), the next-iterate operators are of the form

$$L_h(X, Y) = \frac{N_h(X, Y)}{\alpha_1(K_1 + r_1 X + \alpha_1 K_1 Y)(K_2 + \alpha_2 K_2 X + r_2 Y)},$$

$$L_k(X, Y) = \frac{N_k(X, Y)}{r_2(K_1 + r_1 X + \alpha_1 K_1 Y)(K_2 + \alpha_2 K_2 X + r_2 Y)},$$

where $N_h(X, Y)$ and $N_k(X, Y)$ are quadratic polynomials in $X$ and $Y$. The precise expressions are provided in Appendix A.1 with the expressions for the root-sets and root-curves.

The proof of the following Lemma is based on the fact that if a point $(X, Y)$ is in both root-sets, that is, $(X, Y) \in S_k \cap S_h$, then this point is mapped directly to an equilibrium. The details are provided in Appendix A.3.

**Lemma 3.2.** If $C_{12}, C_{21} > 0$, then

$$S_k \cap S_h \cap \{(X, Y): 0 < X \leq X^*, 0 < Y \leq Y^*\} = E^*$$

and

$$S_k \cap S_h \cap \{(X, Y): X \geq X^*, Y \geq Y^*\} = E^*,$$

where $E^* = (X^*, Y^*)$ is the coexistence equilibrium given in (10).

Lemma 3.2 implies that root-curves associated with the nullclines $Y = h(X)$ and $Y = k(X)$ cannot intersect in $\{(X, Y): 0 < X \leq X^*, 0 < Y \leq Y^*\} \setminus E^*$ or in $\{(X, Y): X \geq X^*, Y \geq Y^*\} \setminus E^*$.

### 3.2 Global Analysis of (3) using the Augmented Phase Portrait

In this section, we illustrate how to use the augmented phase portrait to obtain the global dynamics of (3) based on the signs of the competitive efficiencies defined in (5). However, first we provide some preliminary results.

**Theorem 3.3.** Consider (3) with $X_0, Y_0 \geq 0$ and $X_0 Y_0 = 0$.

(a) If $X_0 = Y_0 = 0$, then $(X_t, Y_t) = E_0$, for all $t \geq 0$. 

b) If $k(X) < h(X)$, then $L_h(X, h(X)) < 0$ for $X \in (0, K_1)$ and $L_k(X, k(X)) > 0$ for $X \in (0, \frac{a_1}{a_2})$.


b) If $X_0 = 0$ and $Y_0 > 0$, then $\lim_{t \to \infty} (X_t, Y_t) = E_2$.

c) If $X_0 > 0$ and $Y_0 = 0$, then $\lim_{t \to \infty} (X_t, Y_t) = E_1$.

The proof is omitted, since it follows immediately from the structure of (3) and the well-known results for the Beverton-Holt model (see [1, Section 3.2]). This theorem could also be proved using the augmented phase portrait approach, since the root-curves associated with each trivial nullcline coincides with its nullcline. This implies that the trivial nullclines, i.e., the $X$ and $Y$ axes, are invariant and also that the interior of the first quadrant is invariant.

3.2.1 Case I: $C_{12} = C_{21} = 0$

By the definition of $C_{ij}$ in (5), $\frac{r_1}{a_1} = K_2$ and $\frac{r_2}{a_2} = K_1$, and so $h(X) = k(X)$, for all $X \in \mathbb{R}$.

The standard phase portrait determined from (7) and (9) is shown in Fig. 3a). Two regions of component-wise monotonicity in $\mathbb{R}^2_+ = (0, \infty)^2$ are identified:

\[ R_1 = \left\{(X, Y) \in \mathbb{R}^2_+: Y < h(X) = k(X)\right\}, \quad R_2 = \left\{(X, Y) \in \mathbb{R}^2_+: h(X) = k(X) < Y\right\}. \]

Figure 3: a) The standard phase portrait in the case when $C_{12} = C_{21} = 0$. Since $h(X) = k(X)$, the nontrivial $X$ and $Y$ nullclines coincide and result in the line of equilibria, $E_X^*$. b) The graph in a) augmented by including the root-curves associated with the nontrivial nullclines for competitors $X$ and $Y$, that overlap their nullclines in this case, and the signs of the next-iterate operators in the regions separated by the root-curves. Each root-curve associated with its nontrivial nullcline is identical to its nontrivial nullcline. Since the next-iterate operators are both negative in $R_1$, any point in $R_1$ is mapped below the competitor $X$ and competitor $Y$ nullclines and therefore remains in $R_1$. Thus, $R_1$ is invariant. Similarly, the positive signs of both next-iterate root-operators in $R_2$ imply that a point in $R_2$ is mapped to a point above both nontrivial nullclines and therefore remains in $R_2$. Thus, $R_2$ is also invariant.

In this case, the standard phase portrait alone cannot be used to prove the stability of the equilibria in $E_X^*$. We need to use the augmented phase portrait that includes the signs of
the next-iterate operators associated with the nullclines to first prove that orbits cannot jump back and forth across the nullclines.

The proof of the following result is due to (15) (see the details in Appendix A.2.

**Lemma 3.4.** Assume \( C_{12} = C_{21} = 0 \).

\[
\begin{align*}
\mathcal{L}_h(X,Y) & = \begin{cases} < 0, & \text{if } (X,Y) \in \mathcal{R}_1, \\ > 0, & \text{if } (X,Y) \in \mathcal{R}_2. \end{cases} \\
\mathcal{L}_h(X,Y) & = \begin{cases} < 0, & \text{if } (X,Y) \in \mathcal{R}_1, \\ > 0, & \text{if } (X,Y) \in \mathcal{R}_2. \end{cases}
\end{align*}
\]

Including the sign of the next-iterate operator in the regions separated by the root-curves, we obtain the augmented phase portrait shown in Fig. 4. From the two ‘–’ signs in \( \mathcal{R}_1 \) and two ‘+’ signs in \( \mathcal{R}_2 \), it follows immediately that orbits cannot jump between regions \( \mathcal{R}_1 \) and \( \mathcal{R}_2 \), i.e., each of these regions is invariant.

**Theorem 3.5.** If \( C_{12} = C_{21} = 0 \), then every equilibrium point \((\hat{X}, \hat{Y}) \in \mathcal{E}_X^*\) is a stable equilibrium and any orbit with \((X_0,Y_0) \neq (0,0)\) converges to a point in \( \mathcal{E}_X^* \).

**Proof.** We use the augmented phase portrait shown in Fig. 4. From the two ‘–’ signs in \( \mathcal{R}_1 \) and two ‘+’ signs in \( \mathcal{R}_2 \), obtained from (16) and (17), it follows immediately that both \( \mathcal{R}_1 \) and \( \mathcal{R}_2 \) are invariant. Select an arbitrary equilibrium point \((\hat{X}, \hat{Y}) \in \mathcal{E}_X^*(E_1 \cup E_2)\) and any open set, \( U \), containing \((\hat{X}, \hat{Y})\). There exists \( \epsilon > 0 \) such that \( U_\epsilon = \{(X,Y) \in (0,\infty)^2 : \| (X,Y) - (\hat{X}, \hat{Y}) \|_\infty < \epsilon \} \subset U \). Take the rectangle \( V \subset U_\epsilon \) such that both its upper left corner and its lower right corner are on the nullcline \( Y = h(X) \). If \((\hat{X}, \hat{Y}) = E_1 \) or \( E_2 \), select \( U \) containing \((\hat{X}, \hat{Y})\), open relative to \([0,\infty]^2\). If \((\hat{X}, \hat{Y}) = E_1 \), let \( U_\epsilon = \{(X,Y) \in (0,\infty) \times [0,\infty) : \| (X,Y) - (\hat{X}, \hat{Y}) \|_\infty < \epsilon \} \subset U \) and take the rectangle \( V \subset U_\epsilon \) with its upper left corner on the nullcline and if \((\hat{X}, \hat{Y}) = E_2 \), let \( U_\epsilon = \{(X,Y) \in [0,\infty) \times (0,\infty) : \| (X,Y) - (\hat{X}, \hat{Y}) \|_\infty < \epsilon \} \subset U \) and take a rectangle \( V \subset U_\epsilon \) with its lower right corner on the nullcline. (If \( K_1 = K_2 \), take \( V = U_\epsilon \).) From the directions field, in all cases, the rectangle \( V \) is positively invariant. \( \square \)

**Remark 3.6.** In the case when \( C_{12} = C_{21} = 0 \), the eigenvalues of the Jacobian matrix evaluated at any \((X,h(X))) \in E_X^*, X \in [0,K_1]\), are \( \lambda_1(X), \lambda_2(X) \) with

\[
0 < \lambda_1(X) = \frac{1 + r_1 \left( 1 - \frac{X}{K_1} \right) + \frac{X}{K_1} r_2}{(1 + r_1)(1 + r_2)} < 1 \quad \text{and} \quad \lambda_2(X) = 1.
\]

Determining the stability using the classical method of calculating the eigenvalues of the Jacobian matrix is therefore inconclusive. Instead, the next theorem provides a global analysis using the augmented phase portrait and the definition of a stable equilibrium point and does not require the calculation of the eigenvalues. It is the invariance of each of the regions \( \mathcal{R}_1 \) and \( \mathcal{R}_2 \) that is the key ingredient. This can be determined from the augmented phase portrait, but not from the standard phase portrait.
3.2.2 Case II: $C_{12}C_{21} < 0$

In this case, competitive efficiencies have opposite signs. We will show that for all positive initial conditions, there is competitive exclusion, that is, the population with the positive competitive efficiency wins the competition and drives the other competitor to extinction.

For competitive efficiencies with opposite signs, the nontrivial nullclines of competitors $X$ and $Y$ do not intersect in the first quadrant and so there is no coexistence equilibrium. We only provide an analysis for the case when $C_{12} < 0$ and $C_{21} > 0$, i.e., $\frac{r_2}{a_1} < K_2$ and $\frac{r_1}{a_2} > K_1$. The proofs in the case when $C_{12} > 0$ and $C_{21} < 0$ follow by interchanging the roles of $X$ and $Y$.

As in Case I, the standard phase portrait is not sufficient to determine the global dynamics. For example, additional information is required to rule out orbits jumping between regions $R_1$ and $R_3$ or jumping out of $R_2$, where:

$$
R_1 := \{(X,Y) \in \mathbb{R}_+^2: Y < h(X)\}, \quad R_2 := \{(X,Y) \in \mathbb{R}_+^2: h(X) \leq Y \leq k(X)\}, \quad R_3 := \{(X,Y) \in \mathbb{R}_+^2: k(X) < Y\}.
$$

To prove this behavior does not occur, we augment the standard phase portrait by including the signs of the next-iterate operators associated with the nontrivial nullclines. We then use the augmented phase portrait, shown in Fig. 5a), in the proof that $E_2$ is globally asymptotically stable and $E_0$ and $E_1$ are unstable (see 3.9). But first we need some preliminary results.

The proof of the next lemma relies on (15) and is provided in Appendix A.4.
Lemma 3.7. Assume $C_{12} < 0$ and $C_{21} > 0$.

a) $\mathcal{L}_h(X,Y) > 0$, for all $(X,Y) \in \mathcal{R}_2 \cup \mathcal{R}_3$.

b) $\mathcal{L}_k(X,Y) < 0$, for all $(X,Y) \in \mathcal{R}_1 \cup \mathcal{R}_2$.

Figure 5: Augmented phase portraits in the case when $C_{12} < 0$ and $C_{21} > 0$. The standard phase portrait is augmented in a) by including only the signs (based on the results in Lemma 3.7) of the next-iterate operators associated with the nullclines $Y = h(X)$ and $Y = k(X)$, needed to prove the global asymptotic stability of $E_2$. This phase portrait is prototypical. An example including the root-curves is shown in b) for parameter values: $\alpha_1 = \alpha_2 = 1, r_1 = \frac{1}{2}, r_2 = \frac{5}{8}, K_1 = \frac{1}{2}, K_2 = 2$. Once the root-curves are included, the signs of the next-iterate operators in all regions can be included.

Next we show how to use the augmented phase portrait in Fig. 5a), to prove that region $\mathcal{R}_2$ is positively invariant.

Proposition 3.8. If $C_{12} < 0$ and $C_{21} > 0$, then $\mathcal{R}_2$ is positively invariant.

Proof. We use the augmented phase portrait shown in Fig. 5a). Let $(X_t,Y_t) \in \mathcal{R}_2$. Based on the black ‘+’ symbol in $\mathcal{R}_2$, obtained from Lemma 3.7a), $\mathcal{L}_h(X_t,Y_t) > 0$ so that $(X_{t+1},Y_{t+1})$ remains above the nullcline $Y = h(X)$. The gray ‘−’ symbol in $\mathcal{R}_2$, obtained from Lemma 3.7b), indicates that $\mathcal{L}_k(X_t,Y_t) < 0$. Thus, $(X_{t+1},Y_{t+1})$ remains below the nullcline $Y = k(X)$. Thus, $(X_{t+1},Y_{t+1}) \in \mathcal{R}_2$. □

Theorem 3.9. If $C_{12} < 0$ and $C_{21} > 0$, then any orbit with initial condition $X_0,Y_0 > 0$ converges to $E_2$. Furthermore, $E_0$ is a repeller and $E_1$ is a saddle.

Proof. Proposition 3.8 and the direction field in $\mathcal{R}_2$ imply that orbits entering $\mathcal{R}_2$ converge to $E_2$. To show that $E_2$ is globally asymptotically stable with respect to all solutions with positive initial conditions, it suffices to show that all such orbits either converge to $E_2$ or eventually enter $\mathcal{R}_2$. We do so using the augmented phase portrait in Fig. 5a).
• Let \((X_0, Y_0) \in \mathcal{R}_1\). The gray ‘−’ symbols in \(\mathcal{R}_1 \cup \mathcal{R}_2\), obtained from Lemma 3.7b), indicate that \(\mathcal{L}_k(X_t, Y_t) < 0\), for all \(t \geq 0\) and so the entire forward orbit must remain below the nullcline \(Y = k(X)\). The orbit cannot remain in \(\mathcal{R}_1\) indefinitely, since the component-wise monotonicity given by the direction field would imply convergence to an equilibrium, but also prevents convergence to any equilibrium in that region. Hence, the orbit must eventually enter \(\mathcal{R}_2\), and hence converge to \(E_2\).

• Let \((X_0, Y_0) \in \mathcal{R}_3\). If the orbit remains in \(\mathcal{R}_3\) indefinitely, by the component-wise monotonicity obtained from the direction field, the orbit must converge to \(E_2\). Otherwise, the black ‘+’ symbol in \(\mathcal{R}_2 \cup \mathcal{R}_3\), obtained from Lemma 3.7b), indicates that \(\mathcal{L}_h(X_t, Y_t) > 0\), for all \(t \geq 0\). The orbit must therefore remain above the nullcline \(Y = h(X)\), and hence must enter \(\mathcal{R}_2\) and once again converge to \(E_2\).

Thus, all orbits with positive initial conditions converge to \(E_2\). By Theorem 3.3 and the direction field, it is clear that \(E_0\) is a repeller and \(E_1\) is a saddle.

This theorem implies that if the competitive efficiency of competitor \(X\) is negative and the competitive efficiency of competitor \(Y\) is positive, then \(Y\) is the sole surviving population. If the sign of the competitive efficiencies are reversed, then population \(X\) is the sole surviving population. This result is stated in the following theorem that can be proven by simply exchanging the parameter indices for \(X\) and \(Y\).

**Theorem 3.10.** If \(C_{12} > 0\) and \(C_{21} < 0\), then any orbit with initial condition \(X_0, Y_0 > 0\) converges to \(E_1\), \(E_0\) is a repeller, and \(E_1\) is a saddle.

Fig. 5b) provides an example for Case II, that includes the root-curves for the parameter choices \(r_1 = \frac{1}{2}, r_2 = \frac{5}{8}, K_1 = \frac{1}{2}, K_2 = 2\), and \(\alpha_1 = \alpha_2 = 1\). Although the precise location of the root-curves is not necessary, as only some of the signs of the next-iterate operators were needed to obtain the global dynamics in Theorem 3.9, the positions of the root-curves are in fact generic for Case II. More precisely, the (gray) root-curve (associated with nullcline, \(Y = k(X)\)), remains above \(Y = k(X)\), intersects \(E_2\), and intersects the \(X\)-axis. The (black) root-curve (associated with the nullcline, \(Y = h(X)\)), remains below \(Y = h(X)\), intersects the \(Y\)-axis, intersects \(E_1\), and is negative, for \(X > K_1\). Above the gray root-curve, the ‘++’ symbols indicate that orbits remain above both nullclines. The direction field in this region implies that orbits converge to \(E_2\) or eventually enter the region between the gray root-curve and the nullcline \(Y = k(X)\). There, the black ‘+’ symbol indicates that an orbit remains above the nullcline \(Y = h(X)\) but the gray ‘−’ symbol indicates that they jump below the nullcline \(Y = k(X)\). Thus, the orbit enters the region bounded by the nontrivial nullclines. The signs in that region imply that an orbit remains in that region and, together with the direction field, imply that the orbit converges to \(E_2\).

### 3.2.3 Case III: \(C_{12}, C_{21} < 0\)

In this case, the nontrivial \(X\) and \(Y\) nullclines intersect exactly once in the interior of the first quadrant, and so there exists a unique coexistence equilibrium \(E^* = (X^*, Y^*)\) with
$X^*, Y^* > 0$. Since the signs of the competitive efficiencies are both negative,

$$h(X) - k(X) \begin{cases} < 0, & \text{if } X < X^*, \\ = 0, & \text{if } X = X^*, \\ > 0, & \text{if } X > X^*. \end{cases} \quad \text{(18)}$$

Since the two nontrivial nullclines intersect in $\mathbb{R}^2_+$, there are four regions of interest:

$\mathcal{R}_1 = \{(X, Y) \in \mathbb{R}^2_+; Y < \min\{h(X), k(X)\}\}$,  $\mathcal{R}_2 = \{(X, Y) \in \mathbb{R}^2_+; k(X) \leq Y \leq h(X)\}\{E^*\}$,
$\mathcal{R}_3 = \{(X, Y) \in \mathbb{R}^2_+; Y > \max\{h(X), k(X)\}\}$,  $\mathcal{R}_4 = \{(X, Y) \in \mathbb{R}^2_+; h(X) \leq Y \leq k(X)\}\{E^*\}$.

The proof of the following Lemma relies on (15) and is provided in Appendix A.5.

**Lemma 3.11.** Assume $C_{12}, C_{21} < 0$.

a) $\mathcal{L}_h(X, Y) > 0$ for $(X, Y) \in \mathcal{R}_4 \cup \mathcal{R}_{34}$, where $\mathcal{R}_{34} := \mathcal{R}_3 \cap \{(X, Y): X < X^*\}$.

b) $\mathcal{L}_h(X, Y) < 0$ for $(X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_{12}$, where $\mathcal{R}_{12} := \mathcal{R}_1 \cap \{(X, Y): X^* < X\}$.

c) $\mathcal{L}_k(X, Y) > 0$ for $(X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_{32}$, where $\mathcal{R}_{32} := \mathcal{R}_3 \cap \{(X, Y): Y < Y^*\}$.

d) $\mathcal{L}_k(X, Y) < 0$ for $(X, Y) \in \mathcal{R}_4 \cup \mathcal{R}_{14}$, where $\mathcal{R}_{14} := \mathcal{R}_1 \cap \{(X, Y): Y^* < Y\}$.

Fig. (6a) includes only the information obtained in Lemma 3.11 about the signs of the next-iterate operators required to obtain the global dynamics in this case. The signs in $\mathcal{D}_1 \cup \mathcal{D}_2$ are not necessary, where:

$$\mathcal{D}_1 := \{(X, Y) \in \mathcal{R}_1; 0 < X \leq X^*, 0 < Y \leq Y^*\} \setminus \{E^*\},$$

$$\mathcal{D}_2 := \{(X, Y) \in \mathcal{R}_3; X^* \leq X, Y^* \leq Y\} \setminus \{E^*\}. \quad \text{(19)}$$

Although, Fig. (6b) is an example that shows that the sign of one of the next-iterate operators can change sign in at least one of these regions, we will show that no orbit can oscillate between $\mathcal{D}_1$ and $\mathcal{D}_2$. This will be sufficient for us to determine the global dynamics using the augmented phase portrait.

**Proposition 3.12.** If $C_{12}, C_{21} < 0$, then regions $\mathcal{R}_2$ and $\mathcal{R}_4$ are positively invariant.

*Proof.* We use the augmented phase portrait shown in Fig. (6a). Assume $(X_t, Y_t) \in \mathcal{R}_4$. The black ‘+’ symbol in $\mathcal{R}_4$, obtained in Lemma 3.11a), implies that $\mathcal{L}_h(X_t, Y_t) > 0$ so that $(X_{t+1}, Y_{t+1})$ is above the nullcline $Y = h(X)$. The gray ‘−’ symbol in $\mathcal{R}_4$, obtained from Lemma 3.11b), implies that $\mathcal{L}_k(X_t, Y_t) < 0$ so that $(X_{t+1}, Y_{t+1})$ lies below the nullcline $Y = k(X)$. Thus, $(X_{t+1}, Y_{t+1}) \in \mathcal{R}_4$.

Next, assume that $(X_t, Y_t) \in \mathcal{R}_2$. Based on the black ‘−’ symbol in $\mathcal{R}_2$, obtained from Lemma 3.11b), $\mathcal{L}_h(X_t, Y_t) < 0$ so that $(X_{t+1}, Y_{t+1})$ lies below the nullcline $Y = h(X)$. Also, the gray ‘+’ symbol in that region obtained from Lemma 3.11b), indicates that $\mathcal{L}_k(X_t, Y_t) > 0$ so that $(X_{t+1}, Y_{t+1})$ lies above the nullcline $Y = k(X)$. Thus, $(X_{t+1}, Y_{t+1}) \in \mathcal{R}_2$. \qed
Figure 6: Augmented phase portraits in the case when $C_{12}, C_{21} < 0$, where $\mathcal{R}_3 = \mathcal{R}_{34} \cup \mathcal{D}_2 \cup \mathcal{R}_{32}$ and $\mathcal{R}_1 = \mathcal{R}_{12} \cup \mathcal{D}_1 \cup \mathcal{R}_{14}$. In a), the standard phase portrait is augmented by including the signs (based on the results in Lemma 3.11) of the next-iterate operators associated with the nullclines $Y = h(X)$ and $Y = k(X)$, needed to determine the global dynamics, and is prototypical in this case. In particular, knowing the signs in regions $\mathcal{D}_1$ and $\mathcal{D}_2$ is not required. In b), an example that includes the root-curves is provided for parameter values, $\alpha_1 = 1$, $\alpha_2 = 3$, $r_1 = 1$, $r_2 = 2$, $K_1 = 2$, and $K_2 = 1.3$.

Using the augmented phase portrait in Fig. 6a), we show the following result by arguing that there cannot be a ‘++’ region in $\mathcal{D}_1$ (see the details in Appendix A.6).

**Lemma 3.13.** Let $C_{12}, C_{21} < 0$. If $(X, Y) \in \mathcal{D}_1$, then $(F(X, Y), G(X, Y)) \notin \mathcal{D}_2$.

**Theorem 3.14.** If $C_{12}, C_{21} < 0$, then every orbit with $X_0, Y_0 > 0$ converges to $E_2$, $E_1$, or $E^*$. Moreover, $E_1$ and $E_2$ are locally asymptotically stable and $E^*$ is unstable.

**Proof.** Since, by Proposition 3.12, regions $\mathcal{R}_2$ and $\mathcal{R}_4$ are positively invariant, and the direction field in $\mathcal{R}_2$ implies that orbits that enter $\mathcal{R}_2$ converge to $E_1$ and orbits that enter $\mathcal{R}_4$ converge to $E_2$, it suffice to show that all solutions either converge to $E^*$ or eventually enter $\mathcal{R}_2 \cup \mathcal{R}_4$.

We use Fig. 6(a) to discuss the global dynamics of orbits with initial conditions outside of $\mathcal{R}_2 \cup \mathcal{R}_4$.

- Let $(X_t, Y_t) \in \mathcal{R}_{14}$. The gray ‘−’ symbol in that region, derived from Lemma 3.11(d), indicates $(X_{t+1}, Y_{t+1})$ is below the line $Y = k(X)$. By the direction field in this region, $(X_{t+1}, Y_{t+1}) \in \mathcal{R}_4 \cup \mathcal{R}_{14}$. If an orbit were to remain in $\mathcal{R}_{14}$ indefinitely, then it would have to converge to an equilibrium. However, the direction field excludes the convergence to the only equilibrium in this region, $E^*$. Thus, the orbit must enter $\mathcal{R}_4$ and then converges to $E_2$.

- Let $(X_t, Y_t) \in \mathcal{R}_{34}$. The black ‘+’ symbol in that region, obtained from Lemma 3.11(h), implies that $(X_{t+1}, Y_{t+1})$ is above the line $Y = h(X)$. Together with the direction...
field, this implies that \((X_{t+1},Y_{t+1}) \in R_{34} \cup R_4\). If an orbit remains in \(R_{34}\) indefinitely, then it could only converge to \(E_2\). Otherwise, it enters \(R_4\) and converges to \(E_2\).

- Let \((X_t,Y_t) \in R_{12}\). Based on the black ‘\(-\)’ symbol in that region, obtained from Lemma \([3.11]\), \((X_{t+1},Y_{t+1})\) is below the line \(Y = h(X)\). By the direction field, \((X_{t+1},Y_{t+1}) \in R_2 \cup R_{12}\). If an orbit were to remain in \(R_{12}\), it would have to converge to an equilibrium. However, the direction field in this region prevents the convergence to the only equilibrium in this region, \(E^*\). Thus, the orbit must enter \(R_2\) and hence converge to \(E_1\).

- Let \((X_t,Y_t) \in R_{32}\). Based on the gray ‘\(+\)’ symbol in that region, obtained from Lemma \([3.11]\), \((X_{t+1},Y_{t+1})\) lies above the nullcline \(Y = k(X)\). Thus, \((X_{t+1},Y_{t+1}) \in R_{32} \cup R_2\). If an orbit were to remain indefinitely in \(R_{32}\), then it would have to converge to an equilibrium. The direction field in this region reveals that such an orbit would have to converge to \(E_1\). Otherwise, the orbit must enter \(R_2\) and also converge to \(E_1\).

- Let \((X_t,Y_t) \in D_1\). If the orbit remains indefinitely in \(D_1\), then it converges to \(E^*\). Otherwise, by Lemma \([3.13]\) there exists \(T > 0\) such that \((X_T,Y_T) \in D_1\) and \((X_{T+1},Y_{T+1}) \in (0,K_1) \times (0,K_2)\). Thus, one of the previous cases applies and hence the orbit converges to \(E_1\) or \(E_2\).

- Let \((X_t,Y_t) \in D_2\). First, assume that \((X_0,Y_0) \in (X^*,K_1) \times (Y^*,K_2)\). If the orbit remains in \(D_2\) indefinitely, then from the direction field, it must converge to \(E^*\). Otherwise, the orbit enters one of the other regions and one of the previous cases applies, so that the orbit converges to \(E_1\) or \(E_2\).

Thus, any orbit with positive initial conditions converges to one of the equilibria, \(E^*, E_1,\) or \(E_2\).

Without calculating the eigenvalues of the Jacobian, we can also conclude that \(E_2\) is locally asymptotically stable because any orbit with initial condition \((X_0,Y_0) \in R_4 \cup R_{34}\) converges to \(E_2\) and the convergence is monotone in a neighbourhood of \(E_2\). Similarly, since any orbit with initial condition \((X_0,Y_0) \in R_2 \cup R_{32}\) converges to \(E_1\), \(E_1\) is locally asymptotically stable. Since the coexistence equilibrium \(E^*\) is on the boundary of all of these regions, \(E^*\) is unstable.

We were able to prove the global dynamics based on the augmented phase portrait in Fig. \((6b)\), without knowing the precise location of the root-curves. If specific parameter values were however chosen, then the root-curves can be obtained numerically and the signs of the next-iterate operators associated with each of the nullclines can be obtained for the entire first quadrant, see Fig. \((6b)\). For the specific example with \(\alpha_1 = 1,\ \alpha_2 = 3,\ r_1 = \frac{1}{2},\ r_2 = 2,\ K_1 = 2,\ and\ K_2 = 1.3,\ the\ root-curves\ were\ obtained.\ The\ black\ solid\ curve\ in\ Fig.\ \((6b)\),\ represents\ the\ root-curve\ associated\ with\ the\ nontrivial\ X-nullcline\ and\ the\ gray\ solid\ curve\ is\ the\ root-curve\ associated\ with\ the\ nontrivial\ Y-nullcline.\ Once\ the\ root-curves\ are\ included,\ the\ corresponding\ signs\ of\ the\ next-iterate\ operators\ can\ be\ added\ in\ every\ region.\ Fig.(6b),\ highlights\ that\ orbits\ in\ the\ \(D_2\) region\ cannot\ jump\ into\ \(D_1\).\ For\ example,\ an\ the\ next\ iterate\ of\ an\ orbit\ in\ \(D_2\) where\ black\ and\ gray\ ‘\(+\)’
symbols are, must remain above both nullclines. Similarly, the next iterate of an orbit in $\mathcal{D}_1$, where black and gray ‘−’ symbols are, must remain below both nullclines and can therefore not enter $\mathcal{D}_2$. Since the proof of Theorem 3.14 was only based on Fig. 6(b), not all signs of the next-iterate operators are necessary to determine the global dynamics.

3.2.4 Case IV: $C_{12}, C_{21} > 0$

In this case, as in Case III, the nontrivial $X$- and $Y$-nullclines intersect exactly once in the interior of the first quadrant, and so there exists a unique coexistence equilibrium $E^* = (X^*, Y^*)$ with $X^*, Y^* > 0$. However, since $C_{12}, C_{21} > 0$,

$$h(X) - k(X) = \begin{cases} > 0, & \text{if } X < X^*, \\ = 0, & \text{if } X = X^*, \\ < 0, & \text{if } X > X^*. \end{cases}$$ (20)

We can again divide the first quadrant into the four regions,

$$\mathcal{R}_1 := \{(X, Y) \in \mathbb{R}^2_+ : Y < \min\{h(X), k(X)\}\}, \mathcal{R}_2 := \{(X, Y) \in \mathbb{R}^2_+ : h(X) \leq Y \leq k(X)\}\setminus\{E^*\},$$

$$\mathcal{R}_3 := \{(X, Y) \in \mathbb{R}^2_+ : Y > \max\{h(X), k(X)\}\}, \mathcal{R}_4 := \{(X, Y) \in \mathbb{R}^2_+ : k(X) \leq Y \leq h(X)\}\setminus\{E^*\}.$$ 

The proof of the next Lemma is provided in Appendix A.7.

Lemma 3.15. Assume $C_{12}, C_{21} > 0$.

a) $\mathcal{L}_h(X, Y) < 0$ for $(X, Y) \in \mathcal{R}_4 \cup \mathcal{R}_4$, where $\mathcal{R}_{14} := \mathcal{R}_1 \cap \{(X, Y) : Y > Y^*\}$.

b) $\mathcal{L}_h(X, Y) > 0$ for $(X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_3$, where $\mathcal{R}_{32} := \mathcal{R}_3 \cap \{(X, Y) : Y < Y^*\}$.

c) $\mathcal{L}_k(X, Y) > 0$ for $(X, Y) \in \mathcal{R}_4 \cup \mathcal{R}_4$, where $\mathcal{R}_{34} := \mathcal{R}_3 \cap \{(X, Y) : X < X^*\}$.

d) $\mathcal{L}_k(X, Y) < 0$ for $(X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_4$, where $\mathcal{R}_{12} := \mathcal{R}_1 \cap \{(X, Y) : X > X^*\}$.

Fig. 7(a) includes the information obtained in Lemma 3.15 about the signs of the next-iterate operators. As for Case III, we do not need to determine the sign of the next-iterate operators in regions $\mathcal{D}_1$ and $\mathcal{D}_2$ to determine the global dynamics.

Proposition 3.16. If $C_{12}, C_{21} > 0$, then regions $\mathcal{R}_2$ and $\mathcal{R}_4$ are positively invariant.

Proof. We use the augmented phase portrait shown in Fig. 7(a). Let $(X_t, Y_t) \in \mathcal{R}_2$. Based on the black ‘+’ symbol in $\mathcal{R}_2$, obtained from Lemma 3.15(b), $\mathcal{L}_h(X_t, Y_t) > 0$, so that $(X_{t+1}, Y_{t+1})$ remains above the nullcline $Y = h(X)$. The gray ‘−’ symbol in $\mathcal{R}_2$, derived from Lemma 3.15(d), indicates that $\mathcal{L}_k(X_t, Y_t) < 0$. Thus, $(X_{t+1}, Y_{t+1})$ remains below the nullcline $Y = k(X)$. Thus, $(X_{t+1}, Y_{t+1}) \in \mathcal{R}_2$.

Next, let $(X_t, Y_t) \in \mathcal{R}_4$. The black ‘−’ symbol in this region, derived from Lemma 3.15(a), indicates that $\mathcal{L}_h(X, Y) < 0$ and so $(X_{t+1}, Y_{t+1})$ remains below the nullcline $Y = h(X)$. Also, the gray ‘+’ symbol in this region, derived from Lemma 3.15(c), indicates that $\mathcal{L}_k(X_t, Y_t) > 0$, so that $(X_{t+1}, Y_{t+1})$ remains above the nullcline $Y = k(X)$. Thus, $(X_{t+1}, Y_{t+1}) \in \mathcal{R}_4$, completing the proof. \(\square\)
Figure 7: Augmented phase portraits in the case when $C_{12}, C_{21} > 0$, where $E_1 = D_1 \cup R_{14} \cup R_{12}$ and $E_3 = D_2 \cup R_{32} \cup R_{34}$. In a), the standard phase portrait is augmented by including only the signs (based on the results in Lemma 3.15) of the next-iterate operators associated with the nullclines $Y = h(X)$ and $Y = k(X)$, necessary to determine the global stability of $E^*$ and is prototypical for this case. An example including root-curves is shown in b) with parameters, $\alpha_1 = \alpha_2 = 1$, $r_1 = r_2 = 2$, $K_1 = K_2 = 1$.

As for Lemma 3.13, the proof of the following result that shows that there is no ‘++’ region in $D_1$, is obtained using the augmented phase portrait, in this case, shown in Fig. 7a) (see details in Appendix A.8).

**Lemma 3.17.** Let $C_{12}, C_{21} > 0$. If $(X, Y) \in D_1$, then $(F(X, Y), G(X, Y)) \notin D_2$, where $D_1$ and $D_2$ are defined in (19).

**Theorem 3.18.** If $C_{12}, C_{21} > 0$, then $E^*$ is globally asymptotically stable with respect to orbits with $X_0, Y_0 > 0$. Furthermore, $E_0$ is a repeller, and $E_1$ and $E_2$ are saddles.

**Proof.** We use the augmented phase portrait in Fig. 7a) to show that all solutions with positive initial conditions converge to $E^*$. First note that by Proposition 3.16, $R_i$, $i = 1, 2$, are positively invariant and that the direction field in these regions implies that any orbit that enters either of these two regions converges to $E^*$.

- Let $(X_t, Y_t) \in R_{14}$. The black ‘−’ symbol, obtained from Lemma 3.15(a), implies that $(X_{t+1}, Y_{t+1})$ must remain below the nullcline $Y = h(X)$. The direction field tells us that $(X_{t+1}, Y_{t+1}) \in R_{14} \cup R_4$. If an orbit were to remain in $R_{14}$ indefinitely, then it must converge to an equilibrium. However, the direction field in this regions prevents the convergence to the only equilibria in this region. Hence, there exists $T > 0$ such that $(X_T, Y_T) \in R_4$ and then the orbit must converge to $E^*$.

- Let $(X_t, Y_t) \in R_{34}$. Based on the gray ‘+’ symbol, obtained from Lemma 3.15(c), $(X_{t+1}, Y_{t+1})$ must remain above the nullcline $Y = k(X)$. From the direction field, it follows that $(X_{t+1}, Y_{t+1}) \in R_{34} \cup R_4$. If an orbit were to remain in $R_{34}$ indefinitely, it
must converge to an equilibrium. However, the direction field in this region prevents the convergence to the only equilibrium in this region, \( E^* \). Hence, there exists \( T > 0 \) such that \((X_T, Y_T) \in \mathcal{R}_4 \) and the orbit must converge to \( E^* \).

- Let \((X_t, Y_t) \in \mathcal{R}_{12} \). The gray ‘–’ symbol, based on Lemma 3.15d), reveals that \((X_{t+1}, Y_{t+1}) \) must remain below the nullcline \( Y = k(X) \). Thus, with the direction field, it follows that \((X_{t+1}, Y_{t+1}) \in \mathcal{R}_{12} \cup \mathcal{R}_2 \). If an orbit were to remain in \( \mathcal{R}_{12} \) indefinitely, then it must converge to an equilibrium. However, the direction field in this region prevents the convergence to the only two equilibria, \( E^* \) and \( E_1 \). Hence, there exists \( T > 0 \) such that \((X_T, Y_T) \in \mathcal{R}_2 \) and the orbit converges to \( E^* \).

- Let \((X_t, Y_t) \in \mathcal{R}_{32} \). The black ‘+’ symbol, based on Lemma 3.15b), implies that \((X_{t+1}, Y_{t+1}) \) remains above the nullcline \( Y = h(X) \). Together with the direction field, \((X_{t+1}, Y_{t+1}) \in \mathcal{R}_{32} \cup \mathcal{R}_2 \). If an orbit were to remain in \( \mathcal{R}_{32} \) indefinitely, then it must converge to an equilibrium. However, the direction field in this region prevents the convergence to the only equilibrium \( E^* \). Thus, there exists \( T > 0 \) such that \((X_T, Y_T) \in \mathcal{R}_2 \) and the orbit converges to \( E^* \).

- Let \((X_t, Y_t) \in \mathcal{D}_1 \). If the orbit remains in \( \mathcal{D}_1 \) indefinitely, then it must converge to \( E^* \). Otherwise, by Lemma 3.17 there exists \( T > 0 \) such that \((X_T, Y_T) \in \mathcal{D}_1 \). However, \((X_{T+1}, Y_{T+1}) \in (0, \frac{r_2}{\alpha_2}) \times (0, \frac{r_1}{\alpha_1}) \) and so one of the previous cases apply.

- Let \((X_t, Y_t) \in \mathcal{D}_2 \). If the orbit remains in \( \mathcal{D}_2 \) indefinitely, then it converges to \( E^* \). Otherwise, the orbit enters one of the other regions, where one of the previous cases apply and the orbit must converge to \( E^* \).

Thus, any orbit with positive initial conditions converges to \( E^* \) and the convergence is eventually monotone. Hence, \( E^* \) is globally asymptotically stable. That \( E_0 \) is a repeller and \( E_1 \) and \( E_2 \) are saddles also follow from Theorem 3.3 and the augmented phase portrait.

Theorem 3.18 does not require the sign of the next-iterate operator in all regions of the first quadrant. However, for specific parameter values, one can graph the root-curves associated with each nullcline, see Fig. 7b). Once the root-curves are obtained, the signs of the next-iterate operators can immediately be included in the phase portrait.

### 4 Extensions and Limitations

While the previous sections focused on the introduction of the augmented phase portrait and how to use it in the analysis of the discrete competition model (3), the method can easily be used for other planar maps and provides an elementary tool to obtain information about the local and global dynamics of solutions. However, just as for the phase plane approach used for the analysis of planar ordinary differential equations, the augmented phase portrait has its limitations. Some of these are discussed in this section.
4.1 Example: Ricker Competition Model

A popular alternative to (3) is the competitive Ricker map:

\[
X_{t+1} = X_t e^{K - X_t - a Y_t}, \quad Y_{t+1} = Y_t e^{L - b X_t - Y_t},
\]

with initial conditions \(X_0, Y_0 \geq 0\), where \(K, L > 0\) represent the carrying capacities of competitor \(X\) and \(Y\), respectively. Here \(a, b > 0\) describe the competitive factor for population \(X\) and \(Y\), respectively. For \(0 < K, L < 1\), the theory of monotone flows was applied, allowing for conclusions regarding the global dynamics given the local stability of equilibria \[17\]. In \[5\], (21) was revisited and conditions were provided for the global stability of the coexistence equilibrium under different restrictions on the parameters. Nevertheless, the conjecture that for (21), local asymptotic stability always implies global asymptotic stability \[14\] remains an open problem. While the augmented phase plane method cannot be used to prove the conjecture, it can be used to identify positively invariant regions and therefore the global dynamics of orbits entering these regions. In turn, the augmented phase portrait also determines regions where solutions might oscillate. This might be helpful to prove or disprove the conjecture.

![Augmented phase portraits](attachment:image.png)

**Figure 8**: Augmented phase portraits for (21). In a), \(K = L = 0.6, a = 0.35,\) and \(b = 0.4\). The augmented phase portrait can be used to prove the global asymptotic stability of the coexistence equilibrium. In b), \(K = 0.9, L = 1.6, a = 0.4,\) and \(b = 0.3\). The augmented phase portrait cannot rule out orbits jumping back and forth between the ‘++’ region below both nullclines and the ‘−−’ region above them.

For the specific model parameters chosen in Fig. 8, the root-curves were obtained numerically, using the built-in function “fimplicit” in Matlab. In contrast to all of the root-curves we have seen thus far, e.g., Fig. 7b), the root-curves in Fig. 8 are neither functions in \(X\) nor \(Y\). In this case, the sign of the next-iterate operators depend on whether it is evaluated at a point that is “inside” or “outside” of the region bounded by the associated root-curve. For points inside (outside) the region bounded by a root-curve, the corresponding next-iterate operator is positive (negative), indicating that the next iterate will lie above (below) its associated nullcline.
From the augmented phase portrait in Fig. 8a), it is possible to determine that the coexistence equilibrium is globally asymptotically stable with respect to the interior of the first quadrant. Based on the signs of the next-iterate operators, the augmented phase portrait identifies two regions as positively invariant: i) the triangular region bounded by the nontrivial nullclines and the $X$-axis with left-corner $K$ and right-corner $\frac{L}{b}$, and ii) the triangular region bounded by the nontrivial nullclines and the $Y$-axis with the lower $Y$-value $L$ and upper value $\frac{K}{a}$. Orbits entering either one of these two regions remain there, and, due to the direction field, must converge to the coexistence equilibrium. The signs of the next-iterate operators together with the direction field can also be used to argue that any orbit in the interior of the first quadrant must enter either i) or ii), and therefore converge to $E^*$.

The coexistence equilibrium for the parameter choice for Fig. 8b) is locally asymptotically stable, as the eigenvalues of the Jacobian are within the unit-circle. However, in this particular example, the augmented phase portrait cannot even be used to determine the local asymptotic stability of the coexistence equilibrium. It however identifies regions of interest. For example, an orbit could oscillate between the small region containing the black and gray ‘+’ symbols, and the region with the black and gray ‘–’ symbols above both nullclines. Furthermore, none of the regions bounded by nullclines is positively invariant. This can be immediately recognized by noting that in all four component-wise monotone regions, there exists at least one root-curve associated with a nullcline that partially lies in this region. This causes a change in the sign of the corresponding next-iterate root operator.

4.2 Example: Model with Mutualism

We consider the following example involving mutualism:

$$
X_{t+1} = \frac{(a + bY_t)X_t}{A + BX_t}, \quad Y_{t+1} = \frac{(c + dX_t)Y_t}{C + DY_t},
$$

with initial conditions $X_0, Y_0 \geq 0$ and positive parameters.

Augmented phase portraits for (22) are shown in Fig. 9 for two different parameter choices. Although, for the choice of parameters in Fig. 9a), the root-curves are not unique, this is not what prevents determining that $E^*$ is globally asymptotically stable with respect the interior of the first quadrant. It is, that we cannot rule out orbits oscillating indefinitely between regions $D_1$ and $D_2$ without converging to $E^*$. What the augmented phase portrait does tell us is that the basin of attraction of $E^*$ is contained in the union of all of the regions that have one ‘+’ and one ‘–’ symbol, the part of the region on the left containing two ‘+’ symbols, where $Y \leq Y^*$, and the part of the region on the bottom-right containing two ‘–’ symbols where $X < X^*$.

From the augmented phase portrait in Fig. 9b), we can conclude that $E^*$ is globally asymptotically stable with respect to initial conditions $(X_0, Y_0) \in (0,6) \times (0,6)$. The problematic regions $D_1$ and $D_2$ in Fig. 9a), are now detached from the equilibrium and are each separate curves outside $[0,6] \times [0,6]$.  

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Figure 9: The augmented phase portrait for (22). In a), \( a = 16, b = 1, A = 4, B = 2, c = 4, d = 1, C = 3, D = 2 \). There are two root-curves associated with each of the nontrivial nullclines. All orbits with initial conditions outside of \( \mathcal{D}_1 \cup \mathcal{D}_2 \), converge to \( E^* \). In b), \( a = 8, b = 1, A = 4, B = 2, c = 4.8, d = 1, C = 3, D = 2 \). All orbits with initial conditions \( (X_0, Y_0) \in (0, 6] \times (0, 6] \), converge to \( E^* \).

4.3 Example: Predator–Prey Model

In [19], we derived and analysed the discrete predator–prey model:

\[ X_{t+1} = \frac{(1 + r)X_t}{1 + \frac{r}{K}X_t + \alpha Y_t}, \quad Y_{t+1} = \frac{(1 + \gamma X_t)Y_t}{1 + d}, \tag{23} \]

with initial conditions \( X_0, Y_0 \geq 0 \), where all parameters are positive and \( X \) and \( Y \) denote the prey and predator populations.

In [19], the root-curve associated with the (nontrivial) prey nullcline was used to discuss the global dynamics of solutions of (23). In the case when no coexistence equilibrium exists, an augmented phase portrait, as in Fig. 10a), was used to determine the global asymptotic stability of the prey-only equilibrium \( E_K = (K, 0) \). When a coexistence equilibrium \( E^* \) exists, as in Fig. 10b), it was shown that the augmented phase portrait excludes the existence of prime period 2 and 3 orbits. The global asymptotic stability of \( E^* \), whenever it is locally asymptotically stable (i.e., \( d < \gamma K < 1 + 2d \)), remains a conjecture.

Just as for the continuous analogue of (23) \( x' = rx \left( 1 - \frac{x}{K} \right) - \alpha xy, \quad y' = y(-d + \gamma x) \), phase plane analysis alone is not enough to obtain a complete picture of the global dynamics when a coexistence equilibrium exists. For the continuous model, additional arguments are needed, including the application of the Dulac criterion, to rule out period orbits, and the Poincaré-Bendixson Theorem. Even though the configuration of the standard phase portraits for the continuous predator-prey model is the same as in Fig. 10, unlike the continuous model for which no periodic orbits are possible and the existence of the coexistence equilibrium implies it is globally asymptotically stable, in [19] it was shown that
Figure 10: Augmented phase portraits for the predator–prey model derived in [19]. In a), where $K\gamma < d$, the prey-only equilibrium $E_K$ is globally asymptotically stable. In b), where $d < \gamma K$, there is a unique interior equilibrium $E^*$. Orbits either converge to $E^*$ eventually monotonically or they cycle around $E^*$ indefinitely visiting each of the regions $\mathcal{R}_i$, $i = 1, 2, 3, 4$, at least once in each cycle.

for the discrete model the coexistence equilibrium undergoes a Neimark-Sacker bifurcation when $\gamma K = 1 + 2d$ and loses it stability.

5 Conclusion

We describe an elementary approach for analyzing planar discrete maps that can provide information about the global dynamics. Standard phase plane analysis has not been very effective in this context, since unlike in the case of planar systems defined by smooth differential equations, orbits of discrete maps can jump over nullclines, as shown in Fig. 2.

To overcome this drawback, we introduce the next-iterate operators associated with the nullclines and their associated root-sets and root-curves. Knowing the sign of the next-iterate operators in a region of the phase plane tells us on which side of the nullcline the operator is associated with, the next iterate will lie. By providing examples, we show that it is sometimes possible to determine the global dynamics of planar maps, by augmenting the standard phase portrait by including the signs of the next-iterate operators, where required. We then call the standard phase portrait that includes these signs, the augmented phase portrait.

In Section 3 we showed how to use the augmented phase plane to determine the global dynamics of a well-studied two species competition model [3]. We provided a more elementary approach, compared to the use of the theory of monotone flows, to show that the relative values of the competitive efficiencies completely determine the global dynamics, just as in the case of the analogous continuous model [1]. Using the augmented phase portrait, we were also able to determine the local stability of all of the equilibria without having to resort to linearization (i.e., finding the eigenvalues of the Jacobian at the equilibrium), even in one case when linearization would have been
inconclusive. We were also able to find the invariant and positively invariant regions and then use the direction field within these regions to conclude convergence of orbits once they enter one of these regions.

We also discuss some extensions and limitations of the augmented phase portrait in Section 4 by considering three examples: a Ricker competition model, a model involving species that display mutualistic behavior, and a predator-prey model. The complexity of root-sets for the Ricker competition model was illustrated in Fig. 8. We provided one set of parameters for which use of the augmented phase portrait could be used to determine the global dynamics completely and one that illustrated that there can be problematic regions in the phase portrait. Next, we addressed a model involving mutualism. Fig. 9a) illustrated that the root-curves do not have to be unique. However, it was not the non-uniqueness of the root-curves that prevented determining the global dynamics from the augmented phase portrait. Instead it was the existence of a ‘++’ region below both nullclines and a ‘– –’ region above both nullclines that, along with the direction field, did not allow ruling out orbits oscillating between these two regions. It is also important to note that although Figs. 8a) and 9b) also have a ‘++’ region and a ‘– –’ region, these do not cause a problem due to the direction field in those regions. Finally, for the predator-prey model, it is possible to use the augmented phase portrait to determine the asymptotic outcome for all orbits in the case that there is no coexistence equilibrium, and in particular prove that the prey-only equilibrium is globally asymptotically stable when it is locally asymptotically stable. The augmented phase portrait also showed that if an orbit does not converge to the coexistence equilibrium, the orbit cycles around it and must visit four different regions at least once in every cycle, thus ruling out prime period 2 and period 3 orbits.

In ongoing research, we continue to explore whether this elementary approach, i.e., using the augmented phase portrait, can be used in other contexts to determine different global properties of discrete planar models such as delay difference equations and general rational maps.

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A Appendix

A.1 Proof of (15)

Substituting the expression for the $X$ nullcline given in [6] in $L_h(X,Y)$, we have

$$L_h(X,Y) = G(X,Y) - h(F(X,Y)) = \frac{(1 + r_2)Y}{1 + \frac{r_2}{K_2}Y + \alpha_2X} - \frac{r_1}{\alpha_1\bar{K}_1} \left( \bar{K}_1 - \frac{(1 + r_1)}{1 + \frac{r_1}{K_1}X + \alpha_1Y} \right)$$

$$= \frac{N_h(X,Y)}{\alpha_1(K_1 + r_1X + \alpha_1\bar{K}_1Y)(K_2 + \alpha_2K_2X + r_2Y)},$$

where

$$N_h(X,Y) = a_0(X) + a_1(X)Y + a_2Y^2 = A_0(Y) + A_1(Y)X + A_2X^2,$$
with

\[
\begin{align*}
  a_0(X) & = -r_1K_2(K_1 - X)(1 + \alpha_2X), \\
  a_1(X) & = -r_1r_2(K_1 - X) - \alpha_1K_2(-r_1(1 + r_2)X + K_1(-1 + r_1 - r_2 + \alpha_2r_1X)), \\
  a_2 & = \alpha_1K_1(\alpha_1K_2(1 + r_2) - r_1r_2), \\
  A_0(Y) & = K_1(1 + \alpha_1Y)(-r_1r_2Y + K_2(-r_1 + \alpha_1(1 + r_2)Y)), \\
  A_1(Y) & = r_1(r_2Y + K_2(1 + \alpha_1(1 + r_2)Y - \alpha_2(K_1 + \alpha_1K_1Y))), \\
  A_2 & = \alpha_2K_2r_1.
\end{align*}
\]

It follows that \( \mathcal{L}_h(X, Y) = 0 \iff Y = r_{h_i}(X) \) or \( X = R_{h_i}(Y) \), \( i = 1, 2 \), where

\[
\begin{align*}
  r_{h_1}(X) & := \begin{cases} 
    -a_1(X) + \sqrt{a_1^2(X) - 4a_0(X)a_2}, & a_2 \neq 0, \\
    \frac{-a_0(X)}{a_1(X)}, & a_2 = 0,
  \end{cases} \\
  r_{h_2}(X) & := \begin{cases} 
    -a_1(X) - \sqrt{a_1^2(X) - 4a_0(X)a_2}, & a_2 \neq 0, \\
    \frac{-a_0(X)}{a_1(X)}, & a_2 = 0,
  \end{cases}
\end{align*}
\]

and

\[
\begin{align*}
  R_{h_1}(Y) & := \frac{-A_1(Y) + \sqrt{A_1^2(Y) - 4A_0(Y)A_2}}{2A_2}, \\
  R_{h_2}(Y) & := \frac{-A_1(Y) - \sqrt{A_1^2(Y) - 4A_0(Y)A_2}}{2A_2}.
\end{align*}
\]

Substituting the expression for the \( Y \) nullcline given in (8) in \( \mathcal{L}_k(X, Y) \), we have

\[
\begin{align*}
  \mathcal{L}_k(X, Y) = G(X, Y) - k(F(X, Y)) & = \frac{(1 + r_2)Y}{1 + \frac{r_2}{K_2}Y + \alpha_2X} - \frac{K_2}{r_2} \left( \frac{r_2 - \alpha_2}{1 + \frac{r_2}{K_2}X + \alpha_1Y} \right) \\
  &= \frac{N_k(X, Y)}{r_2(K_1 + r_1X + \alpha_1K_1Y)(K_2 + \alpha_2K_2X + r_2Y)},
\end{align*}
\]

with

\[
N_k(X, Y) = b_0(X) + b_1(X)Y + b_2Y^2 = B_0(Y) + B_1(Y)X + B_2X^2,
\]

where

\[
\begin{align*}
  b_0(X) & = K_2^2(1 + \alpha_2X)(K_1(\alpha_2(1 + r_1)X - r_2) - r_1r_2X), \\
  b_1(X) & = K_2r_2(r_1X + K_1(1 + \alpha_2(1 + r_1)X - \alpha_1(K_2 + \alpha_2K_2X))), \\
  b_2 & = \alpha_1K_2K_2, \\
  B_0(Y) & = -K_1K_2r_2(K_2 - Y)(1 + \alpha_1Y), \\
  B_1(Y) & = K_2(r_1r_2(Y - K_2) + \alpha_2K_1((1 + r_1)r_2Y + K_2(1 + r_1 - r_2(1 + \alpha_1Y)))), \\
  B_2 & = \alpha_2K_2^2(\alpha_2K_1(1 + r_1) - r_1r_2).
\end{align*}
\]

We therefore have

\[
\mathcal{L}_k(X, Y) = 0 \iff Y = r_{k_i}(X) \text{ or } X = R_{k_i}(Y), \quad i = 1, 2,
\]

where

\[
\begin{align*}
  r_{k_1}(X) & := \frac{-b_1(X) + \sqrt{b_1^2(X) - 4b_0(X)b_2}}{2b_2}, \\
  r_{k_2}(X) & := \frac{-b_1(X) - \sqrt{b_1^2(X) - 4b_0(X)b_2}}{2b_2}.
\end{align*}
\]
and
\[ R_{k_1}(Y) := \begin{cases} \frac{-B_1(Y) + \sqrt{B_1^2(Y) - 4B_0(Y)B_2}}{2B_2}, & B_2 \neq 0, \\ \frac{B_0(Y)}{B_1(Y)}, & B_2 = 0. \end{cases} \]
\[ R_{k_2}(Y) := \begin{cases} \frac{-B_1(Y) - \sqrt{B_1^2(Y) - 4B_0(Y)B_2}}{2B_2}, & B_2 \neq 0, \\ \frac{B_0(Y)}{B_1(Y)}, & B_2 = 0. \end{cases} \]

**A.2 Proof of Lemma 3.4**

**Proof.** Substituting \( K_2 = \frac{r_2}{\alpha_1} \) and \( K_1 = \frac{r_2}{\alpha_2} \) in (24), we have \( a_2 = \frac{\alpha_1 r_1 r_2}{\alpha_1} > 0 \) and therefore, by (25), \( r_{h_1}(X) = \frac{r_1(r_2 - \alpha_2 X)}{\alpha_1 r_2} = h(X) \) and \( r_{h_2}(X) = \frac{-\alpha_2 X + 1}{\alpha_1} < 0 \). Thus, there is a unique positive root-curve, \( r_h(X) = r_{h_1}(X) = h(X) \), associated with the positive \( X \) nullcline, \( Y = h(X) \), that is defined for \( 0 < X < \frac{r_2}{\alpha_2} = K_1 \). Since the next-iterate operator associated with \( Y = h(X) \) only changes sign at this root-curve, we have with (11),

\[ \mathcal{L}_h(X, Y) \begin{cases} < 0, & \text{if } (X, Y) \in \mathcal{R}_1, \\ > 0, & \text{if } (X, Y) \in \mathcal{R}_2, \end{cases} \]

so that (16) follows.

Substituting \( K_2 = \frac{r_2}{\alpha_1} \) and \( K_1 = \frac{r_2}{\alpha_2} \) in (28), we have \( B_2 = \frac{\alpha_2 r_1 r_2}{\alpha_1^2} > 0 \), and therefore, by (30), \( X = R_{k_1}(Y) = \frac{r_1}{\alpha_2} \left( 1 - \frac{Y}{K_2} \right) = k^{-1}(Y) \) and \( X = R_{k_2}(Y) = \frac{-\alpha_1 Y + 1}{\alpha_2} < 0 \). Thus, there is again a unique positive root-curve \( X = R_{k_1}(Y) = k^{-1}(Y) \) that is positive for \( 0 < Y < K_2 \) associated with the positive \( Y \) nullcline, \( Y = k(X) \). Hence, the next-iterate root operator associated with the positive \( Y \) nullcline only changes sign at the nullcline \( Y = k(X) \), and with (12), it follows that

\[ \mathcal{L}_k(X, Y) \begin{cases} < 0, & \text{if } (X, Y) \in \mathcal{R}_1, \\ > 0, & \text{if } (X, Y) \in \mathcal{R}_2, \end{cases} \]

and (17) follows. \( \Box \)

**A.3 Proof of Lemma 3.2**

**Proof.** First, recall that if \( C_{12} \cdot C_{21} > 0 \), then \( E^* \in \mathcal{E} \). Clearly, \( E^* \) is in the intersection of the sets. Let \( (\bar{X}, \bar{Y}) \in S_k \cap S_h \). Then, by Remark 2.7 \( F(\bar{X}, \bar{Y}) = X^* \) and \( G(\bar{X}, \bar{Y}) = Y^* \). That is,

\[ F(\bar{X}, \bar{Y}) - F(X^*, Y^*) = \frac{1 + r_1}{m_1(\bar{X}, \bar{Y}) m_1(X^*, Y^*)} (\bar{X} - X^* + \alpha_1 (\bar{Y} Y^* - X^* \bar{Y})) \]
\[ G(\bar{X}, \bar{Y}) - G(X^*, Y^*) = \frac{1 + r_2}{m_2(\bar{Y}, \bar{X}) m_2(Y^*, X^*)} (\bar{Y} - Y^* + \alpha_2 (X^* \bar{Y} - \bar{X} Y^*)) , \]

where \( m_i(u, v) = 1 + \frac{r_i}{K_i} u + \alpha_i v > 0 \), for \( i = 1, 2 \).

We use proof by contradiction to show that no point is also in \( (\bar{X}, \bar{Y}) \in \{(X, Y); 0 < X \leq X^*, 0 < Y \leq Y^*\} \setminus E^* \) or \( (\bar{X}, \bar{Y}) \in \{(X, Y); X \geq X^*, Y \geq Y^*\} \setminus E^* \). Since \( \bar{X} \leq X^* \) and
$\bar{Y} \leq Y^*$ or $X \geq X^*$ and $\bar{Y} \geq Y^*$, but $(\bar{X}, \bar{Y}) \neq E^*$, we have without loss of generality $\bar{X} \neq X^*$,

$$0 > (\bar{X} - X^*) = \alpha_1(X^*\bar{Y} - \bar{X}Y^*),$$
$$0 \geq (\bar{Y} - Y^*) = -\alpha_2(X^*\bar{Y} - \bar{X}Y^*),$$

yielding a contradiction.

\[\square\]

### A.4 Proof of Lemma 3.7

**Proof.** a) Assume that $(X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_3$. By (24),

$$a_2 = \alpha_1 K_1 (\alpha_1 K_2 (1 + r_2) - r_1 r_2) \geq \alpha_1 K_1 \left(\alpha_1 \frac{r_1}{\alpha_1} (1 + r_2) - r_1 r_2\right) = \alpha_1 K_1 r_1 > 0.$$  

We consider two sub-cases: a)(i) $X \geq K_1$ and a)(ii) $X < K_1$.

a)(i) Assume that $X \geq K_1$. By (24), $a_1(X)$ is linear in $X$, and since $C_{21} > 0$,

$$a_1'(X) = r_1 (r_2 + \alpha_1 K_2 (1 - \alpha_2 K_1 + r_2)) > r_1 (r_2 + \alpha_1 K_2) > 0$$

and therefore

$$a_1(X) \geq a_1(K_1) = \alpha_1 K_1 K_2 (1 + r_2 + r_1 (r_2 - \alpha_2 K_1)) > \alpha_1 K_1 K_2 (1 + r_2) > 0.$$  

Thus, $-\frac{a_1(X)}{a_2} < 0$. Also, $a_0(X) a_2 > 0$, and since the term under the radical in (25) is less than $a_1^2(X)$, we have $Y = r_{h_1}(X) < 0$ and $\bar{Y} = r_{h_2}(X) < 0$. Since the sign of the associated next-iterate operator can only change sign at a root-curve, $\mathcal{L}_h(X, Y)$ has the same sign for any $X \geq K_1$. Since,

$$\lim_{Y \to \infty} \mathcal{L}_h(K_1, Y) = \lim_{Y \to \infty} G(K_1, Y) - h(F(K_1, Y)) = \frac{1 + r_2}{r_2} K_2 - h(0) > K_2 - \frac{r_1}{\alpha_1} > 0,$$

$\mathcal{L}_h(X, Y) > 0$ for all $X \geq K_1$.

a)(ii) Assume that $X \in (0, K_1)$. Since, by (24), $a_2 > 0$ and $a_0(X) < 0$, by (25), $Y = r_{h_1}(X) < 0$ and $Y = r_{h_2}(X) > 0$, and so $S_h$ is uniquely determined for $X \in (0, K_1)$ by the root-curve $Y = r_{h_1}(X)$. Since there is no coexistence equilibrium, by Lemma 2.5, $Y = r_{h_1}(X)$ cannot intersect the nullcline $Y = h(X)$ for any $0 < X < K_1$, so that $Y = r_{h_1}(X)$ must lie either entirely above or entirely below $Y = h(X)$. Since $h(X) < h(K)$, for $0 < X < K_1$, by Lemma 3.1a, $\mathcal{L}_h(X, h(X)) > 0$. By (11), $\mathcal{L}_h(X, 0) < 0$. Thus, $\mathcal{L}_h(X, Y)$ must have already changed sign in $\mathcal{R}_1$, and so $Y = r_{h_1}(X)$ must lie below $Y = h(X)$. Thus, $\mathcal{L}_h(X, Y) > 0$, for all $0 < X < K_1$, such that $X \in \mathcal{R}_2 \cup \mathcal{R}_3$.

By a(i) and a(ii), $\mathcal{L}_h(X, Y) > 0$, for all $(X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_3$.

b) Assume that $(X, Y) \in \mathcal{R}_1 \cup \mathcal{R}_2$. The sign of $b_0(X)$, defined in (27), is the same as the sign of the factor

$$\tilde{b}_0 = (K_1(\alpha_2 (1 + r_1) X - r_2) - r_1 r_2 X) = X (\alpha_2 K_2 (1 + r_1) - r_1 r_2) - r_2 K_1,$$

a linear function of $X$. $\tilde{b}_0(0) = -r_2 K_1 < 0$, and since $C_{21} > 0$, $\tilde{b}_0 \left(\frac{r_2}{\alpha_2}\right) = \frac{r_1 r_2 K_2^2 (r_2 + 1) (\alpha_2 K_1 - r_2)}{\alpha_2} < 0$. Hence, $b_0(X) < 0$, for all $X \in \left[0, \frac{r_2}{\alpha_2}\right]$. By (27), $b_2 > 0$ so that by (29), $Y = r_{k_1}(X) > 0$ and
This implies that \( Y = r_{k_2}(X) < 0 \) for all \( X \in \left(0, \frac{\alpha_2}{r_{k_2}}\right) \). Hence, only one root-curve is positive for \( X \in \left(0, \frac{\alpha_2}{r_{k_2}}\right) \). By Lemma 3.1b), since \( h(X) < k(X) \), \( \mathcal{L}_k(X, k(X)) < 0 \) for all \( X \in \left(0, \frac{\alpha_2}{r_{k_2}}\right) \). Since \( k(X) \) is decreasing and \( F(X, Y) \) is increasing in \( X \),

\[
\mathcal{L}_k(X, 0) = -k(F(X, 0)) < -k(F(K_1, 0)) < -k(K_1) < 0.
\]

Therefore, the sign of the next-iterate operator associated with \( Y = k(X) \) did not change sign for \( X \in \left(0, \frac{\alpha_2}{r_{k_2}}\right) \) and so \( \mathcal{L}_k(X, 0) < 0 \), for all \( X \in \mathcal{R}_1 \cup \mathcal{R}_2 \).

A.5 Proof of Lemma 3.11

Proof. First consider \( a) \) and \( b) \). Since \( C_{12} < 0 \), \( K_2 > \frac{r_1}{\alpha_1} \), and so the sign of \( a_2 \) is given by the sign of

\[
\alpha_1 K_2 (1 + r_2) - r_1 r_2 > \alpha_1 \frac{r_1}{\alpha_1} (1 + r_2) - r_1 r_2 = r_1 > 0.
\]

Since \( a_2 > 0 \) and \( a_0(X) < 0 \), for all \( X \in (0, K_1) \), we have by (25) \( r_{h_2}(X) < 0 \) and \( r_{h_1}(X) > 0 \), for all \( X \in (0, K_1) \). Hence, the function \( Y = r_{h_1}(X) \) determines \( \mathcal{S}_h \) uniquely in the regions considered in \( a) \) and \( b) \).

\( a) \) Assume that \( (X, Y) \in \mathcal{R}_4 \cup \mathcal{R}_{3\alpha} \). By (11), \( \mathcal{L}_h(0, X) < 0 \) for all \( X \in (0, X^*) \) and by (18) and Lemma 3.1b), \( \mathcal{L}_h(X, h(X)) > 0 \) for all \( X \in (0, X^*) \). Therefore, the associated next-iterate operator, \( \mathcal{L}_h(X, Y) \) must already have changed sign and become positive below \( Y = h(X) \) when \( X \in (0, X^*) \). Thus, the unique positive root-curve, \( Y = r_{h_1}(X) \), must lie below the line \( Y = h(X) \) for all \( X \in (0, X^*) \). We conclude that \( \mathcal{L}_h(X, Y) > 0 \), for all \( (X, Y) \in \mathcal{R}_4 \cup \mathcal{R}_{3\alpha} \).

\( b) \) Assume that \( (X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_{12} \). By Lemma 2.5, the only points where \( Y = r_{h_1}(X) \) and the nullcline \( Y = h(X) \) intersect are the equilibrium points \( E_1 \) and \( E^* \). We again use (18), Lemma 3.1b), and (11) to conclude that \( \mathcal{L}_h(X, h(X)) < 0 \) for \( X^* < X < K_1 \). Since, by (11), \( \mathcal{L}_h(X, 0) < 0 \) for all \( X \in (X^*, K_1) \), we have by continuity that the next-iterate operator associated with \( Y = h(X) \) must change sign above the nullcline \( Y = h(X) \) for \( X \in (X^*, K_1) \). Thus, the root-curve \( Y = r_{h_1}(X) \) must lie above the nullcline \( Y = h(X) \) for \( X^* < X < K_1 \) and hence \( \mathcal{L}_h(X, Y) < 0 \) for all \( (X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_{12} \).

Next consider \( c) \) and \( d) \). Since \( C_{21} < 0 \), \( K_1 > \frac{r_2}{\alpha_2} \), and so

\[
B_2 = \alpha_2 K_2^2 \left( \alpha_2 K_1 (1 + r_1) - r_1 r_2 \right) > \alpha_2 K_2^2 r_2 > 0.
\]

Since \( B_2 > 0 \) and \( B_0(Y) < 0 \) for all \( Y \in (0, K_2) \), we have by (29) that \( R_{k_2}(Y) < 0 \) and \( R_{h_1}(Y) > 0 \) for all \( Y \in (0, K_2) \). Hence, for \( Y \in (0, K_2) \), the function \( X = R_{h_1}(Y) \) determines \( \mathcal{S}_h \) uniquely in the regions considered in \( c) \) and \( d) \).

\( c) \) Assume that \( (X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_{3\alpha} \). For \( Y \in (0, Y^*) \), \( X > X^* \), so that by (18) and Lemma 3.1b), \( \mathcal{L}_k(X, k(X)) > 0 \). Since, by (14), \( \mathcal{L}_k(0, Y) < 0 \), this implies that the sign of the next-iterate operator associated with \( Y = k(X) \) must have changed sign to the left of \( X = k^{-1}(Y) \), which in turn means that the root-curve \( X = R_{h_1}(Y) \) must be below the line \( Y = k(X) \) for \( Y \in (0, Y^*) \). Hence, \( \mathcal{L}_k(X, Y) > 0 \) for all \( (X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_{3\alpha} \).
d) Assume that \((X,Y) \in \mathcal{R}_4 \cup \mathcal{R}_{14}\). By Lemma 2.5, the only points where \(X = R_{h_1}(Y)\) and the nullcline \(Y = h(X)\) intersect at the equilibrium points \(E_2\) and \(E^*\). For \(Y \in (Y^*, K_2)\) and \(X \in (0, X^*)\) by (18) and Lemma 3.11, \(\mathcal{L}_k(X, k(X)) < 0\) for \(X \in (0, X^*)\). Since \(X = R_{h_1}(Y)\) uniquely determines \(S_k\) for \(Y \in (0, K_2)\) and \(\mathcal{L}_k(0, Y) < 0\) for \(Y \in (0, K_2)\), the next-iterate operator associated with \(Y = k(X)\) did not change sign to the left of \(X = k^{-1}(Y)\). Therefore, the next-iterate operator changes sign above the nullcline \(Y = k(X)\) (i.e., to the right of \(X = k^{-1}(X)\)). Hence, \(\mathcal{L}_k(X, Y) < 0\) for all \((X,Y) \in \mathcal{R}_4 \cup \mathcal{R}_{14}\).

\[\Box\]

### A.6 Proof of Lemma 3.13

**Proof.** The proof relies on the signs of the next-iterate operators indicated in the augmented phase portrait shown in Fig. 6a), based on Lemma 3.11. By Fig. 6a), \(\mathcal{R}_{14}\) has a gray ‘+’ symbol, so that \(\mathcal{L}_k(X, Y) < 0\) in that region. In \(\mathcal{R}_{12}\), the black ‘−’ symbol indicates that \(\mathcal{L}_h(X, Y) < 0\) in that region. An orbit in \(\mathcal{D}_1\) can only enter \(\mathcal{D}_2\) if there is a sub-region of \(\mathcal{D}_1\) with a black ‘+’ symbol and a gray ‘+’ symbol, as the orbit would have to jump over both nullclines. Since the sign can only change at root-curves and both root-curves cannot cross within \(\mathcal{D}_1\) by Lemma 3.2, it suffices to show that the root-curve associated with the nullcline \(Y = k(X)\) remains below the root-curve associated with the nullcline \(Y = h(X)\) in \(\mathcal{D}_1\). In the proof of Lemma 3.11d) and d), it was shown that \(S_k\) is determined uniquely by the root-curve \(X = R_{h_1}(Y)\) for \(Y \in (0, K_2)\). Also, \(B_2 > 0\), \(B_0(0) = -K_1 K_2^2 r_2 < 0\), and therefore \(X = R_{h_1}(Y)\) intersects the \(X\)-axis at a value \(X \in (0, \frac{a_1}{\alpha_1}]\) noting the gray ‘+’ symbols in region \(\mathcal{R}_2 \cup \mathcal{R}_3\).

In the proof of Lemma 3.11b) and b), it was shown that \(S_h\) is determined uniquely by the root-curve \(Y = r_{h_1}(X)\) for \(X \in (0, K_1)\). By (24), \(a_2 > 0\) and since \(a_0(0) = -K_1 K_2 r_1 < 0\), it follows by (25) that \(r_{h_1}(0) > 0\), and so \(Y = r_{h_1}(X)\) intersects the \(Y\)-axis at a value \(Y \in (0, \frac{a_1}{\alpha_1}]\), noting the black ‘+’ symbols in \(\mathcal{R}_4 \cup \mathcal{R}_{14}\). Hence, by Lemma 3.2, the root-curves do not intersect in \(\mathcal{D}_1\), \(X = R_{h_1}(Y)\) must remain to the right of (below) the root-curve \(Y = r_{h_1}(X)\). Hence, no sub-region of \(\mathcal{D}_1\) exists where both \(\mathcal{L}_h(X, Y)\) and \(\mathcal{L}_k(X, Y)\) are positive.

\[\Box\]

### A.7 Proof of Lemma 3.15

**Proof.** First consider a) and b). Since \(C_{12} > 0\), \(K_2 < \frac{r_1}{\alpha_1}\), and so the sign of \(A_0(Y)\) is given by the sign of

\[-r_1 r_2 Y + K_2(-r_1 + \alpha_1(1 + r_2)Y) = -r_2 Y(r_1 - \alpha_1 K_2) - K_2(r_1 - \alpha_1 Y)
\]

\[< -K_2(r_1 - \alpha_1 Y)\]

Thus, \(A_0(Y) < 0\) for all \(Y \in (0, \frac{a_1}{\alpha_1}]\). Since \(A_2 > 0\), we have by (20) that \(R_{h_2}(Y) < 0\) and \(R_{h_1}(Y) > 0\) for all \(Y \in (0, \frac{a_1}{\alpha_1}]\). Hence, the function \(X = R_{h_1}(Y)\) determines \(S_h\) uniquely in the regions considered in a) and b). Further note that for \(Y \in (0, \frac{a_1}{\alpha_1}]\), we have by (13),

\[\mathcal{L}_h(0, Y) = G(0, Y) - \frac{r_1}{\alpha_1} = \frac{(1 + r_2)Y}{1 + \frac{r_2}{K_2^2} Y} - \frac{r_1}{\alpha_1} = \frac{(1 + r_2 - \frac{r_1}{\alpha_1 K_2} r_2)Y - \frac{r_1}{\alpha_1}}{1 + \frac{r_2}{K_2^2} Y} < 0\]

because \(Y < \frac{a_1}{\alpha_1}\) and \(1 + r_2 - \frac{r_1}{\alpha_1 K_2} r_2 < 1\).

\[\Box\]
a) Assume that \((X,Y) \in \mathcal{R}_4 \cup \mathcal{R}_{14}\). By \([20]\) and Lemma \([3.1b]\), \(L_h(X, h(X)) < 0\) for all \(X \in (0, X^*)\), i.e., \(L_h(h^{-1}(Y), Y) < 0\) for all \(Y \in (Y^*, \frac{\alpha_1}{\alpha_2})\). Since by \([31]\), \(L_h(0, Y) < 0\). This implies that the next-iterate operator \(L_h(X, Y)\) did not change sign between the \(Y\)-axis and the nullcline \(Y = h(X)\) for \(Y \in (Y^*, \frac{\alpha_1}{\alpha_2})\). Therefore, the associated root-curve \(X = R_{h_1}(Y)\) must be on the right of \(X = h^{-1}(Y)\) for \(Y \in (Y^*, \frac{\alpha_1}{\alpha_2})\) and so \(L_h(X, Y) < 0\) for all \((X, Y) \in \mathcal{R}_4 \cup \mathcal{R}_{14}\).

b) Assume that \((X,Y) \in \mathcal{R}_2 \cup \mathcal{R}_{32}\). By Lemma \([2.5]\) the only points where \(X = R_{h_1}(Y)\) and the nullcline \(Y = h(X)\) intersect are the equilibrium points \(E_1\) and \(E^*\). We again use \([18]\) and Lemma \([3.1b]\) to conclude that \(L_h(h^{-1}(Y), Y) = L_h(X, h(X)) > 0\) for all \(X^* < X < K_1\), i.e., \(L_h(h^{-1}(Y), Y) > 0\) for \(0 < Y < Y^*\). Since, by \([31]\), \(L_h(0, Y) < 0\) for \(Y \in (0, Y^*) \subset \left(0, \frac{\alpha_1}{\alpha_2}\right)\), we have by continuity of \(L_h(X, Y)\) that the next-iterate operator associated with \(Y = h(X)\) must change sign between the \(Y\)-axis and the nullcline \(Y = h(X)\). Hence, the root-curve \(X = R_{h_1}(Y)\) must lie to the left of \(Y = h(X)\) for \(Y \in (0, Y^*)\). Hence, \(L_h(X, Y) > 0\) for all \((X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_{32}\).

Next consider \(c)\) and \(d)\). Since \(C_{21} > 0, K_1 < \frac{\alpha_2}{\alpha_1}\). By \([27]\), the sign of \(b_0(X)\) depends on a factor that is linear in \(X\), for \(X > 0\). Furthermore, \(b_0(0) < 0\) and

\[
b_0 \left( \frac{r_2}{\alpha_2} \right) = \frac{K_2^2 r_1 (\alpha_2 K_1 - r_2) r_2 (1 + r_2)}{\alpha_2} < 0.
\]

It follows that \(b_0(X) < 0\) for all \(X \in \left(0, \frac{\alpha_2}{\alpha_1}\right)\). Since \(b_2 > 0\), we have by \([29]\) that \(r_{k_2}(X) < 0\) and \(r_{k_1}(X) > 0\) for all \(X \in \left(0, \frac{\alpha_2}{\alpha_1}\right)\). Hence, the function \(Y = r_{k_1}(X)\) determines \(S_h\) uniquely in the regions considered in \(c)\) and \(d)\).

c) Assume that \((X,Y) \in \mathcal{R}_4 \cup \mathcal{R}_{34}\). For \(X \in (0, X^*), Y > Y^*, \) so that by \([18]\) and Lemma \([3.1b]\), \(L_k(X, k(X)) > 0\). By \([12]\), \(L_k(X, 0) = -k(F(X, 0))\). Since for \(0 < X \leq K_1\), we have \(0 < F(X, 0) \leq K_1\) and therefore also \(k(F(X, 0)) > 0\). For \(K_1 < X < \frac{\alpha_2}{\alpha_1}\), the direction field indicates that \(F(X, 0) < X < \frac{\alpha_2}{\alpha_1}\), implying that \(k(F(X, 0)) > 0\). Hence, for \(X \in \left(0, \frac{\alpha_2}{\alpha_1}\right)\), we have by \([12]\) that \(L_k(X, 0) < 0\). Since the next-iterate operator is continuous and \(L_k(X, k(X)) > 0\) but \(L_k(X, 0) < 0\), the sign of \(L_k(X,Y)\) must have changed sign below \(Y = k(X)\). This means in turn that the root-curve \(Y = r_{k_1}(X)\) must lie below the nullcline \(Y = k(X)\) for \(X \in (0, X^*)\). Hence, \(L_k(X,Y) > 0\), for all \((X, Y) \in \mathcal{R}_4 \cup \mathcal{R}_{34}\).

d) Assume that \((X,Y) \in \mathcal{R}_2 \cup \mathcal{R}_{12}\). By Lemma \([2.5]\) the only points where \(Y = r_{k_1}(X)\) and the nullcline, \(Y = k(X)\), intersect are the equilibrium points, \(E_2\) and \(E^*\). For \(X \in (X^*, K_1)\) and \(0 < Y < Y^*\), by \([18]\) and Lemma \([3.1b]\), \(L_k(X, k(X)) < 0\) for \(X \in (0, X^*)\). Since \(Y = r_{k_1}(X)\) uniquely determines \(S_k\), for \(X \in \left(0, \frac{\alpha_2}{\alpha_1}\right)\), and \(L_k(X, 0) < 0\) for \(X \in \left(0, \frac{\alpha_2}{\alpha_1}\right)\), we know that \(L_k(X,Y)\) did not change sign below \(Y = k(X)\). Therefore, \(L_k(X,Y)\) changes sign above the nullcline \(Y = k(X)\) and so \(L_k(X,Y) < 0\) for all \((X, Y) \in \mathcal{R}_2 \cup \mathcal{R}_{12}\).

\(\blacksquare\)
A.8 Proof of Lemma 3.17

Proof. The proof relies on the signs of the next-iterate operators included in the augmented phase portrait shown in Fig. 7a), based on Lemma 3.15.

If there is a point \((X_t, Y_t) \in \mathcal{D}_1\) such that \((X_{t+1}, Y_{t+1}) \in \mathcal{D}_2\), then there must be a ‘++’ region in \(\mathcal{D}_1\), since the orbit would have to jump across both nullclines in order to enter \(\mathcal{D}_2\). Thus, it suffices to show that there is no ‘++’ region in \(\mathcal{D}_1\). In the proof of Lemma 3.15 a) and b), we proved that \(S_k\) is determined by a unique positive root-curve \(X = R_{h_1}(Y)\) for all \(0 < Y < \frac{\alpha_1}{a_1}\). By (26), \(A_2 > 0\) and since \(A_0(0) = -K_1K_2r_1 < 0\), from (26), \(R_{h_1}(0) > 0\). Thus, \(X = R_{h_1}(Y)\) intersects the X-axis at a value \(X \in (0, K_1]\). This implies that every point to the left of \(X = R_{h_1}(Y)\) satisfies \(L_h(X, Y) < 0\), since there are black ‘–’ symbols in region \(R_4 \cup R_1\), noting also that by Lemma 2.5, \(X = R_{h_1}(Y)\) cannot intersect \(Y = h(X)\) except at \(E^*\) and/or \(E_1\). Thus, in order for a ‘++’ region to exist in \(\mathcal{D}_1\), the nonnegative root-curve associated with \(Y = k(X)\), namely \(Y = r_{k_1}(X)\) that uniquely determines \(S_k\) for \(0 < X < \frac{\alpha_1}{a_2}\) (see proof of Lemma 3.15 c) and d)) would have to be to the right of (below) \(X = R_{h_1}(Y)\) in \(\mathcal{D}_1\). However, \(b_0(0) < 0\), and since \(b_2 > 0\), it follows that \(r_{k_1}(0) > 0\), and so \(r_{k_1}(X)\) intersects the Y-axis at a value \(Y \in (0, K_2]\) due to the gray ‘+’ symbols in \(R_4 \cup R_3\). Thus, \(X = R_{h_1}(Y)\) is below \(Y = r_{k_1}(X)\), at least for some \(X \in (0, K_1]\). Since, by Lemma 3.2, the root-curves cannot intersect in \(\mathcal{D}_1\), \(Y = R_{h_1}(Y)\) must remain to the right of (below) the root-curve \(Y = r_{k_1}(X)\). Hence, no ‘++’ region can exist in \(\mathcal{D}_1\). \(\square\)

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