ANALYSIS OF A DISCRETE TWO-SPECIES COMPETITION MODEL

ANALYSIS OF A TWO-SPECIES DISCRETE COMPETITION MODEL ASSUMING A SINGLE-CYCLE MATURATION DELAY

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Abstract

We introduce and analyze a discrete-time, two-species competition model that requires one cycle before newborn cohort can contribute to the growth of the population. Our formulation admits all of the outcomes of the classical discrete Lotka-Volterra like competition model: both species die out; one species wins the competition independent of the initial conditions; there is a unique coexistence fixed point that is a saddle and the winning species depends on the initial conditions; or there is a unique coexistence fixed point that is globally asymptotically stable. It also admits two novel bistable regimes. In the first regime, one stable and one unstable interior fixed point coexist with a stable and unstable boundary fixed point. In the second regime, the two boundary fixed points are saddles and there are three interior fixed points; two are attractors and the one in between them is a saddle. Using monotone dynamical systems theory, we show that every forward orbit converges to some fixed point. In the general case, where the two species' parameters need not coincide, we derive sufficient conditions for extinction, exclusion, and unique coexistence. We also establish sufficient conditions for each of the novel bistable regimes to occur provided we know how many interior fixed points exist. In the symmetric case where certain ratios of the parameters of each species are identical, the first of the bistable regimes is ruled out and we obtain necessary and sufficient conditions for the second case. Finally, we illustrate each regime with phase portraits and bifurcation diagrams.

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Table of Contents

List of Figures

List of Tables

Chapter 1

Introduction and Motivation

Many species exhibit different survival probabilities between newborn and adult cohorts, even when no direct juvenile–adult competition occurs. An experimental study on the cardinalfish *Apogon notatus* [13] showed that females defended their breeding territories to guard newly spawned eggs from predators. Consequently, the eggs experienced higher survival probability than the adults. Likewise, an experimental study at Cape Crozier, Ross Island [1] showed that the adults of Adélie penguins suffered high mortality due to breeding, especially among younger adults where the annual survivorship is only 54.7%. In contrast, a study across six colonies at Cape Bird, Antarctica [9] found that 56.2% of Adélie eggs hatched successfully and 63.3% of hatched chicks survived to fledging. Similarly, [28] described that male three-spined stickleback constructed and defended nests, actively guarded eggs and fry, indicating a higher survival probability for newborns.

However, many discrete-time competition models do not account for such differences and incorporate adults and juveniles in a single stage or age class. For example, the two-species competition models introduced in [20, 21] model each species population as a single rational function that ignores the stage or age structure. It was shown in [7] that the Leslie-Gower discrete competition model only admits the same classical outcomes of the two species continuous Lotka-Volterra competition model as in [22]. Such simplifications can miss important dynamical behavior.

To address this issue, many stage-structured competition models have been studied (see e.g., [5, 6, 32]). For example, the juvenile-adult model in [6] separates each species into juvenile and adult stages and is given by a four-dimensional discrete-time competition system. Not only does it recover all the outcomes of [7], but it also reveals stable and unstable two-cycles. In [32], a three-stage, two-species competition model was introduced and shown to capture the same classical outcomes. When the survivorship functions take the Ricker form, it can exhibit a period doubling bifurcation and chaos. While these models capture richer dynamics, their high dimensionality makes global stability analysis more complicated.

Recently, [27] separates a single species population into mature and immature cohorts incorporating a reproduction delay, τ, to model age classes. It separates the model into an adult survival term and a juvenile survival term where the survival probability of the newborns to maturity involves $\tau + 1$ breeding cycles. The adult survivors and newborns formulation can be easily generalized to include more than one species. In this thesis, we extend that framework, assuming $\tau = 0$, to two competing species, assuming that it requires only one cycle after birth for newborns to become mature and contribute to the growth of the population. We obtain a planar competition model. We show that this model not only exhibits the classical outcomes, but also admits multiple interior attractors separated by a saddle, even though it is only two-dimensional. In order to study the global dynamics of the model, we employ tools from the theory of monotone dynamical systems (see

[3, 4, 8, 10, 15–19, 24, 30] and references therein). In particular, we show our model falls into the class of *competitive maps*, in which each species' population increases as its competitor's population decreases. To establish global convergence, we combine results in [25] and [8, 15, 16]. We carry out this analysis first in the general (asymmetric) case, deriving sufficient conditions for extinction, exclusion, and coexistence and we reveal two novel bistable regimes. Under the simplifying assumption of symmetry, (i.e., certain ratios of the parameters are identical for each species), we obtain a complete classification of the global dynamics.

1.1 Organization of the Thesis

The rest of this thesis is structured as follows:

- Chapter 2 introduces the preliminaries, including notation, definitions, and theorems on monotone dynamical systems that are used throughout the thesis.
- Chapter 3 develops the core results for the mature–immature two-species competition model in the general case, i.e., for arbitrary positive parameters. It is shown that there can be at most three interior fixed points and every forward orbit must converge to some fixed point. It also establishes sufficient conditions for global stability of the origin, for a unique interior fixed point to exist, and identifies the bistable regimes in which orbits converge either to a stable boundary fixed point or to a stable interior fixed point. In particular, whenever three interior fixed points exist, both boundary fixed points are unstable and the two stable interior fixed points are separated by the unstable saddle in the middle. This conclusion holds for both general and symmetric cases. However, the regime with one stable interior fixed point and one stable boundary fixed point occurs only in the general case.
- Chapter 4 restricts the discussion to the case where both species have identical parameters, which we call the symmetric case of the model. This simplification allows us to make stronger conclusions regarding global dynamics of the model and allows us to determine the basins of attraction in the bistable regimes.
- Chapter 5 presents numerical illustrations of all the qualitative regimes derived earlier, including schematic phase portraits for the symmetric and general cases. Bifurcation diagrams are presented that highlight the possible sequences of bifurcations that include transcritical bifurcations and a pitchfork bifurcation in the symmetric model and one or two saddle–node bifurcations in the general case.
- Chapter 6 summarizes the main results, discusses their implications for biology, and outlines future directions.

Through this, we aim to present a comprehensive analysis of the global dynamics of the planar two-species competition model with single-cycle maturation, thereby contributing to the broader literature on discrete competition models and provides a bridge between higher order stage and or age structured models and the classical planar competition models.

Chapter 2

Mathematical Background and Preliminaries

2.1 Notation

- $\mathbb{R}$ denotes the set of real numbers.
- $\mathbb{R}_+ = \{r \in \mathbb{R} : r \geqslant 0\}$ denotes the set of non-negative real numbers.
- $\mathbb{Z} = \{\dots, -2, -1, 0, 1, 2, \dots\}$ denotes the set of all integers.
- $\mathbb{N} = \{0, 1, 2, \dots\}$ denotes the set of nonnegative integers.
- $\mathbb{N}_+ = \{1, 2, 3, \dots\}$ denotes the set of positive integers.
- $\mathbb{R}^n$ is the n-dimensional real vector space.
- For a subset $A \subset \mathbb{R}^n$, $\mathrm{int}A$ denotes the interior of A. In particular, $\mathrm{int}\mathbb{R}^n_+ = \{\mathbf{x} \in \mathbb{R}^n : x_i > 0 \text{ for all } i\}$.
- Vectors in $\mathbb{R}^n$ are denoted in boldface; e.g., $\mathbf{x} \in \mathbb{R}^n$ for $n > 1$.
- $\mathbb{R}^n_+$ refers to the nonnegative orthant in $\mathbb{R}^n$, i.e., $\{\mathbf{x} = (x_1, \dots, x_n) \in \mathbb{R}^n \; : x_i \geqslant 0 \text{ for all } i\}$.
- $C^m(U)$ denotes the class of functions that are m-times continuously differentiable on domain U. In particular, if $\mathbf{T} \in C^m(U)$, that means $\mathbf{T}$ is an m-times continuously differentiable map from $U \subset \mathbb{R}^n$ into $\mathbb{R}^n$.
- For a smooth vector-valued map $\mathbf{T} : \Omega \subset \mathbb{R}^n \to \mathbb{R}^n$, $D\mathbf{T}(\mathbf{x})$ denotes the Jacobian matrix of $\mathbf{T}$ at the point $\mathbf{x}$.
- For a real-valued function $f : \mathbb{R} \to \mathbb{R}$, we write the first derivative as $f'(x)$ (or $\frac{d}{dx}f(x)$), the second derivative as $f''(x)$, and for higher-order derivatives we use the notation $f^{(n)}(x)$.

We use boldface letters for all vectors (e.g. $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n$) and vector valued functions (e.g. $\mathbf{T} : \Omega \to \mathbb{R}^n$). Scalars or parameters (e.g. t, α, β, f) are written in standard italic type. Unless otherwise stated, all norms and inner products are the usual Euclidean ones.

2.2 Standard Definitions in Discrete Dynamical Systems

The terminology presented here is standard in many texts on dynamical systems; see, for example, [11, 23, 31].

Let $\mathcal{X}$ be a metric space, and let $\Omega \subset \mathcal{X}$ be a subset. Consider a continuous map

$$\mathbf{T} : \Omega \to \Omega.$$

For an initial point $\mathbf{x}_0 \in \Omega$, define the iterative sequence

$$\mathbf{x}_{t+1} = \mathbf{T}(\mathbf{x}_t), \quad t \geqslant 0,$$

so that

$$\mathbf{x}_t = \mathbf{T}^t(\mathbf{x}_0), \quad t \geqslant 0.$$

i.e., $\mathbf{T}^t$ denotes the tth iterate of the map, $\mathbf{T}$.

Definition 2.2.1 (Spectral Radius)**.** For a square matrix A the spectral radius is

$$\rho(A) := \max\{\, |\lambda| : \lambda \text{ is an eigenvalue of } A\}.$$

Definition 2.2.2 (Forward Orbit)**.** For $\mathbf{z} \in \Omega$, we define its forward orbit by

$$\mathcal{O}^+(\mathbf{z}) := \{\mathbf{T}^t(\mathbf{z}) : t = 0, 1, 2, \dots\}.$$

Definition 2.2.3 (Forward-Invariant Set)**.** The subset $\Omega \subset \mathcal{X}$ is called forward invariant under the map $\mathbf{T} : \Omega \to \Omega$ if

$$\mathbf{T}(\Omega) \subset \Omega.$$

Definition 2.2.4 (Fixed Point)**.** A point $\mathbf{x}^* \in \Omega$ is a fixed point of $\mathbf{T}$ if

$$\mathbf{T}(\mathbf{x}^*) = \mathbf{x}^*.$$

Definition 2.2.5 (Periodic Point)**.** A point $\mathbf{x} \in \Omega$ is said to be periodic with period $p > 0$ if

$$\mathbf{T}^p(\mathbf{x}) = \mathbf{x},$$

and p is the smallest positive integer for which this holds. The set

$$\mathcal{O}_p(\mathbf{x}) := \{\mathbf{x}, \mathbf{T}(\mathbf{x}), \dots, \mathbf{T}^{p-1}(\mathbf{x})\}$$

is called the periodic orbit of $\mathbf{x}$, and p is referred to as the prime period of $\mathbf{x}$.

Definition 2.2.6 (Stability and Asymptotic Stability)**.** A fixed point $\mathbf{x}^*$ is called stable if, for every $\varepsilon > 0$, there exists $\delta > 0$ such that

$$\|\mathbf{x}_0 - \mathbf{x}^*\| < \delta \Longrightarrow \|\mathbf{x}_t - \mathbf{x}^*\| < \varepsilon \text{ for all } t \geqslant 0.$$

If in addition $\mathbf{x}_t \to \mathbf{x}^*$ as $t \to \infty$ whenever $\|\mathbf{x}_0 - \mathbf{x}^*\| < \delta$, then $\mathbf{x}^*$ is called asymptotically stable.

Definition 2.2.7 (Global Asymptotic Stability)**.** A fixed point $\mathbf{x}^*$ is globally asymptotically stable if it is asymptotically stable and all orbits in Ω converge to $\mathbf{x}^*$. Equivalently,

$$\lim_{t \to \infty} \mathbf{x}_t = \mathbf{x}^* \text{ for every } \mathbf{x}_0 \in \Omega.$$

Definition 2.2.8 (Basin of Attraction)**.** Let $\mathbf{x}^* \in \Omega$ be a fixed point of $\mathbf{T}$. The basin of attraction of $\mathbf{x}^*$ is

$$\mathcal{B}(\mathbf{x}^*) := \{\mathbf{x}_0 \in \Omega : \lim_{t\to\infty} \mathbf{T}^t(\mathbf{x}_0) = \mathbf{x}^*\}.$$

Definition 2.2.9 (ω-Limit Set)**.** For $\mathbf{x}_0 \in \Omega$, the ω-limit set of $\mathbf{x}_0$ is

$$\omega(\mathbf{x}_0) = \{\mathbf{y} \in \Omega : \text{there exists } t_k \to \infty \text{ with } \mathbf{x}_{t_k} \to \mathbf{y}\}.$$

Definition 2.2.10 (Hyperbolic Fixed Point, Stable Manifold)**.** If $\mathbf{x}^*$ is a hyperbolic fixed point of a smooth map $\mathbf{T}$ (meaning the Jacobian $D\mathbf{T}(\mathbf{x}^*)$ has no eigenvalues on the unit circle), then the stable manifold of $\mathbf{x}^*$ is

$$W^s(\mathbf{x}^*) = \{\mathbf{x} \in \Omega : \lim_{t\to\infty} \mathbf{T}^t(\mathbf{x}) = \mathbf{x}^*\}.$$

2.3 Cone-Induced Partial Orders

Definition 2.3.1 (Positive Cone [15])**.** A nonempty subset Y_+ of a Banach space Y is said to be a positive cone if it satisfies

(1) $Y_+ + Y_+ \subset Y_+$;

(2) $\mathbb{R}_+ \cdot Y_+ \subset Y_+$;

(3) $Y_+ \cap (-Y_+) = \{0\}$;

(4) $Y_+ \neq \{0\}$.

Here, Y_+ is viewed as the positive elements in Y: $\mathbf{y} \in Y_+ \iff \mathbf{y} \geqslant 0$.

Definition 2.3.2 (Cone-Induced Partial Order [15, 25])**.** Given a positive cone $Y_+ = K \subset \mathbb{R}^n$, we define a partial order $\leqslant_K$ on $\mathbb{R}^n$ by

$$\mathbf{x} \leqslant_K \mathbf{y} \iff \mathbf{y} - \mathbf{x} \in K.$$

We then write

$$\mathbf{x} <_K \mathbf{y} \quad \iff \quad \mathbf{x} \leqslant_K \mathbf{y} \text{ and } \mathbf{x} \neq \mathbf{y},$$

and

$$\mathbf{x} \ll_K \mathbf{y} \quad \iff \quad \mathbf{y} - \mathbf{x} \in \text{int}K.$$

If the cone K is taken to be the positive orthant, i.e.,

$$K = \mathbb{R}^n_+ = \{\mathbf{x} \in \mathbb{R}^n : x_i \geqslant 0 \text{ for } i = 1, \ldots, n\},$$

then we omit the subscript K in the above definition.

Definition 2.3.3 (Comparability [2, 15])**.** Let $(\mathbb{R}^n, \leqslant_K)$ be a partially ordered set induced by the cone K. Two points $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n$ are said to be comparable if either

$$\mathbf{x} \leqslant_K \mathbf{y} \quad \text{or} \quad \mathbf{y} \leqslant_K \mathbf{x}.$$

Otherwise, $\mathbf{x}$ and $\mathbf{y}$ are said to be incomparable.

Definition 2.3.4 (Order Intervals [2, 15]). For $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n$ with $\mathbf{x} \leqslant_K \mathbf{y}$, the closed order interval $[\mathbf{x}, \mathbf{y}]_K$ is defined by

$$[\mathbf{x}, \mathbf{y}]_K = \{\mathbf{z} \in \mathbb{R}^n : \mathbf{x} \leqslant_K \mathbf{z} \leqslant_K \mathbf{y}\}.$$

If $\mathbf{x} \ll_K \mathbf{y}$, the open order interval $[[\mathbf{x}, \mathbf{y}]]_K$ is defined by

$$[[\mathbf{x}, \mathbf{y}]]_K = \{\mathbf{z} \in \mathbb{R}^n : \mathbf{x} \ll_K \mathbf{z} \ll_K \mathbf{y}\}.$$

Definition 2.3.5 (Order-Convex Sets [2, 15]). A subset $\Omega \subset \mathbb{R}^n$ is order-convex (with respect to $\leqslant_K$) if for any $\mathbf{x}, \mathbf{y} \in \Omega$ and $\mathbf{x} \leqslant_K \mathbf{y}$, we have

$$[\mathbf{x}, \mathbf{y}]_K \subset \Omega.$$

2.4 Order-Preserving Maps

Let $\Omega \subset \mathbb{R}^n$ and let $\mathbf{T} : \Omega \to \Omega$ be continuous.

Definition 2.4.1 (Order-Preserving, Strictly, and Strongly Order-Preserving [15, 25]). We say $\mathbf{T}$ is:

- order-preserving if, for all $\mathbf{x}, \mathbf{y} \in \Omega$,

$$\mathbf{x} \leqslant_K \mathbf{y} \Longrightarrow \mathbf{T}(\mathbf{x}) \leqslant_K \mathbf{T}(\mathbf{y}),$$

- strictly order-preserving if, for all $\mathbf{x}, \mathbf{y} \in \Omega$,

$$\mathbf{x} <_K \mathbf{y} \Longrightarrow \mathbf{T}(\mathbf{x}) <_K \mathbf{T}(\mathbf{y}),$$

- strongly order-preserving if, for all $\mathbf{x}, \mathbf{y} \in \Omega$,

$$\mathbf{x} \ll_K \mathbf{y} \Longrightarrow \mathbf{T}(\mathbf{x}) \ll_K \mathbf{T}(\mathbf{y}).$$

2.5 Planar Competitive Maps

Consider the discrete-time dynamical system defined by

$$\mathbf{x}_{t+1} = \mathbf{T}(\mathbf{x}_t), \quad t = 0, 1, 2, \ldots,$$

where $\mathbf{x}_t \in \Omega \subset \mathbb{R}^n$ and $\mathbf{T} : \Omega \to \Omega$ a $C^1(\Omega)$ map. Let $\mathbf{x}_0 \in \Omega$ be the initial condition. Take any $\mathbf{x}, \mathbf{y} \in \Omega$ with $\mathbf{x} = (x_1, x_2)$ and $\mathbf{y} = (y_1, y_2)$. Consider the cone

$$K = \{(u, v) \in \mathbb{R}^2 : u \geqslant 0,\ v \leqslant 0\},$$

which induces the partial order

$$\mathbf{x} = (x_1, x_2) \leqslant_K \mathbf{y} = (y_1, y_2) \quad \Longleftrightarrow \quad (x_1 \leqslant y_1) \text{ and } (x_2 \geqslant y_2).$$

Accordingly, we define

$$\mathbf{x} <_K \mathbf{y} \quad \Longleftrightarrow \quad (x_1 \leqslant y_1,\ x_2 \geqslant y_2,\ \mathbf{x} \neq \mathbf{y}),$$

and

$$\mathbf{x} \ll_K \mathbf{y} \quad \Longleftrightarrow \quad (x_1 < y_1) \text{ and } (x_2 > y_2).$$

Definition 2.5.1 (Competitive, Strictly and Strongly Competitive Maps [15, 25]). Let $\Omega \subset \mathbb{R}^2$ and $\mathbf{T} : \Omega \to \Omega$ be continuous. We say $\mathbf{T}$ is:

1. Competitive if
$$\mathbf{x} \leqslant_K \mathbf{y} \Longrightarrow \mathbf{T}(\mathbf{x}) \leqslant_K \mathbf{T}(\mathbf{y}) \quad \text{for all } \mathbf{x}, \mathbf{y} \in \Omega,$$

2. Strictly Competitive if
$$\mathbf{x} <_K \mathbf{y} \Longrightarrow \mathbf{T}(\mathbf{x}) <_K \mathbf{T}(\mathbf{y}) \quad \text{for all } \mathbf{x}, \mathbf{y} \in \Omega,$$

3. Strongly Competitive if
$$\mathbf{x} <_K \mathbf{y} \Longrightarrow \mathbf{T}(\mathbf{x}) \ll_K \mathbf{T}(\mathbf{y}) \quad \text{for all } \mathbf{x}, \mathbf{y} \in \Omega.$$

Remark 2.5.1 ([4, Proposition 3.1]; [19, Proposition 2.1]). If $\mathbf{T}$ is differentiable, a sufficient condition for $\mathbf{T}$ to be strongly competitive is that, for every $\mathbf{x} \in \Omega$, the Jacobian matrix

$$D\mathbf{T}(\mathbf{x}) = \begin{bmatrix} \frac{\partial T_1}{\partial x_1}(\mathbf{x}) & \frac{\partial T_1}{\partial y_1}(\mathbf{x}) \\ \frac{\partial T_2}{\partial x_1}(\mathbf{x}) & \frac{\partial T_2}{\partial y_1}(\mathbf{x}) \end{bmatrix}$$

has the sign configuration
$$\begin{bmatrix} + & - \\ - & + \end{bmatrix},$$

i.e.,
$$\frac{\partial T_1}{\partial x_1}(\mathbf{x}) > 0, \quad \frac{\partial T_1}{\partial y_1}(\mathbf{x}) < 0, \quad \frac{\partial T_2}{\partial x_1}(\mathbf{x}) < 0, \quad \frac{\partial T_2}{\partial y_1}(\mathbf{x}) > 0.$$

Definition 2.5.2 (K-positive and Strongly K-positive Linear Maps [15, 25]). Let $F : \mathbb{R}^2 \to \mathbb{R}^2$ be a linear map and let $K \subset \mathbb{R}^2$ be a cone. We say that:

1. F is K-positive if
$$F(K) \subseteq K,$$
that is, for every $\mathbf{x} \in K$, we have $F(\mathbf{x}) \in K$.

2. F is strongly K-positive if
$$F(K \backslash \{0\}) \subset \operatorname{int} K,$$
that is, for every nonzero $\mathbf{x} \in K$, we have $F(\mathbf{x}) \in \operatorname{int} K$.

Lemma 2.5.1 ([25], page 5). *A 2×2 matrix M is called K-positive, if the diagonal entries are non-negative and off diagonal entries are non-positive.*

Definition 2.5.3 ([15, 25]). We say that $\mathbf{T} : \Omega \subset \mathbb{R}^2_+ \to \Omega$ satisfies condition $(O+)$ if for every $\mathbf{x} = (x_1, x_2), \mathbf{y} = (y_1, y_2) \in \Omega$,
$$\mathbf{T}(\mathbf{x}) \ll \mathbf{T}(\mathbf{y}) \quad \Longrightarrow \quad \mathbf{x} \leqslant \mathbf{y},$$

i.e., if
$$T_1(\mathbf{x}) < T_1(\mathbf{y}) \quad \text{and} \quad T_2(\mathbf{x}) < T_2(\mathbf{y}),$$

then
$$x_1 \leqslant y_1 \quad \text{and} \quad x_2 \leqslant y_2.$$

Lemma 2.5.2 ([25, Lemma 4.3]). *If $\mathbf{T} : \Omega \subset \mathbb{R}^2_+ \to \Omega$ is C^1 and:*

(a) *Ω contains order intervals and is $\leqslant_K$ convex.*

(b) $\det(D\mathbf{T}(\mathbf{x})) > 0$ *for* $\mathbf{x} \in \Omega$.

(c) *$D\mathbf{T}(\mathbf{x})$ is K-positive in Ω.*

(d) *$\mathbf{T}$ is injective.*

then $\mathbf{T}$ is competitive and condition (O+) holds.

Theorem 2.5.1 ([25, Theorem 4.2])**.** *Let $\mathbf{T} : \Omega \subset \mathbb{R}^2_+ \to \Omega$ be a competitive map satisfying condition (O+). Then for every $\mathbf{x}$ in Ω, the forward orbit $\{\mathbf{T}^t(\mathbf{x})\}_{t\geqslant 0}$ is eventually componentwise monotone. Moreover, if the orbit of $\mathbf{x}$ has compact closure in Ω, then it converges to a fixed point of $\mathbf{T}$.*

The following results originate from [8] and are presented here in the form given by [15]. They require the following hypothesis that they refer to as (G).

Hypothesis 2.5.1. *Let $\Omega = [\mathbf{a}, \mathbf{b}]_K = \{\mathbf{x} \in \mathbb{R}^2 : \mathbf{a} \leqslant_K \mathbf{x} \leqslant_K \mathbf{b}\}$ where $\mathbf{a}, \mathbf{b} \in \mathbb{R}^2$ and $\mathbf{a} <_K \mathbf{b}$. The map $\mathbf{T}\colon \Omega \subset \mathbb{R}^2 \to \Omega$ is order preserving and $\mathbf{T}(\Omega)$ has compact closure in Ω.*

Theorem 2.5.2 (Order Interval Trichotomy [8, Proposition 1]; [15, Theorem 5.1])**.** *Assume Hypothesis 2.5.1. Then at least one of the following holds:*

(a) *there exists a fixed point $\mathbf{c} \in \Omega$ such that $\mathbf{a} <_K \mathbf{c} <_K \mathbf{b}$*

(b) *there exists an entire orbit $\{\mathbf{x}_n\}_{n\in\mathbb{Z}} \subset \Omega$ with $\lim_{t\to-\infty} \mathbf{x}_t = \mathbf{a}$ and $\lim_{t\to+\infty} \mathbf{x}_t = \mathbf{b}$ that is nondecreasing in the K-order and strictly increasing if $\mathbf{T}$ is strictly order preserving.*

(c) *there exists an entire orbit $\{\mathbf{x}_t\}_{t\in\mathbb{Z}} \subset \Omega$ with $\lim_{t\to-\infty} \mathbf{x}_t = \mathbf{b}$ and $\lim_{t\to+\infty} \mathbf{x}_t = \mathbf{a}$ that is nonincreasing in the K-order and strictly decreasing if $\mathbf{T}$ is strictly order preserving.*

Corollary 2.5.1 ([8, Theorem 4]; [15, Corollary 5.2])**.** *Assume Hypothesis 2.5.1, and let $\mathbf{a}$ and $\mathbf{b}$ be stable fixed points of $\mathbf{T}$. Then there is a third fixed point in $\Omega = [\mathbf{a}, \mathbf{b}]_K$.*

Proposition 2.5.1 ([15, Proposition 5.3])**.** *Consider (a),(b),(c) in Theorem 2.5.2. Assume Hypothesis 2.5.1.*

(i) *If $\mathbf{a} \ll_K \mathbf{b}$, at most one of (b),(c) can hold.*

(ii) *If $\mathbf{T}$ is strongly order preserving, then exactly one of (a),(b),(c) can hold.*

2.6 Useful Definitions and Theorems

Theorem 2.6.1 (Bolzano–Poincare–Miranda (see e.g., [29]))**.** *Let*

$$I_n = \{\, x \in \mathbb{R}^n : |x_i| < q,\ 1 \leqslant i \leqslant n\},$$

and

$$G = (g_1, g_2, \ldots, g_n) : I_n \to \mathbb{R}^n$$

be a continuous mapping defined on the closure of I_n such that $G(x) \neq \mathbf{0}$ for all x on the boundary of I_n. Assume further that for each i,

$$g_i(x_1, \ldots, x_{i-1}, -q, x_{i+1}, \ldots, x_n) \geqslant 0 \quad \textit{and} \quad g_i(x_1, \ldots, x_{i-1}, +q, x_{i+1}, \ldots, x_n) \leqslant 0$$

on the respective boundary faces. Then there exists at least one point $x^* \in I_n$ *such that*

$$G(x^*) = \mathbf{0}.$$

Definition 2.6.1 (P-matrix, [14])**.** A real $n \times n$ matrix is called a P-matrix if every principal minor (i.e., the determinant of every principal submatrix) is positive.

Theorem 2.6.2 ([14, Theorem 4])**.** *Let* $\Omega \subset \mathbb{R}^n$ *be a rectangular region (open or closed) and* $\mathbf{T} : \Omega \to \mathbb{R}^n$ *be* C^1*. If* $D\mathbf{T}(\mathbf{x})$ *is a* P*-matrix for every* $\mathbf{x} \in \Omega$*, then* $\mathbf{T}$ *is injective on* Ω*.*

Chapter 3

The Two-Species Competition Model

3.1 The Model

We formulate a competition model between two species X_t and Y_t based on the formulation of a single species model introduced in [27]. For each species, we consider that the species at time $t+1$ consists of the individuals that were alive at time t and survive to time $t+1$ as well as individuals born at the beginning of the time period $(t, t+1)$ that survive until time $t+1$. Thus, the general form for a species Z at time $t+1$ is then

$$Z_{t+1} = s_t Z_t + \widetilde{s}_t g Z_t, \tag{3.1.1}$$

where the first term represents the survival of the individuals that were alive at time t, determined by the fraction $s_t \in [0, 1]$. The second term, $\widetilde{s}_t g Z_t$ represents the newborn individuals (gZ_t, $g > 0$) that survive until time $t+1$, determined by the newborn survival probability $\widetilde{s}_t \in [0, 1]$.

To include competition in the single species model, the general model construction aligns with the model derivation technique for single species introduced in [27] where they also allowed for incorporation of a delay in the reproduction terms.

We consider the following model of two-species competition. Here, the equations for X_t and Y_t are of the form of (3.1.1) and we assume that the adult survival probability, s_t, is subject to natural mortality, intra-specific competition, and inter-specific competition. We assume that immediately after time t, populations X_t, Y_t produce $r_1 X_t, r_2 Y_t$ newborns, where $r_1, r_2 > 0$ are the number of offspring per adult of species of X and Y, respectively. On the other hand, the newborn survival probability $\widetilde{s_t}$ is subject to natural mortality and intra-specific competition within the newborn cohort.

$$X_{t+1} = \frac{X_t}{1 + d_1 + C_{11} X_t + C_{12} Y_t} + \frac{r_1 X_t}{(1 + D_1) + C_1 r_1 X_t}, \tag{3.1.2a}$$

$$Y_{t+1} = \frac{Y_t}{1 + d_2 + C_{22} Y_t + C_{21} X_t} + \frac{r_2 Y_t}{(1 + D_2) + C_2 r_2 Y_t}. \tag{3.1.2b}$$

Here, the survival probability of the adults of species X is given by $s_t^{(X)} = \frac{1}{1+d_1+C_{11}X_t+C_{12}Y_t}$, where $d_1 > 0$ is the natural mortality coefficient of adults of species X, $C_{11} > 0$ is the intra-specific competition coefficient for individuals of adults, and $C_{12} > 0$ is the inter-specific competition coefficient for adults of species X due to competition with adults of species Y. A similar structure is obtained for adults of species Y, $s_t^{(Y)}$, with a respective description of the parameters. We also model the survival of the newborn cohort of species X as $\tilde{s}_t^{(X)} = \frac{1}{1+D_1+C_1 r_1 X_t}$, where $D_1 > 0$ is the natural mortality coefficient of the newborns of species X and $C_1 > 0$ measures the intra-specific competition among its newborn individuals. A similar expression holds for $\tilde{s}_t^{(Y)}$ with the corresponding parameters.

Next, we nondimensionalize system (3.1.2) by letting

$$X_t = \frac{x_t}{C_{11}},\ Y_t = \frac{y_t}{C_{22}},\ \alpha_1 = \frac{C_{12}}{C_{22}},\ \alpha_2 = \frac{C_{21}}{C_{11}},\ \mu_1 = \frac{C_1}{C_{11}},\ \mu_2 = \frac{C_2}{C_{22}},\ \delta_1 = \frac{1+D_1}{r_1},\ \delta_2 = \frac{1+D_2}{r_2}.$$

This yields

$$x_{t+1} = \frac{x_t}{1+d_1+x_t+\alpha_1 y_t} + \frac{x_t}{\delta_1+\mu_1 x_t}, \tag{3.1.3a}$$
$$y_{t+1} = \frac{y_t}{1+d_2+y_t+\alpha_2 x_t} + \frac{y_t}{\delta_2+\mu_2 y_t}, \tag{3.1.3b}$$

where

$$d_i, \alpha_i, \mu_i, \delta_i > 0 \quad \text{for} \quad i = 1, 2.$$

Let $\mathbf{z}_t = (x_t, y_t)$ and $\mathbf{f}(x,y) = (f_1(x,y), f_2(x,y))$ where

$$f_1(x,y) = \frac{1}{1+d_1+x+\alpha_1 y} + \frac{1}{\delta_1+\mu_1 x}, \quad f_2(x,y) = \frac{1}{1+d_2+y+\alpha_2 x} + \frac{1}{\delta_2+\mu_2 y}. \tag{3.1.4}$$

Define

$$\mathbf{T}(x,y) = (T_1(x,y), T_2(x,y)) = (x f_1(x,y), y f_2(x,y)), \tag{3.1.5}$$

so that $\mathbf{T} : \mathbb{R}_+^2 \to \mathbb{R}_+^2$ matches the right-hand sides of (3.1.3). We now introduce the symmetric case by letting

$$d_1 = d_2, \quad \delta_1 = \delta_2, \quad \mu_1 = \mu_2, \quad \alpha_1 = \alpha_2, \tag{3.1.6}$$

Next, we establish well-posedness of system (3.1.3).

3.2 Analysis of the two-species model

3.2.1 Well-Posedness

We first show that the model is well-posed, i.e, solutions with nonnegative initial conditions remain nonnegative and all solutions are bounded.

For any $\mathbf{z} = (x,y) \in \mathbb{R}_+^2$, let

$$\mathcal{O}^+(\mathbf{z}) := \{\mathbf{T}^t(\mathbf{z}) : t = 0, 1, 2, \dots\}.$$

Define

$$\mathcal{A} := \left[0, 1 + \frac{1}{\mu_1}\right] \times \left[0, 1 + \frac{1}{\mu_2}\right].$$

Lemma 3.2.1. *Consider* (3.1.5). *Then,* $\mathbf{T}(\mathbb{R}_+^2) \subseteq \mathcal{A}$ *and all solutions starting in* $\mathrm{int}\mathbb{R}_+^2$ *remain positive.*

Proof. First observe that every term in $\mathbf{T}$ (see (3.1.5)) is strictly positive, so any orbit starting in $\mathrm{int}\mathbb{R}^2_+$ remains positive. Next, for any $(x,y) \in \mathbb{R}^2_+$:

$$T_1(x,y) = \frac{x}{1+d_1+x+\alpha_1 y} + \frac{x}{\delta_1+\mu_1 x} \leqslant \frac{x}{1+d_1+x} + \frac{x}{\mu_1 x} \leqslant 1 + \frac{1}{\mu_1}.$$

A similar argument shows $0 \leqslant T_2(x,y) \leqslant 1 + \frac{1}{\mu_2}$. This implies

$$\mathbf{T}(\mathbb{R}^2_+) \subseteq \left[0, 1+\frac{1}{\mu_1}\right] \times \left[0, 1+\frac{1}{\mu_2}\right] = \mathcal{A}$$

Since $\mathcal{A}$ is compact and forward invariant under $\mathbf{T}$, every forward orbit enters $\mathcal{A}$ in at most one step and remains there, completing the proof. □

Remark 3.2.1. Any fixed point $\mathbf{x}^*$ of $\mathbf{T}$ must satisfy $\mathbf{x}^* = \mathbf{T}(\mathbf{x}^*) \in \mathbf{T}(\mathbb{R}^2_+) \subseteq \mathcal{A}$.

Having established that all fixed points lie in $\mathcal{A}$, we now show that $\mathbf{T}$ also admits forward invariant sets, including the coordinate axes, and under symmetry, the diagonal.

Lemma 3.2.2. *The following sets are forward invariant under* $\mathbf{T}$*:*

$$\{(x,0) : x \geqslant 0\}, \quad \{(0,y) : y \geqslant 0\}.$$

Moreover, if $\mathbf{T}$ *satisfies the symmetry assumption,* (3.1.6)*, then the diagonal* $\{(x,x) : x \geqslant 0\}$ *is also forward invariant under* $\mathbf{T}$*.*

Proof. For any $x \geqslant 0$, one has

$$\mathbf{T}(x,0) = (T_1(x,0),0) \in \{(x,0) : x \geqslant 0\}, \quad \mathbf{T}(0,x) = (0,T_2(0,x)) \in \{(0,y) : y \geqslant 0\}.$$

Finally, under the symmetry assumption (3.1.6), we have $T_1(x,x) = T_2(x,x)$. Thus,

$$\mathbf{T}(x,x) = (T_1(x,x), T_1(x,x)) \in \{(x,x) : x \geqslant 0\}.$$

□

3.2.2 Properties of Nullclines

Setting $T_1(x,y) = xf_1(x,y) = x$ and $T_2(x,y) = yf_2(x,y) = y$ in system (3.1.3), yields the nullclines,

$$x\text{-nullclines: } x = 0 \quad \text{or} \quad y = \ell_1(x) = \frac{1}{\alpha_1(\mu_1 x + \delta_1 - 1)} - \frac{x+d_1}{\alpha_1}. \tag{3.2.1a}$$

$$y\text{-nullclines: } y = 0 \quad \text{or} \quad x = \widehat{\ell}_2(y) = \frac{1}{\alpha_2(\mu_2 y + \delta_2 - 1)} - \frac{y+d_2}{\alpha_2}. \tag{3.2.1b}$$

Note that we express the nontrivial y-nullcline as a function of y rather than x here to emphasize that it has a horizontal asymptote. We will express it as a function of x later, as well.

Define the vertical asymptote of $y = \ell_1(x)$ as

$$x_{\text{asy}} := \frac{1-\delta_1}{\mu_1},$$

and the horizontal asymptote of $y = \widehat{\ell}_2(y)$ as

$$y_{\text{asy}} := \frac{1-\delta_2}{\mu_2}.$$

For every $x \neq x_{\text{asy}}$, a direct calculation shows

$$\lim_{x\to x_{\text{asy}}^-} \ell_1(x) = -\infty, \quad \lim_{x\to x_{\text{asy}}^+} \ell_1(x) = +\infty, \quad \lim_{x\to-\infty} \ell_1(x) = +\infty, \quad \lim_{x\to+\infty} \ell_1(x) = -\infty. \tag{3.2.2}$$

On each side of $x = x_{\text{asy}}$, $\ell_1(x)$ is C^2. The derivatives of $y = \ell_1(x)$ are

$$\ell_1'(x) = -\frac{\mu_1}{\alpha_1(\mu_1 x + \delta_1 - 1)^2} - \frac{1}{\alpha_1}, \tag{3.2.3}$$

$$\ell_1''(x) = \frac{2\mu_1^2}{\alpha_1(\mu_1 x + \delta_1 - 1)^3}. \tag{3.2.4}$$

This implies $\ell_1(x)$ is strictly decreasing on both $(-\infty, x_{\text{asy}})$ and (x_{asy}, ∞), concave on $(-\infty, x_{\text{asy}})$ and convex on (x_{asy}, ∞). By continuity and strict monotonicity, $\ell_1(x) : (-\infty, x_{\text{asy}}) \to \mathbb{R}$ is a bijection which implies $y = \ell_1(x)$ admits a continuous inverse. Clearly, if $x_{\text{asy}} < 0$, then the branch of $y = \ell_1(x)$ to the left of x_{asy} never enters the first quadrant. Even if $x_{\text{asy}} > 0$, since $0 < \delta_1 < 1$, it follows that

$$\ell_1(x) \leqslant \ell_1(0) = \frac{1}{\alpha_1(\delta_1 - 1)} - \frac{d_1}{\alpha_1} < 0, \quad \forall x \in (0, x_{\text{asy}}). \tag{3.2.5}$$

So the left branch never enters the first quadrant in all cases. By reflecting the graph of $\ell_1(x)$ with respect to $y = x$, one sees that $x = \widehat{\ell}_2(y)$ satisfies the corresponding properties. In particular,

$$\lim_{y\to y_{\text{asy}}^-} \widehat{\ell}_2(y) = -\infty, \quad \lim_{y\to y_{\text{asy}}^+} \widehat{\ell}_2(y) = +\infty, \quad \lim_{y\to-\infty} \widehat{\ell}_2(y) = +\infty, \quad \lim_{y\to+\infty} \widehat{\ell}_2(y) = -\infty. \tag{3.2.6}$$

Similarly, even if $y_{\text{asy}} > 0$,

$$\widehat{\ell}_2(y) \leqslant \widehat{\ell}_2(0) < 0, \quad \forall y \in (0, y_{\text{asy}}).$$

This implies the branch of $x = \widehat{\ell}_2(y)$ below $y = y_{\text{asy}}$ never enters the first quadrant, as well.

The properties of the branches of $y = \ell_1(x)$ and $x = \widehat{\ell}_2(y)$ that lie outside of the first quadrant are illustrated in Figure 3.1.

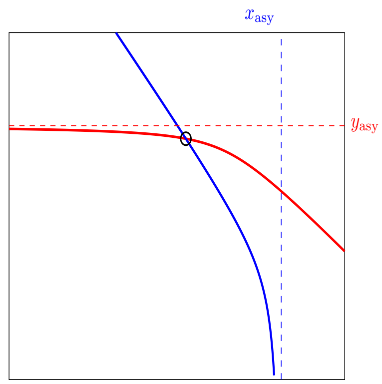


Figure 3.1: The blue dashed line is $x = x_{\text{asy}}$ and the red dashed line is $y = y_{\text{asy}}$. The blue solid curve is the branch of the x-nullcline to the left of x_{asy} and the red solid curve is the branch of the y-nullcline above $y = y_{\text{asy}}$. The intersection is labeled with a black circle.

With the above properties of the nullclines in mind, we show that the branch to the left of x_{asy} of $\ell_1(x)$ and the branch above the y_{asy} of $\widehat{\ell_2}(y)$ must intersect at least once outside of the first quadrant.

Lemma 3.2.3. *The two nontrivial nullclines*

$$y = \ell_1(x) \quad \textit{and} \quad x = \widehat{\ell_2}(y)$$

defined in (3.2.1)*, intersect at least once outside of the first quadrant.*

Proof. Define

$$h(x) := \widehat{\ell_2}(\ell_1(x)).$$

Note that

$$y = \ell_1(x) \quad \text{and} \quad x = \widehat{\ell_2}(y) \iff x = \widehat{\ell_2}(\ell_1(x)).$$

So an intersection of the nullclines is equivalent to a fixed point of $h(x)$. Since

$$\lim_{x \to -\infty} h(x) = -\infty \quad \text{and} \quad \lim_{x \to x_{\text{asy}}^-} h(x) = +\infty,$$

the continuity and Intermediate Value Theorem ensure at least one intersection $\hat{x} \in (-\infty, x_{\text{asy}})$ with $h(\hat{x}) = \hat{x}$. By (3.2.5), either $\hat{x} < 0$ or $\ell_1(\hat{x}) < 0$, so at least one intersection lies outside of the first quadrant. ☐

Remark 3.2.2. Any fixed point in $\text{int}\mathbb{R}^2_+$ of (3.1.3) must lie to the right of $x = x_{\text{asy}}$ and above $y = y_{\text{asy}}$.

Next, we find an alternative expression for the branch of the y-nullcline that is above $y = y_{\text{asy}}$. This will be used to determine a sufficient condition for a unique interior fixed point

$$y = \ell_2^+(x) := \frac{-\left[(\delta_2 - 1) + \mu_2(d_2 + \alpha_2 x)\right] + \sqrt{\left(\delta_2 - 1 - \mu_2(d_2 + \alpha_2 x)\right)^2 + 4\mu_2}}{2\mu_2}. \tag{3.2.7}$$

Define

$$\widetilde{S}(x) := \frac{-\mu_2(\alpha_2 x + d_2) + \delta_2 - 1}{\sqrt{\left[-\mu_2(\alpha_2 x + d_2) + \delta_2 - 1\right]^2 + 4\mu_2}} - 1. \tag{3.2.8}$$

A direct calculation yields

$$(\ell_2^+)'(x) = \frac{\alpha_2}{2}\widetilde{S}(x), \tag{3.2.9}$$

$$(\ell_2^+)''(x) = \frac{2\alpha_2^2\mu_2^2}{\Big((-\mu_2(\alpha_2 x + d_2) + \delta_2 - 1)^2 + 4\mu_2\Big)^{3/2}}. \tag{3.2.10}$$

3.2.3 Existence and Number of Fixed Points

In this subsection, we establish the existence conditions and number of fixed points in $\mathbb{R}_+^2$. In order to do this, we require the following lemma on the behavior of the functions f_i for $i = 1, 2$ in implicit form.

Lemma 3.2.4. *Consider* (3.1.4) *with* $(x, y) \in \mathbb{R}_+^2$. *Let* $i \in \{1, 2\}$.

(a) If $\delta_i \geqslant 1 + \frac{1}{d_i}$, *then* $f_i(x, y) \leqslant 1$ *for all* $(x, y) \in \mathbb{R}_+^2$ *with equality if and only if* $(x, y) = (0, 0)$.

(b) If $0 < \delta_i < 1 + \frac{1}{d_i}$, *then there exists at least one* $(x, y) \in \mathbb{R}_+^2$ *such that* $f_i(x, y) = 1$.

(c) If

$$0 < \delta_1 < 1 + \frac{1}{d_1 + \alpha_1\Big(1 + \frac{1}{\mu_2}\Big)} \quad \text{and} \quad 0 < \delta_2 < 1 + \frac{1}{d_2 + \alpha_2\Big(1 + \frac{1}{\mu_1}\Big)},$$

then there exists at least one point $(x^*, y^*) \in \operatorname{int}\mathcal{A}$ *such that*

$$f_1(x^*, y^*) = 1 = f_2(x^*, y^*).$$

Proof. (a) We first compute the partial derivatives of both $f_1(x, y)$ and $f_2(x, y)$:

$$\begin{aligned}
\frac{\partial f_1}{\partial x}(x, y) &= -\frac{1}{(1 + d_1 + x + \alpha_1 y)^2} - \frac{\mu_1}{(\delta_1 + \mu_1 x)^2}, \quad \frac{\partial f_1}{\partial y}(x, y) = -\frac{\alpha_1}{(1 + d_1 + x + \alpha_1 y)^2}, \\
\frac{\partial f_2}{\partial x}(x, y) &= -\frac{\alpha_2}{(1 + d_2 + y + \alpha_2 x)^2}, \quad \frac{\partial f_2}{\partial y}(x, y) = -\frac{1}{(1 + d_2 + y + \alpha_2 x)^2} - \frac{\mu_2}{(\delta_2 + \mu_2 y)^2}.
\end{aligned} \tag{3.2.11}$$

From (3.2.11), we see

$$\frac{\partial f_i}{\partial x}(x, y) < 0, \quad \frac{\partial f_i}{\partial y}(x, y) < 0 \quad \forall\, (x, y) \in \mathbb{R}_+^2,$$

so each f_i is strictly decreasing in both variables and each attains its maximum value at $(0, 0)$. A direct evaluation gives

$$f_i(0, 0) = \frac{1}{1 + d_i} + \frac{1}{\delta_i}.$$

If $\delta_i = 1 + 1/d_i$, then $f_i(0, 0) = 1$ and since each f_i is strictly decreasing,

$$f_i(x, y) < 1 \quad \forall\, (x, y) \in \mathbb{R}_+^2 \backslash \{(0, 0)\},$$

so $f_i(x,y) \leqslant 1$ everywhere with equality only at $(0,0)$. If instead, $\delta_i > 1 + 1/d_i$ then $f_i(0,0) < 1$ and monotonicity gives

$$f_i(x,y) \leqslant f_i(0,0) < 1, \quad \forall (x,y) \in \mathbb{R}^2_+.$$

(b) A direct calculation shows

$$f_i(0,0) > 1 \iff \delta_i < 1 + \frac{1}{d_i},$$

while

$$\lim_{x,y\to\infty} f_i(x,y) = 0 < 1.$$

Since $f_i(x,y)$ is continuous on $\mathbb{R}^2_+$, the Intermediate Value Theorem guarantees at least one $(x^*, y^*) \in \mathbb{R}^2_+$ with $f_i(x^*, y^*) = 1$.

(c) By (3.2.11), both f_1 and f_2 are strictly decreasing in each variable. Hence, on $x = 0$, $f_1(0,y)$ decreases for $y \in [0, 1 + 1/\mu_2]$ (so its minimum occurs at $y = 1 + 1/\mu_2$) and $f_2(0,y)$ decreases for $y \in [0, 1 + 1/\mu_1]$ (so its minimum occurs at $y = 1 + 1/\mu_1$). On $y = 0$, $f_1(x,0)$ decreases for $x \in [0, 1 + 1/\mu_1]$ (maximum at $x = 0$) and $f_2(x,0)$ decreases for $x \in [0, 1 + 1/\mu_2]$ (maximum at $x = 0$). Hence on $\mathcal{A}$, it suffices to check when

$$f_1\big(0, 1 + 1/\mu_2\big) > 1, \quad f_1\big(1 + 1/\mu_1, 0\big) < 1, \quad f_2\big(0, 1 + 1/\mu_1\big) > 1, \quad f_2\big(1 + 1/\mu_2, 0\big) < 1.$$

By calculations,

$$f_1(0, 1 + 1/\mu_2) = \frac{1}{1 + d_1 + \alpha_1\big(1 + \frac{1}{\mu_2}\big)} + \frac{1}{\delta_1} > 1 \iff \delta_1 < 1 + \frac{1}{d_1 + \alpha_1\big(1 + \frac{1}{\mu_2}\big)}.$$

and

$$f_1(1 + 1/\mu_1, 0) = \frac{1}{1 + d_1 + 1 + \frac{1}{\mu_1}} + \frac{1}{\delta_1 + \mu_1\big(1 + \frac{1}{\mu_1}\big)} < 1,$$

holds for all $\delta_1 > 0$ and $d_1 > 0$ and therefore adds no further restrictions, noting that the left-hand side of the inequality is a decreasing function of both d_1 and δ_1 and

$$\frac{1}{2 + \frac{1}{\mu_1}} + \frac{1}{\mu_1\big(1 + \frac{1}{\mu_1}\big)} = \frac{\mu_1^2 + 3\mu_1 + 1}{2\mu_1^2 + 3\mu_1 + 1} < 1.$$

Similarly for f_2,

$$f_2(0, 1 + 1/\mu_1) > 1 \iff \delta_2 < 1 + \frac{1}{d_2 + \alpha_2\big(1 + \frac{1}{\mu_1}\big)}.$$

By Theorem 2.6.1, there exists $(x^*, y^*) \in \mathrm{int}\mathcal{A}$ with

$$f_1(x^*, y^*) = 1 = f_2(x^*, y^*),$$

provided the conditions in *(c)* of the lemma hold. □

We now show how the nullclines determine when boundary or interior fixed points exist.

Proposition 3.2.1. *Consider system* (3.1.3)*. The following statements hold:*

(a) ***(Trivial Fixed Point)*** $\mathbf{E}_0 = (0,0)$ *always exists.*

(b) ***(Boundary Fixed Points)*** *A positive boundary fixed point* $\mathbf{E}_x = (\overline{x}, 0)$ *(respectively,* $\mathbf{E}_y = (0, \overline{y})$*) where* $\overline{x} > 0$ *(respectively,* $\overline{y} > 0$*) exists if and only if*

$$0 < \delta_1 < 1 + \frac{1}{d_1} \quad \left(\textit{respectively,} \quad 0 < \delta_2 < 1 + \frac{1}{d_2}\right),$$

where

$$\overline{x} := \frac{-\left(\mu_1 d_1 + \delta_1 - 1\right) + \sqrt{\left[\mu_1 d_1 - (\delta_1 - 1)\right]^2 + 4\mu_1}}{2\mu_1}, \tag{3.2.12}$$

and

$$\overline{y} := \frac{-\left(\mu_2 d_2 + \delta_2 - 1\right) + \sqrt{\left[\mu_2 d_2 - (\delta_2 - 1)\right]^2 + 4\mu_2}}{2\mu_2}. \tag{3.2.13}$$

Under the symmetry assumption (3.1.6), $\overline{x} = \overline{y}$ *where*

$$\overline{x} = \frac{-\left(\mu d + \delta - 1\right) + \sqrt{\left[\mu d - (\delta - 1)\right]^2 + 4\mu}}{2\mu}.$$

$\mathbf{E}_x$ *(respectively,* $\mathbf{E}_y$*) coalesces with* $\mathbf{E}_0$*, whenever* $\delta_1 = 1 + \frac{1}{d_1}$ *(respectively,* $\delta_2 = 1 + \frac{1}{d_2}$*).*

(c) ***(Interior Fixed Points)*** *A sufficient condition for at least one interior fixed point* $\mathbf{E}^*$ *to exist is*

$$0 < \delta_1 < 1 + \frac{1}{d_1 + \alpha_1\left(1 + \frac{1}{\mu_2}\right)} \quad \textit{and} \quad 0 < \delta_2 < 1 + \frac{1}{d_2 + \alpha_2\left(1 + \frac{1}{\mu_1}\right)}.$$

A necessary condition for at least one interior fixed point to exist is

$$\delta_1 < 1 + \frac{1}{d_1} \quad \textit{and} \quad \delta_2 < 1 + \frac{1}{d_2},$$

i.e., both nontrivial boundary fixed points exist.

Proof. a) It is obvious. *(b)* This follows from Lemma 3.2.4(b) and noting that when $x \equiv 0$ or $y \equiv 0$ then system (3.1.3) reduces to a special case of the single-species growth models considered in Theorem 4.5 of [26] where for the growth model it was proved at most one positive fixed point exists. *(c)* This follows immediately from Lemma 3.2.4(c). □

We now prove there are at most three intersections of the x- and y-nullclines with both components positive and hence, at most three interior fixed points.

Proposition 3.2.2. *System* (3.1.3) *admits at most three interior fixed points in* $\mathbb{R}^2_+$*. If* $\alpha_1\alpha_2 = 1$*, it admits at most two.*

Proof. Setting $f_i(x, y) = 1$, $i = 1, 2$ and simplifying, each nullcline can be expressed as a conic in

$\mathbb{R}^2$:

$$
\begin{aligned}
f_1(x,y) = 1 \quad &\Longleftrightarrow \quad Q_1(x,y) \;=\; \mu_1 x^2 + (d_1\mu_1 + \delta_1 - 1)x + \alpha_1(\delta_1 - 1)y \\
&\qquad\qquad + \; \alpha_1\mu_1\, xy + d_1\delta_1 - d_1 - 1 \;=\; 0, &(3.2.14)\\
f_2(x,y) = 1 \quad &\Longleftrightarrow \quad Q_2(x,y) \;=\; \mu_2 y^2 + (d_2\mu_2 + \delta_2 - 1)y + \alpha_2(\delta_2 - 1)x \\
&\qquad\qquad + \; \alpha_2\mu_2\, xy + d_2\delta_2 - d_2 - 1 \;=\; 0. &(3.2.15)
\end{aligned}
$$

Hence, any interior fixed point satisfies

$$Q_1(x,y) = 0 \quad \text{and} \quad Q_2(x,y) = 0.$$

A necessary condition for an interior fixed point to exist is that

$$Q(x,y) := f_1(x,y) - f_2(x,y) = Q_1(x,y) - Q_2(x,y) = 0.$$

Setting $Q(x,y) = 0$, we obtain

$$
\begin{aligned}
Q(x,y) = \mu_1 x^2 + (\alpha_1\mu_1 - \alpha_2\mu_2)xy - \mu_2 y^2 + \big(d_1\mu_1 + \delta_1 - 1 - \alpha_2(\delta_2 - 1)\big)x \\
+ \big(\alpha_1(\delta_1 - 1) - d_2\mu_2 - \delta_2 + 1\big)y + \big[d_1(\delta_1 - 1) + d_2(1 - \delta_2)\big] = 0.
\end{aligned} \tag{3.2.16}
$$

For every $x \neq x_{\text{asy}}$, $Q_1(x,y) = 0$ is equivalent to $y = \ell_1(x)$ so substituting $y = \ell_1(x)$ into $Q_2(x,y) = 0$ gives

$$\widetilde{Q}(x) = \eta_4 x^4 + \eta_3 x^3 + \eta_2 x^2 + \eta_1 x + \eta_0 = 0, \tag{3.2.17}$$

where η_j are provided in Appendix A.1. Thus, $\widetilde{Q}(x)$ has at most four real roots (at most three when $\alpha_1\alpha_2 = 1$, since then $\eta_4 = 0$). Each $(x^*, \ell_1(x^*))$ yields an intersection of the two nullclines. Hence $y = \ell_1(x)$ and $x = \widehat{\ell}_1(y)$ intersect at most four times (three times if $\alpha_1\alpha_2 = 1$) in $\mathbb{R}^2$ and at least one of those intersections always lies outside the first quadrant (Lemma 3.2.3). So, there are at most three intersections in $\mathbb{R}^2_+$ (two when $\alpha_1\alpha_2 = 1$), and hence at most three interior fixed points (two when $\alpha_1\alpha_2 = 1$). □

Remark 3.2.3. If there is a unique interior fixed point, we refer to it as $\mathbf{E}^*$. If there are two interior fixed points, we refer to them as $\mathbf{E}_1^*$ and $\mathbf{E}_2^*$. If there are three interior fixed points, we refer to them as $\mathbf{E}_1^*$, $\mathbf{E}_2^*$, and $\mathbf{E}_3^*$.

We now derive sufficient conditions for system (3.1.3) to admit a unique interior fixed point. To do so, we collect nullcline derivatives needed in Lemma 3.2.5.

Lemma 3.2.5. *Consider system* (3.1.3). *If*

$$\delta_1 < 1 + \frac{1}{d_1 + \alpha_1(1 + \frac{1}{\mu_2})}, \quad \delta_2 < 1 + \frac{1}{d_2 + \alpha_2(1 + \frac{1}{\mu_1})}, \quad \alpha_1\alpha_2 < 1 + \frac{\mu_1}{(\mu_1 + \delta_1 - 1)^2}, \tag{3.2.18}$$

then there exists a unique interior fixed point.

Proof. By Proposition 3.2.1(c), the first two conditions in (3.2.18) imply that there is at least one interior fixed point. We show the third condition implies that there is at most one interior fixed point.

Define $\tilde{h}(x) := \ell_1(x) - \ell_2^+(x)$. Since $\ell_1(x), \ell_2^+(x)$ (see (3.2.3)) are C^1 on $I = (x_{\text{asy}}, 1 + \frac{1}{\mu_1}]$,

$\tilde{h} \in C^1(I)$. Next, we find conditions so that

$$\ell_1'(x) < (\ell_2^+)'(x), \quad \forall\, x \in \left(x_{\text{asy}}, 1 + \frac{1}{\mu_1}\right]. \tag{3.2.19}$$

Then, $\tilde{h}(x)$ is strictly decreasing and hence has at most one root for $\tilde{h}(x) = 0$. In order to show this, it suffices to determine an upper bound for $\ell_1'(x)$ and a lower bound for $(\ell_2^+)'(x)$. By (3.2.4), $\ell_1''(x) > 0$ for all $x > x_{\text{asy}}$. Therefore, the maximum of $\ell_1'(x)$ occurs at $x = 1 + \frac{1}{\mu_1}$. A direct computation shows

$$\ell_1'(x) \leqslant -\frac{1}{\alpha_1}\left(1 + \frac{\mu_1}{(\mu_1 + \delta_1 - 1)^2}\right), \quad \forall x \in \left(x_{\text{asy}}, 1 + \frac{1}{\mu_1}\right]. \tag{3.2.20}$$

Similarly by (3.2.10), $(\ell_2^+)''(x) > 0$ for any $x \in \mathbb{R}$. Therefore, the minimum of $(\ell_2^+)'(x)$ occurs as x approaches the left end point of I. By (3.2.8), $\widetilde{S}(x) \in (-2, 0)$ for every $x \in \mathbb{R}$. It follows that

$$(\ell_2^+)'(x) \in (-\alpha_2, 0), \quad \forall\, x \geqslant x_{\text{asy}}. \tag{3.2.21}$$

Combining (3.2.20) and (3.2.21), a sufficient condition for (3.2.19) to hold is

$$-\frac{1}{\alpha_1}\left(1 + \frac{\mu_1}{(\mu_1 + \delta_1 - 1)^2}\right) < -\alpha_2.$$

This inequality is equivalent to

$$0 < \alpha_1\alpha_2 < 1 + \frac{\mu_1}{(\mu_1 + \delta_1 - 1)^2}. \tag{3.2.22}$$

Therefore, under (3.2.22), $\tilde{h}'(x)$ satisfies

$$\tilde{h}'(x) = \ell_1'(x) - (\ell_2^+)'(x) < 0, \quad \forall\, x \in \left(x_{\text{asy}}, 1 + \frac{1}{\mu_1}\right].$$

This implies $\tilde{h}(x)$ has at most one root in $\left(x_{\text{asy}}, 1 + \frac{1}{\mu_1}\right]$. This completes the proof. $\square$

The sufficient conditions for multiple interior fixed points rely on the local stability of $\mathbf{E}_x$ and $\mathbf{E}_y$ and the order perseveration property of $\mathbf{T}$, and hence will be discussed later.

3.2.4 All Forward Orbits Converge Monotonically to a Fixed Point

In this section, we show that every forward orbit is componentwise monotone and converges to a fixed point using the theory of monotone dynamical systems. First we compute the Jacobian matrix of system (3.1.3) to obtain.

$$D\mathbf{T}(x,y)$$
$$= \begin{bmatrix} \frac{1}{(1+d_1+x+\alpha_1 y)} - \frac{\alpha_1 x}{(1+d_1+x+\alpha_1 y)^2} + \frac{1}{\delta_1+\mu_1 x} - \frac{x}{(\delta_1+\mu_1 x)^2} & -\frac{\alpha_1 x}{(1+d_1+x+\alpha_1 y)^2} \\ -\frac{\alpha_2 y}{(1+d_2+y+\alpha_2 x)^2} & \frac{1}{(1+d_2+y+\alpha_2 x)} - \frac{\alpha_2 y}{(1+d_2+y+\alpha_2 x)^2} + \frac{1}{\delta_2+\mu_2 y} - \frac{y}{(\delta_2+\mu_2 y)^2} \end{bmatrix} \tag{3.2.23}$$
$$= \begin{bmatrix} \frac{\delta_1}{(\delta_1+\mu_1 x)^2} + \frac{1+d_1+\alpha_1 y}{(1+d_1+x+\alpha_1 y)^2} & -\frac{\alpha_1 x}{(1+d_1+x+\alpha_1 y)^2} \\ -\frac{\alpha_2 y}{(1+d_2+y+\alpha_2 x)^2} & \frac{\delta_2}{(\delta_2+\mu_2 y)^2} + \frac{1+d_2+\alpha_2 x}{(1+d_2+y+\alpha_2 x)^2} \end{bmatrix}.$$

We note for any $(x, y) \in \mathbb{R}^2_+$ and positive parameters, that

$$\frac{\partial T_1}{\partial x} > 0, \quad \frac{\partial T_1}{\partial y} \leqslant 0, \quad \frac{\partial T_2}{\partial x} \leqslant 0, \quad \frac{\partial T_2}{\partial y} > 0.$$

where $\frac{\partial T_1}{\partial y} = 0$ if and only if $x = 0$ and $\frac{\partial T_2}{\partial x} = 0$ if and only if $y = 0$. Hence, for any $x, y \geqslant 0$, $D\mathbf{T}(x, y)$ has the sign pattern

$$D\mathbf{T}(x,y) = \begin{bmatrix} > 0 & \leqslant 0 \\ \leqslant 0 & > 0 \end{bmatrix}. \tag{3.2.24}$$

Remark 3.2.4. Each T_i is rational with positive denominator for $(x, y) \in \mathbb{R}^2_+$. Hence, $\mathbf{T} \in C^1(\mathbb{R}^2_+)$.

Define

$$K := \{(u, v) : u \geqslant 0, v \leqslant 0\} \subset \mathbb{R}^2.$$

The partial ordering $\leqslant_K$ on $\mathbb{R}^2_+$ becomes

$$(x_1, y_1) \leqslant_K (x_2, y_2) \iff x_1 \leqslant x_2, \quad y_1 \geqslant y_2.$$

Remark 3.2.5. By Lemma 2.5.1 and the sign pattern (3.2.24), $D\mathbf{T}(x, y)$ is K-positive for every $(x, y) \in \mathbb{R}^2_+$.

We note a geometric fact about the K–order that will be used in the proof that system (3.1.3) is a competitive dynamical system.

Lemma 3.2.6. *Any closed rectangle $\Omega = [A, B] \times [C, D] \subset \mathbb{R}^2_+$ contains order intervals and is $\leqslant_K$–convex.*

Proof. Consider $\Omega = [A, B] \times [C, D] \subset \mathbb{R}^2_+$. Take any $\mathbf{u}, \mathbf{v}, \mathbf{z} \in \Omega$ with $\mathbf{u} \leqslant_K \mathbf{z} \leqslant_K \mathbf{v}$. It follows from the definition that

$$A \leqslant u_1 \leqslant z_1 \leqslant v_1 \leqslant B, \quad D \geqslant u_2 \geqslant z_2 \geqslant v_2 \geqslant C.$$

Thus, it is clear that $\mathbf{z} \in \Omega$ for any $\mathbf{z} \in [\mathbf{u}, \mathbf{v}]_K$. □

Lemma 3.2.7. *Consider* (3.1.5). $\mathbf{T}$ *is competitive on* $\mathbb{R}^2_+$ *and strongly competitive (strongly K-order preserving) on* $\text{int}\mathbb{R}^2_+$.

Proof. Since T_1 is non-decreasing in x and non-increasing in y, while T_2 is non-increasing in x and non-decreasing in y, for any $(x_1, y_1), (x_2, y_2) \in \mathbb{R}^2_+$ with $x_1 \leqslant x_2, y_1 \geqslant y_2$, we have

$$\begin{cases} T_1(x_1, y_1) \leqslant T_1(x_2, y_2) \\ T_2(x_1, y_1) \geqslant T_2(x_2, y_2) \end{cases},$$

with equality in both lines if and only if $(x_1, y_1) = (x_2, y_2)$. Therefore,

$$(x_1, y_1) \leqslant_K (x_2, y_2) \implies (T_1(x_1, y_1), T_2(x_1, y_1)) \leqslant_K (T_1(x_2, y_2), T_2(x_2, y_2)),$$

and so $\mathbf{T}$ is K-order preserving, and therefore competitive on $\mathbb{R}^2_+$ by Definition 2.5.1. Moreover, by (3.1.5), the off-diagonal derivatives are strict whenever $x, y > 0$. Remark 2.5.1 then yields that $\mathbf{T}$ is strongly K-order preserving (i.e., strongly competitive) on $\text{int}\mathbb{R}^2_+$. □

We next verify that $\mathbf{T}$ has a positive Jacobian determinant everywhere and use a P-matrix criterion to deduce global injectivity.

Lemma 3.2.8. *Consider* (3.1.5). $\mathbf{T}$ *is orientation-preserving on* $\mathbb{R}^2_+$.

Proof. It is straightforward to show that for any $(x, y) \in \mathbb{R}^2_+$,

$$\det(D\mathbf{T}(x, y)) = \frac{\partial T_1}{\partial x}\frac{\partial T_2}{\partial y} - \frac{\partial T_1}{\partial y}\frac{\partial T_2}{\partial x} > 0.$$

After simplification, one can see that the determinant $\det(D\mathbf{T})$ is always positive, since

$$\begin{aligned}
\det(D\mathbf{T}(x, y)) &= \left(\frac{\delta_1}{(\delta_1 + \mu_1 x)^2} + \frac{1 + d_1 + \alpha_1 y}{(1 + d_1 + x + \alpha_1 y)^2}\right)\left(\frac{\delta_2}{(\delta_2 + \mu_2 y)^2} + \frac{1 + d_2 + \alpha_2 x}{(1 + d_2 + y + \alpha_2 x)^2}\right) \\
&\quad - \frac{\alpha_1\alpha_2 xy}{(1 + d_1 + x + \alpha_1 y)^2(1 + d_2 + y + \alpha_2 x)^2}, \\
&= \frac{\delta_1\delta_2}{(\delta_1 + \mu_1 x)^2(\delta_2 + \mu_2 y)^2} + \frac{\delta_1(1 + d_2 + \alpha_2 x)}{(\delta_1 + \mu_1 x)^2(1 + d_2 + y + \alpha_2 x)^2} \\
&\quad + \frac{\delta_2(1 + d_1 + \alpha_1 y)}{(\delta_2 + \mu_2 y)^2(1 + d_1 + x + \alpha_1 y)^2} + \frac{(1 + d_1 + \alpha_1 y)(1 + d_2 + \alpha_2 x) - \alpha_1\alpha_2 xy}{(1 + d_1 + x + \alpha_1 y)^2(1 + d_2 + y + \alpha_2 x)^2}, \\
&= \frac{\delta_1\delta_2}{(\delta_1 + \mu_1 x)^2(\delta_2 + \mu_2 y)^2} + \frac{\delta_1(1 + d_2 + \alpha_2 x)}{(\delta_1 + \mu_1 x)^2(1 + d_2 + y + \alpha_2 x)^2} \\
&\quad + \frac{\delta_2(1 + d_1 + \alpha_1 y)}{(\delta_2 + \mu_2 y)^2(1 + d_1 + x + \alpha_1 y)^2} + \frac{(1 + d_1)(1 + d_2) + (1 + d_1)\alpha_2 x + (1 + d_2)\alpha_1 y}{(1 + d_1 + x + \alpha_1 y)^2(1 + d_2 + y + \alpha_2 x)^2}, \\
&> 0.
\end{aligned}$$

Hence, $\mathbf{T}$ is orientation preserving on $\mathbb{R}^2_+$. □

Having shown $\det(D\mathbf{T}) > 0$ everywhere, we now use Definition 2.6.1 of a P-matrix and apply Theorem 2.6.2 to conclude global injectivity of $\mathbf{T}$.

Lemma 3.2.9. *Consider* (3.1.5). *The Jacobian* $D\mathbf{T}(x, y)$ *is a* P*-matrix on* $\mathbb{R}^2_+$ *and* $\mathbf{T}$ *is globally injective on* $\mathbb{R}^2_+$.

Proof. Since for any $(x, y) \in \mathbb{R}^2_+$,

$$\frac{\partial T_1}{\partial x}(x, y) > 0, \quad \frac{\partial T_2}{\partial y}(x, y) > 0 \quad \text{(see sign pattern (3.2.24))},$$

and

$$\det D\mathbf{T}(x, y) > 0 \quad \text{(Lemma 3.2.8)},$$

both 1×1 principal minors and the 2×2 principal minor of $D\mathbf{T}$ are strictly positive. Hence $D\mathbf{T}(x, y)$ is a P-matrix on $\mathbb{R}^2_+$. Applying Theorem 2.6.2 with $\Omega = \mathbb{R}^2_+$ and using the differentiability of $\mathbf{T}$ from Remark 3.2.4, we conclude $\mathbf{T}$ is globally injective on $\mathbb{R}^2_+$. ☐

Remark 3.2.6. The conclusion that $\mathbf{T}$ is injective on $\mathbb{R}^2_+$ can also be proven by Theorem 4.1 [30] that states that if $\mathbf{T}$ is competitive and locally invertible in the first quadrant, then $\mathbf{T}$ is globally injective on $\mathbb{R}^2_+$.

We next verify that $\mathbf{T}$ satisfies the four hypotheses of Lemma 2.5.2 (and hence condition $(O+)$ of Definition 2.5.3).

Lemma 3.2.10. $\mathbf{T}$ *satisfies condition $(O+)$ defined in Definition 2.5.3.*

Proof. We show that all four conditions (a)-(d) of Lemma 2.5.2 hold for $\mathbf{T}$ on $\mathbb{R}^2_+$. (a) This follows from Lemma 3.2.6. (b) This follows from Lemma 3.2.8. (c) This follows from Remark 3.2.5.(d) This follows from Lemma 3.2.9. Thus, all assumptions of Lemma 2.5.2 are satisfied, and the claim follows. ☐

Since $\mathbf{T}$ is competitive and $(O+)$ holds, Theorem 2.5.1 applies.

Theorem 3.2.1. *Consider system* (3.1.3). *For every $(x, y) \in \mathbb{R}^2_+$, the forward orbit $\{\mathbf{T}^t(x, y)\}_{t \geqslant 0}$ converges to a fixed point of* $\mathbf{T}$.

Proof. By Lemma 3.2.7, $\mathbf{T}$ is competitive. By Lemma 3.2.10, condition $(O+)$ is satisfied. By Lemma 3.2.1, every forward orbit eventually enters the compact absorbing rectangle $\mathcal{A}$, and hence has compact closure in $\mathbb{R}^2_+$. Therefore, all the hypotheses of Theorem 2.5.1 are satisfied. It follows that each orbit is eventually componentwise monotone and converges to a fixed point of $\mathbf{T}$. ☐

3.2.5 Stability and Global Dynamics

In order to determine the relative positions of the interior fixed points with respect to each other and the boundary fixed points and determine their stability and the global dynamics of system (3.1.3), we require the following results.

First we determine the relative positions of the interior fixed points with respect to the boundary fixed points.

Lemma 3.2.11. *Consider system* (3.1.3). *Let $\mathbf{E}^*_j = (x^*_j, y^*_j)$ be any interior fixed point of $\mathbf{T}$. Then*

$$\mathbf{E}_y \ll_K \mathbf{E}^*_j \ll_K \mathbf{E}_x.$$

Proof. By Proposition 3.2.1, the interior fixed point $\mathbf{E}^*_j$ can only exist if boundary fixed points $\mathbf{E}_x$ and $\mathbf{E}_y$ also exist. On the nonnegative x-axis, $f_1(x, 0) = 1$ determines a unique point $\overline{x} > 0$. For each $x > 0$, the strictly decreasing function $f_1(x, y) = 1$ has exactly one root given by $y = \ell_1(x) > 0$. Assume for contradiction that $x^*_j \geqslant \overline{x}$, then we obtain

$$f_1(x^*_j, 0) \leqslant f_1(\overline{x}, 0) = 1,$$

so the unique y with $f_1(x^*_j, y) = 1$ must satisfy $y \leqslant 0$, contradicting $y^*_j > 0$. Hence $0 < x^*_j < \overline{x}$. Similarly, assuming $y^*_j \geqslant \overline{y} > 0$ leads to $x^* < 0$ which is a contradiction. Thus, every interior fixed point must satisfy

$$0 < x^*_j < \overline{x}, \quad 0 < y^*_j < \overline{y}.$$

Equivalently,

$$\mathbf{E}_y \ll_K \mathbf{E}_j^* \ll_K \mathbf{E}_x.$$

□

To show that if there are two unstable fixed points that are order related by $\ll_K$ then there is a third fixed point in between, we require the following results.

Lemma 3.2.12. *Let $\mathbf{E}_i \neq \mathbf{E}_j$ be two fixed points of $\mathbf{T}$ with $\mathbf{E}_i <_K \mathbf{E}_j$, and let*

$$\mathcal{A}_1 := [\mathbf{E}_i, \mathbf{E}_j]_K = \{\mathbf{z} \in \mathbb{R}_+^2 : \mathbf{E}_i \leqslant_K \mathbf{z} \leqslant_K \mathbf{E}_j\}.$$

Then $\mathbf{T}(\mathcal{A}_1) \subset \mathcal{A}_1$ and $\mathbf{T}(\mathcal{A}_1)$ has compact closure in $\mathcal{A}_1$.

Proof. By Lemma 3.2.7, $\mathbf{T}$ is order preserving with respect to $\leqslant_K$ in $\mathbb{R}_+^2$. For any $\mathbf{z} \in [\mathbf{E}_i, \mathbf{E}_j]_K$, we have

$$\mathbf{E}_i \leqslant_K \mathbf{z} \leqslant_K \mathbf{E}_j \implies \mathbf{T}(\mathbf{E}_i) \leqslant_K \mathbf{T}(\mathbf{z}) \leqslant_K \mathbf{T}(\mathbf{E}_j).$$

Since $\mathbf{T}(\mathbf{E}_i) = \mathbf{E}_i$ and $\mathbf{T}(\mathbf{E}_j) = \mathbf{E}_j$, it follows that

$$\mathbf{E}_i \leqslant_K \mathbf{T}(\mathbf{z}) \leqslant \mathbf{E}_j \implies \mathbf{T}(\mathbf{z}) \in \mathcal{A}_1.$$

Hence, $\mathbf{T}(\mathcal{A}_1) \subset \mathcal{A}_1$. Since $\mathcal{A}_1 \subset \mathbb{R}_+^2$ is compact and $\mathbf{T}$ is continuous, $\mathbf{T}(\mathcal{A}_1)$ has compact closure in $\mathcal{A}_1$. □

Therefore, Lemma 3.2.12 shows that Hypothesis 2.5.1 of Theorem 2.5.2 is satisfied. We now show that if two order related fixed points are unstable, a third fixed point must exist.

Lemma 3.2.13. *Consider system* (3.1.3)*. Let $\mathbf{E}_i \neq \mathbf{E}_j$ be two fixed points of $\mathbf{T}$ in $\mathbb{R}_+^2$ with $\mathbf{E}_i \ll_K \mathbf{E}_j$ and*

$$\rho(D\mathbf{T}(\mathbf{E}_i)) > 1, \quad \rho(D\mathbf{T}(\mathbf{E}_j)) > 1,$$

where $\rho(\cdot)$ denotes the spectral radius. Then there exists a third fixed point $\mathbf{E}_k$ such that

$$\mathbf{E}_k \in [[\mathbf{E}_i, \mathbf{E}_j]]_K.$$

This lemma was first proved as Corollary 1 in [16]; see also Corollary 5.4 in [15]. A self-contained proof is included here for completeness.

Proof. Since $\mathbf{E}_i \ll_K \mathbf{E}_j$ and by Lemma 3.2.12, Hypothesis 2.5.1 holds, Theorem 2.5.2 and Proposition 2.5.1 apply to $[\mathbf{E}_i, \mathbf{E}_j]_K$. Therefore, at least one of (a), (b), (c) in Theorem 2.5.2 is satisfied, while (b) and (c) cannot both hold by Proposition 2.5.1(i).

Assume (a) holds. Then, there exists a fixed point such that $\mathbf{E}_k \in [[\mathbf{E}_i, \mathbf{E}_j]]_K$, and we are done.

Without loss of generality assume (b) holds (the argument for (c) is identical by relabeling $\mathbf{E}_i$ and $\mathbf{E}_j$). Then, there exists an entire orbit

$$\{\mathbf{x}_t\}_{t \in \mathbb{Z}} \subset [\mathbf{E}_i, \mathbf{E}_j]_K$$

that is non-decreasing with respect to $\leqslant_K$, and

$$\lim_{t \to -\infty} \mathbf{x}_t = \mathbf{E}_i, \quad \lim_{t \to +\infty} \mathbf{x}_t = \mathbf{E}_j.$$

Since $\lim_{t\to+\infty} \mathbf{x}_t = \mathbf{E}_j$, for any $\varepsilon > 0$ there exists $t_0 > 0$ with $\|\mathbf{x}_t - \mathbf{E}_j\| < \varepsilon$ for all $t \geqslant t_0$. Define

$$U_\varepsilon = \big\{\mathbf{z} \in [\mathbf{E}_i, \mathbf{E}_j]_K : \mathbf{x}_{t_0} \leqslant_K \mathbf{z} \leqslant_K \mathbf{E}_j\big\} = [\mathbf{x}_{t_0}, \mathbf{E}_j]_K.$$

Let

$$B_\varepsilon(\mathbf{E}_j) = \big\{\mathbf{z} \in \mathbb{R}^2 : ||\mathbf{z} - \mathbf{E}_j|| < \varepsilon\big\}.$$

Take any $\mathbf{z} \in U_\varepsilon$. Write $\mathbf{x}_{t_0} = (x_{t_0,1}, x_{t_0,2})$, $\mathbf{z} = (z_1, z_2)$ and $\mathbf{E}_j = (E_{j,1}, E_{j,2})$. Since $\mathbf{T}$ is order preserving with respect to $\leqslant_K$, we obtain

$$\mathbf{x}_{t_0} \leqslant_K \mathbf{z} \leqslant_K \mathbf{E}_j \iff \begin{cases} 0 \leqslant x_{t_0,1} \leqslant z_1 \leqslant E_{j,1}, \\ x_{t_0,2} \geqslant z_2 \geqslant E_{j,2} \geqslant 0. \end{cases}$$

By $0 \leqslant x_{t_0,1} \leqslant z_1 \leqslant E_{j,1}$, we obtain

$$0 \leqslant E_{j,1} - z_1 \leqslant E_{j,1} - x_{t_0,1} \implies |z_1 - E_{j,1}| \leqslant |x_{t_0,1} - E_{j,1}|,$$

and by $x_{t_0,2} \geqslant z_2 \geqslant E_{j,2} \geqslant 0$, we obtain

$$x_{t_0,2} - E_{j,2} \geqslant z_2 - E_{j,2} \geqslant 0 \implies 0 \leqslant |z_2 - E_{j,2}| \leqslant |x_{t_0,2} - E_{j,2}|.$$

Hence,

$$||\mathbf{z} - \mathbf{E}_j||_2 \leqslant ||\mathbf{x}_{t_0} - \mathbf{E}_j||_2 < \varepsilon \implies \mathbf{z} \in B_\varepsilon(\mathbf{E}_j).$$

This shows $\mathbf{E}_j \in U_\varepsilon \subset B_\varepsilon(\mathbf{E}_j)$. For any $\mathbf{z} \in U_\varepsilon$, order-preservation of $\mathbf{T}$ gives

$$\mathbf{x}_{t_0} \leqslant_K \mathbf{x}_{t_0+1} = \mathbf{T}(\mathbf{x}_{t_0}) \leqslant_K \mathbf{T}(\mathbf{z}) \leqslant_K \mathbf{T}(\mathbf{E}_j) = \mathbf{E}_j.$$

Hence, $\mathbf{T}(\mathbf{z}) \in U_\varepsilon$ and $\mathbf{T}(U_\varepsilon) \subseteq U_\varepsilon$. For any $\varepsilon > 0$, there is a forward invariant set U_ε of $\mathbf{E}_j$ contained in the open ball $B_\varepsilon(\mathbf{E}_j)$. Hence, $\mathbf{E}_j$ is locally stable, contradicting $\rho\big(D\mathbf{T}(\mathbf{E}_j)\big) > 1$. Therefore, (b) contradicts the local instability of $\mathbf{E}_j$. Similarly, (c) contradicts the local instability of $\mathbf{E}_i$. Thus, only (a) can occur, and there exists a fixed point $\mathbf{E}_k$ with $\mathbf{E}_k \in [[\mathbf{E}_i, \mathbf{E}_j]]_K$. ☐

Next, we consider the convergence of the orbits.

Theorem 3.2.2. *Consider system* (3.1.3)*. If* $\mathbf{E}_0$ *is the only boundary fixed point, then every forward orbit that starts on an axis converges to* $\mathbf{E}_0$*. If* $\mathbf{E}_x$ *exists than any forward orbit with* $x > 0$ *and* $y = 0$ *converges to* $\mathbf{E}_x$*. Similarly, if* $\mathbf{E}_y$ *exists than any orbit with* $y > 0$ *and* $x = 0$ *converges to* $\mathbf{E}_x$*.*

Proof. On the axes, (3.1.3) reduces to a special case of the single species growth model in [26] and Theorem 4.5 applies. ☐

Theorem 3.2.3. *The trivial fixed point* $\mathbf{E}_0 = (0,0)$ *of system* (3.1.3) *is globally asymptotically stable with respect to* $\mathbb{R}^2_+$ *if and only if*

$$\delta_i \geqslant 1 + \frac{1}{d_i}, \quad \textit{for } i = 1, 2.$$

Proof. By Proposition 3.2.1(a), if $\delta_i \geqslant 1 + \frac{1}{d_i}$ for $i = 1, 2$, then $\mathbf{E}_0$ is the only fixed point in the first quadrant. Hence, by Theorem 3.2.1, every orbit with initial conditions in $\mathbb{R}^2_+$ converges to $\mathbf{E}_0$. On the other hand, if $\delta_i < 1 + \frac{1}{d_i}$ for at least one of $i = 1$ or 2, then at least one of $\mathbf{E}_x$ or $\mathbf{E}_y$ exists, and so by Theorem 3.2.2, $\mathbf{E}_0$ is unstable. ☐

Next, we analyze the local stability of the boundary fixed points.

Proposition 3.2.3. *Consider system* (3.1.3)*. When* $\mathbf{E}_x$ *and* $\mathbf{E}_y$ *are hyperbolic, the following statements hold.*

(a) $\mathbf{E}_x$ *is locally asymptotically stable if and only if*

$$0 < \delta_1 < 1 + \frac{1}{d_1} \qquad \text{and} \qquad \left[\delta_2 \geqslant 1 + \frac{1}{d_2}\right] \cup \left[1 < \delta_2 < 1 + \frac{1}{d_2}, \alpha_2 > \alpha_2^*\right].$$

(b) $\mathbf{E}_y$ *is locally asymptotically stable if and only if*

$$0 < \delta_2 < 1 + \frac{1}{d_2} \qquad \text{and} \qquad \left[\delta_1 \geqslant 1 + \frac{1}{d_1}\right] \cup \left[1 < \delta_1 < 1 + \frac{1}{d_1}, \alpha_1 > \alpha_1^*\right].$$

where

$$\alpha_i^* = \frac{(1 + d_i - d_i\delta_i)\left[\sqrt{(\mu_j d_j - (\delta_j - 1))^2 + 4\mu_j} + \mu_j d_j + \delta_j - 1\right]}{2(\delta_i - 1)(1 + d_j - d_j\delta_j)}, \; i, j \in \{1, 2\}, i \neq j. \tag{3.2.25}$$

Proof. (a) The Jacobian of (3.1.3) is given in (3.2.23) and (3.2.24). Since $f_1(\overline{x}, 0) = 1$, at $\mathbf{E}_x$, $D\mathbf{T}(\mathbf{E_x})$ is upper triangular, the eigenvalues are given by

$$\begin{aligned}
\lambda_1(\mathbf{E}_x) &= 1 - \frac{\overline{x}}{(1 + d_1 + \overline{x})^2} - \frac{\mu_1\,\overline{x}}{(\delta_1 + \mu_1\overline{x})^2} = \frac{1 + d_1}{(1 + d_1 + \overline{x})^2} + \frac{\delta_1}{(\delta_1 + \mu_1\overline{x})^2} > 0,\\
\lambda_2(\mathbf{E}_x) &= \frac{1}{1 + d_2 + \alpha_2\overline{x}} + \frac{1}{\delta_2}.
\end{aligned}$$

By Proposition 3.2.1(b), $\overline{x} > 0 \iff 0 < \delta_1 < 1 + \frac{1}{d_1}$ with $\overline{x}$ given by (3.2.12), so

$$0 < \lambda_1(\mathbf{E}_x) < 1 \iff 0 < \delta_1 < 1 + \frac{1}{d_1}.$$

For $\lambda_2(\mathbf{E}_x)$, one checks easily if $0 < \delta_2 \leqslant 1$, then

$$\lambda_2(\mathbf{E}_x) = \frac{1}{1 + d_2 + \alpha_2\overline{x}} + \frac{1}{\delta_2} > 1.$$

Hence a necessary condition for $\lambda_2(\mathbf{E}_x) < 1$ is $\delta_2 > 1$. When $\delta_2 > 1$, one has

$$\lambda_2(\mathbf{E}_x) < 1 \iff 1 + d_2 + \alpha_2\overline{x} > \frac{\delta_2}{\delta_2 - 1} \iff \alpha_2 > \frac{\frac{\delta_2}{\delta_2 - 1} - (1 + d_2)}{\overline{x}} = \alpha_2^*,$$

where α_2^* is given in (3.2.25). When $1 < \delta_2 < 1 + \frac{1}{d_2}$, we have $d_2(\delta_2 - 1) < 1$ and $\overline{x} > 0$. This implies that $\alpha_2^* > 0$. If $\delta_2 \geqslant 1 + \frac{1}{d_2}$, then $\alpha_2^* \leqslant 0$ and $\lambda_2(\mathbf{E}_x)$ is always less than one and the claim follows.

(b) By exchanging the indices, a similar argument applies to $\mathbf{E}_y$ and the conclusion follows. □

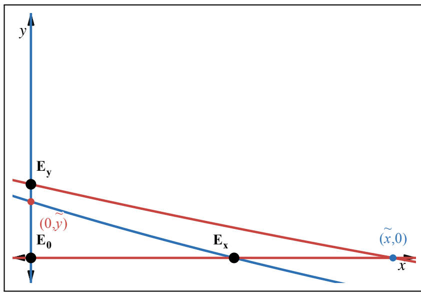
Next, we present the geometric interpretation of the Proposition 3.2.3. Define

$$\tilde{y} = \frac{1 - d_1(\delta_1 - 1)}{\alpha_1(\delta_1 - 1)}, \quad \tilde{x} = \frac{1 - d_2(\delta_2 - 1)}{\alpha_2(\delta_2 - 1)}. \tag{3.2.26}$$

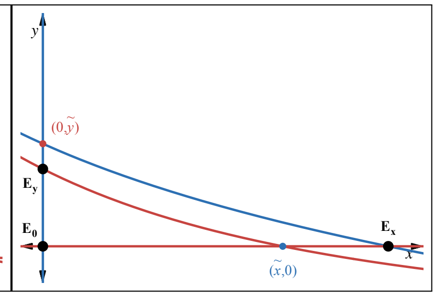
On the y-axis, $f_1(0, y) = 1$ gives the intercept $y = \tilde{y}$. On the x-axis, $f_2(x, 0) = 1$ gives the intercept $x = \tilde{x}$. Assume $1 < \delta_i < 1 + \frac{1}{d_i}$. A direct calculation shows

$$\tilde{x} < \overline{x} \iff \alpha_2 > \alpha_2^*, \quad \tilde{y} < \overline{y} \iff \alpha_1 > \alpha_1^*. \tag{3.2.27}$$

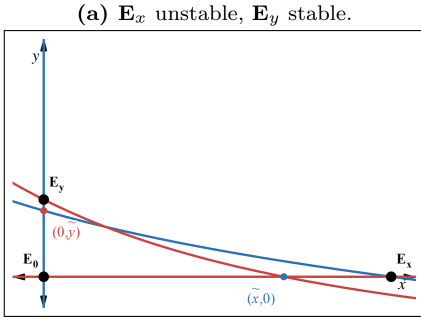
In view of Proposition 3.2.3, (3.2.27) shows the local stability of $\mathbf{E}_x$ and $\mathbf{E}_y$ can be translated to the relative positions of $(\tilde{x}, 0)$ and $\mathbf{E}_x$, and $(0, \tilde{y})$ and $\mathbf{E}_y$. We illustrate this by Figure 3.2.



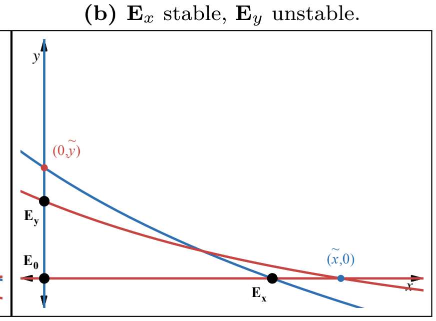
(a) $\mathbf{E}_x$ unstable, $\mathbf{E}_y$ stable.



(b) $\mathbf{E}_x$ stable, $\mathbf{E}_y$ unstable.



(c) Both $\mathbf{E}_x$ and $\mathbf{E}_y$ are locally stable.



(d) Both $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable.

Figure 3.2: The blue curves are the x-nullclines and the red curves are the y-nullclines. The figures illustrate all possible relative positions of axis intercepts $(\tilde{x}, 0)$ and $(0, \tilde{y})$ with respect to the boundary fixed points $\mathbf{E}_x$ and $\mathbf{E}_y$ which in turn determine their local stability.

The following Lemma shows when both $\mathbf{E}_x$ and $\mathbf{E}_y$ are locally asymptotically stable, then there is a unique interior fixed point.

Lemma 3.2.14. *Consider system* (3.1.3)*. If*

$$1 < \delta_i < 1 + \frac{1}{d_i} \quad \textit{and} \quad \alpha_i > \alpha_i^*, \quad i = 1, 2,$$

then there is a unique interior fixed point.

Proof. Under the assumption, Proposition 3.2.3 shows both $\mathbf{E}_x$ and $\mathbf{E}_y$ are both locally asymptotically stable. Let $h(x) = \ell_1(x) - \ell_2(x)$ where $\ell_1(x)$ and $\ell_2^+(x)$ are given in (3.2.1a) and (3.2.7). By calculations,

$$\lim_{x \to x_{\text{asy}}^+} h(x) = +\infty, \quad \lim_{x \to +\infty} h(x) = -\infty, \quad h(0) = \tilde{y} - \overline{y} < 0, \quad h(\overline{x}) = 0 - \ell_2^+(\overline{x}) > 0.$$

Choose $\varepsilon > 0$ with $x_{\text{asy}} + \varepsilon < 0$ and $M > \overline{x}$ large so that

$$h(x_{\text{asy}} + \varepsilon) > 0, \quad h(M) < 0.$$

Since $h(x)$ is continuous on (x_{asy}, ∞), the Intermediate Value Theorem and Proposition 3.2.2 ensure that there is exactly one root in each of the intervals

$$(x_{\text{asy}} + \varepsilon, 0) \subset (x_{\text{asy}}, 0), \quad (0, \overline{x}), \quad (\overline{x}, M) \subset (\overline{x}, \infty).$$

Since only the middle root lies in the first quadrant, there is a unique interior fixed point. $\square$

Here, we illustrate Lemma 3.2.14 with Figure 3.3.

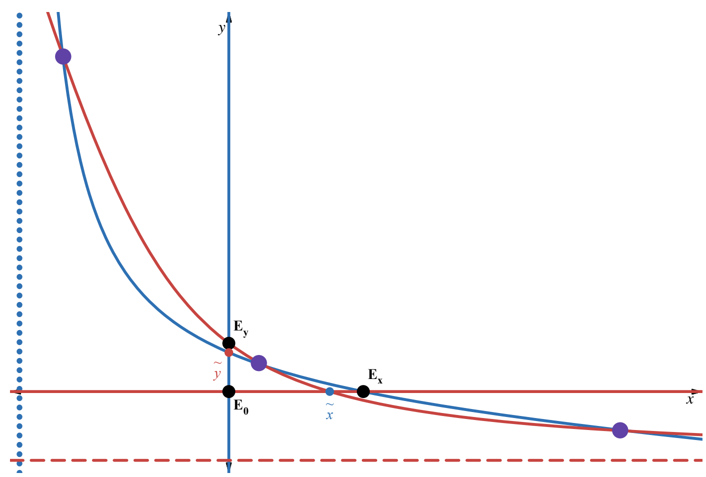


Figure 3.3: Illustration of the proof of Lemma 3.2.14. The intersections are labeled in purple.

We now state the corresponding global stability results when only one of $\mathbf{E}_x$ or $\mathbf{E}_y$ exists.

Theorem 3.2.4. *Consider system* (3.1.3). *Then, the following hold:*

(a) If $\quad \delta_2 \geqslant 1 + \frac{1}{d_2} \quad$ *and* $\quad 0 < \delta_1 < 1 + \frac{1}{d_1},$
then $\mathbf{E}_x$ *is globally asymptotically stable with respect to* $\text{int}\mathbb{R}^2_+$.

(b) If $\quad \delta_1 \geqslant 1 + \frac{1}{d_1} \quad$ *and* $\quad 0 < \delta_2 < 1 + \frac{1}{d_2},$
then $\mathbf{E}_y$ *is globally asymptotically stable with respect to* $\text{int}\mathbb{R}^2_+$.

Proof. (a) By Proposition 3.2.3(a), $\mathbf{E}_x$ is locally asymptotically stable while Proposition 3.2.1(b) shows $\mathbf{E}_y$ does not exists. By Theorem 3.2.3, $\mathbf{E}_0$ is unstable whenever any other fixed point exist. Thus, Theorem 3.2.1 implies that every orbit with initial conditions in $\text{int}\mathbb{R}^2_+$ converges to $\mathbf{E}_x$, and the conclusion follows. *(b)* Similarly, the result for $\mathbf{E}_y$ follows. $\square$

Next, we describe global convergence when system (3.1.3) has either no interior fixed points (with existence of both boundary fixed points) or exactly two interior fixed points. The results are summarized in Theorem 3.2.5.

Theorem 3.2.5. *Assume system* (3.1.3) *satisfies one of the following conditions:*

(i) $1 < \delta_2 < 1 + \frac{1}{d_2}, \quad \alpha_2 > \alpha_2^*, \quad$ *and* $\quad \left[\delta_1 \leqslant 1 \text{ or } (1 < \delta_1 < 1 + \frac{1}{d_1}, \alpha_1 < \alpha_1^*)\right]$,
or

(ii) $1 < \delta_1 < 1 + \frac{1}{d_1}, \quad \alpha_1 > \alpha_1^*, \quad$ *and* $\quad \left[\delta_2 \leqslant 1 \text{ or } (1 < \delta_2 < 1 + \frac{1}{d_2},\ \alpha_2 < \alpha_2^*)\right]$.

Then, either there are no interior fixed points or there are two and one of the following holds:

(a) If there is no interior fixed point, in regime (i), every interior orbit converges to $\mathbf{E}_x$ *and in regime (ii), every interior orbit converges to* $\mathbf{E}_y$*.*

(b) If, there are two interior fixed points, $\mathbf{E}_1^* \ll_K \mathbf{E}_2^*$*, in regime (i), every interior orbit converges to either* $\mathbf{E}_1^*$ *or* $\mathbf{E}_x$ *and in regime (ii), every interior orbit converges to either* $\mathbf{E}_2^*$ *or* $\mathbf{E}_y$*.*

Proof. We prove both *(a)* and *(b)* for regime (i). The exact same argument applies to regime (ii) by exchanging indices.

First note that, under the conditions in regime (i), Proposition 3.2.3(a) implies that $\mathbf{E}_x$ is locally asymptotically stable and $\mathbf{E}_y$ is unstable. We show that there must be an even number of interior fixed points in this case. We proceed using proof by contradiction. Suppose that there is a unique fixed point $\mathbf{E}^*$. Since $\mathbf{E}_x$ is asymptotically stable, if $\mathbf{E}^*$ is also asymptotically stable, by Corollary 2.5.1, there is a second interior fixed point $\mathbf{E}_2^*$ with $\mathbf{E}_2^* \in [[\mathbf{E}^*, \mathbf{E}_x]]_K$ yielding a contradiction. Since $\mathbf{E}_y$ is unstable, if $\mathbf{E}^*$ is also unstable, then Lemma 3.2.13 implies there is at least a second interior fixed point $\mathbf{E}_2^* \in [[\mathbf{E}_y, \mathbf{E}^*]]_K$, contradicting that $\mathbf{E}^*$ is the only interior fixed point. If we suppose instead that there are exactly three interior fixed points, a similar argument implies there must be at least four interior fixed points again proving a contradiction. Since, by Proposition 3.2.2, there can be at most three interior fixed points, there must be either two interior fixed points or no interior fixed points.

(a) If no interior fixed point exists, then $\mathbf{E}_x$ is the only attractor. Proposition 3.2.3 and Theorem 3.2.1 immediately imply convergence of interior orbits to $\mathbf{E}_x$.

(b) Let the two interior fixed points be ordered as $\mathbf{E}_1^* \ll_K \mathbf{E}_2^*$, since $\mathbf{E}_x$ is locally asymptotically stable and $\mathbf{E}_y$ is unstable, it follows that $\mathbf{E}_1^*$ is locally asymptotically stable and $\mathbf{E}_2^*$ is unstable. Theorem 3.2.1 then ensures every interior orbit converges to either $\mathbf{E}_2^*$ or $\mathbf{E}_x$. ☐

We now consider the parameter regime in which there are an odd number of interior fixed points, i.e., one or three.

Theorem 3.2.6. *Consider system* (3.1.3)*.*

(a) If $\quad 0 < \delta_i \leqslant 1 \quad$ *and* $\quad 0 < \alpha_1\alpha_2 < 1 + \frac{\mu_1}{(\mu_1+\delta_1-1)^2} \quad$ *for* $i = 1, 2$,
then there is a unique interior fixed point, $\mathbf{E}^*$ *that is globally asymptotically stable with respect to* $\mathrm{int}\mathbb{R}_+^2$*.*

(b) If $\quad 1 < \delta_i < 1 + \frac{1}{d_i} \quad$ *and* $\quad \alpha_i > \alpha_i^* \quad$ *for* $i = 1, 2$,
then there is a unique interior fixed point $\mathbf{E}^*$ *that is unstable, and every interior orbit converges to either* $\mathbf{E}_x$ *or* $\mathbf{E}_y$*.*

(c) If $\quad 1 < \delta_i < 1 + \frac{1}{d_i} \quad$ *and* $\quad \alpha_i < \alpha_i^* \quad$ *for* $\quad i = 1, 2$,
then exactly one of the following holds:

(i) there is a unique interior fixed point, $\mathbf{E}^*$ *that is globally asymptotically stable with respect to* $\mathrm{int}\mathbb{R}_+^2$*; or*

(ii) there are three interior fixed points $\mathbf{E}_1^* \ll_K \mathbf{E}_2^* \ll_K \mathbf{E}_3^*$ *and every interior orbit converges to* $\mathbf{E}_1^*$ *or* $\mathbf{E}_3^*$.

Proof. *(a)* By Proposition 3.2.3, both $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable under the given conditions. Lemma 3.2.5 ensures a unique interior fixed point $\mathbf{E}^*$. By Lemma 3.2.11, $\mathbf{E}_y \ll_K \mathbf{E}^* \ll_K \mathbf{E}_x$. Assume for contradiction that $\mathbf{E}^*$ is unstable. By Lemma 3.2.13, there is a second interior fixed point $\mathbf{E}_2^*$ with $\mathbf{E}_2^* \in [[\mathbf{E}_y, \mathbf{E}^*]]_K$, contradicting the uniqueness of $\mathbf{E}^*$. Hence $\mathbf{E}^*$ is locally asymptotically stable. By Theorem 3.2.1, every interior orbit converges to $\mathbf{E}^*$.

(b) By Proposition 3.2.3, both $\mathbf{E}_x$ and $\mathbf{E}_y$ are locally asymptotically stable under the given conditions. By Lemma 3.2.14, there is a unique interior fixed point $\mathbf{E}^*$. Lemma 3.2.11 then gives $\mathbf{E}_y \ll_K \mathbf{E}^* \ll_K \mathbf{E}_x$. Assume for contradiction that $\mathbf{E}^*$ is locally asymptotically stable. Corollary 2.5.1 will yield a second interior fixed point, again contradicting uniqueness. Hence $\mathbf{E}^*$ is unstable. By Theorem 3.2.1, every interior orbit converges to either $\mathbf{E}_x$ or $\mathbf{E}_y$.

(c) Under the given conditions, Proposition 3.2.3 shows both $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable. Lemma 3.2.13 implies there is at least one interior fixed point. Assume for contradiction that there are exactly two interior fixed points $\mathbf{E}_1^*, \mathbf{E}_3^*$ with $\mathbf{E}_1^* \ll_K \mathbf{E}_3^*$. If both $\mathbf{E}_1^*, \mathbf{E}_3^*$ are stable, then Corollary 2.5.1 implies a third fixed point $\mathbf{E}_2^*$ in $[[\mathbf{E}_1^*, \mathbf{E}_3^*]]_K$. If both $\mathbf{E}_1^*, \mathbf{E}_3^*$ are unstable, then Lemma 3.2.13 yields a third one in $[[\mathbf{E}_1^*, \mathbf{E}_3^*]]_K$. If one is stable ($\mathbf{E}_1^*$) and one is unstable ($\mathbf{E}_3^*$), applying Lemma 3.2.13 to $[[\mathbf{E}_3^*, \mathbf{E}_x]]_K$ again yields a third one in $[[\mathbf{E}_3^*, \mathbf{E}_x]]_K$. Hence, in all cases, there can not be two interior fixed points. Since Proposition 3.2.2 bounds the total number to three, there can be either one or three interior fixed points.

If there is a unique interior fixed point $\mathbf{E}^*$, the same argument as in *(a)* applies and the conclusion follows. If there are three interior fixed points, we order them as $\mathbf{E}_1^* \ll_K \mathbf{E}_2^* \ll_K \mathbf{E}_3^*$. Since both $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable, $\mathbf{E}_1^*$ and $\mathbf{E}_3^*$ must be stable. Also, $\mathbf{E}_2^*$ must be unstable. Otherwise $\mathbf{E}_2^*$ and $\mathbf{E}_1^*$ are both locally asymptotically stable and Corollary 2.5.1 yields a third one in between, a contradiction. The convergence to $\mathbf{E}_1^*$ and $\mathbf{E}_3^*$ follows from Theorem 3.2.1 □

Proposition 3.2.2 allows at most three interior fixed points and parts *(b) (c)(ii)* of Theorem 3.2.6 imply the following result.

Corollary 3.2.1. *Consider system* (3.1.3). *If there are three interior fixed points, then the following ordering is the only possibility:*

$$\mathbf{E}_y \text{ (unstable)} \ll_K \mathbf{E}_1^* \text{ (stable)} \ll_K \mathbf{E}_2^* \text{ (unstable)} \ll_K \mathbf{E}_3^* \text{ (stable)} \ll_K \mathbf{E}_x \text{ (unstable)}.$$

It is worth emphasizing that when there are three interior fixed points, $\mathbf{E}_2^*$ is always unstable. We leave the bifurcation analysis of the fixed points to Chapter 5.

Chapter 4

Global Dynamics Assuming Symmetry

In this chapter, we assume system (3.1.3) satisfies the symmetry conditions

$$d_1 = d_2 = d, \quad \delta_1 = \delta_2 = \delta, \quad \mu_1 = \mu_2 = \mu, \quad \alpha_1 = \alpha_2 = \alpha. \tag{4.0.1}$$

Biologically, (4.0.1) means that certain ratios of the parameters of the two species are identical based on the change of varaibles given in (3.1.3).

4.1 Existence of Interior Fixed Points under Symmetry

Under (4.0.1), $Q(x, y) = f_1(x, y) - f_2(x, y) = 0$ defined in (3.2.16) factors as

$$Q(x, y) = L_1(x, y)L_2(x, y) = 0, \tag{4.1.1}$$

where

$$L_1(x, y): \ x - y, \qquad L_2(x, y): \ \mu(x + y) + d\mu + \delta - 1 - \alpha(\delta - 1). \tag{4.1.2}$$

Any fixed point $(x^*, y^*) \in \mathrm{int}\mathbb{R}^2$ must satisfy

$$\textbf{Case 1}: \begin{cases} L_1(x^*, y^*) = 0, \\ f_i(x^*, y^*) = 1, \quad i = 1 \text{ or } 2. \end{cases} \quad \text{or} \quad \textbf{Case 2}: \begin{cases} L_2(x^*, y^*) = 0, \\ f_i(x^*, y^*) = 1, \quad i = 1 \text{ or } 2. \end{cases} \tag{4.1.3}$$

In order to determine the existence conditions of all interior fixed points, we now analyze the two cases above.

4.1.1 Case 1: $(L_1 = 0)$

Lemma 4.1.1. *Consider system* (3.1.3) *with* (4.0.1). *The fixed point* $\mathbf{E}_2^* = (x_2^*, x_2^*)$ *lies in the interior of the first quadrant if and only if* $0 < \delta < 1 + \frac{1}{d}$. *If* $\delta = 1 + \frac{1}{d}$, $\mathbf{E}_2^*$ *disappears through* $\mathbf{E}_0$.

Proof. Since $y = \ell_1(x)$ (see (3.2.3)) is strictly decreasing and $L_1 = 0$ (see (4.1.2)) is strictly increasing, they intersect at most once in the first quadrant and hence there is at most one interior fixed point. On $L_1 = 0$, $y = x$ and (3.2.14) becomes

$$\widetilde{A}_1 x^2 + \widetilde{B}_1 x + \widetilde{C}_1 = 0, \tag{4.1.4}$$

where $\widetilde{A}_1 = \mu(1+\alpha), \widetilde{B}_1 = d\mu + (1+\alpha)(\delta - 1),$ and $\widetilde{C}_1 = d(\delta-1) - 1$. Since $\widetilde{A}_1 \neq 0$, the roots are

$$x_{\pm} = \frac{-\widetilde{B}_1 \pm \sqrt{\widetilde{B}_1^2 - 4\widetilde{A}_1\widetilde{C}_1}}{2\widetilde{A}_1}.$$

A direct calculation shows that $x_+ > x_-$ and

$$x_+ > 0 \iff \widetilde{C}_1 < 0 \iff 0 < \delta < 1 + \frac{1}{d}.$$

Hence, $\mathbf{E}_2^* = (x_2^*, x_2^*)$, where $x_2^* = x_+$.

□

4.1.2 Case 2: $(L_2 = 0)$

In this case, we consider all the fixed points that are on $L_2 = 0$. Define

$$\tilde{k}_1 := \frac{d\mu + \delta - 1 - \alpha(\delta - 1)}{\mu}. \tag{4.1.5}$$

Solving $L_2(x, y) = 0$ for y yields

$$y = -x - \tilde{k}_1. \tag{4.1.6}$$

Substituting (4.1.6) into $f_1(x, y) = 1$ and simplifying, we obtain a quadratic equation in x:

$$\widetilde{A}_2 x^2 + \widetilde{B}_2 x + \widetilde{C}_2 = 0, \tag{4.1.7}$$

where

$$\widetilde{A}_2 = \mu(1-\alpha), \quad \widetilde{B}_2 = d\mu + \delta - 1 - \alpha(\delta-1) - \alpha\mu\tilde{k}_1, \quad \widetilde{C}_2 = d(\delta-1) - 1 - \alpha(\delta-1)\tilde{k}_1. \tag{4.1.8}$$

We therefore consider the following cases:

1. **Case 2.1:** $\widetilde{A}_2 \neq 0, \widetilde{B}_2 \neq 0, \widetilde{C}_2 \neq 0$.
2. **Case 2.2:** One or more of $\widetilde{A}_2, \widetilde{B}_2, \widetilde{C}_2$ is zero: **(a)** $\widetilde{A}_2 = 0$, **(b)** $\widetilde{B}_2 = 0$, **(c)** $\widetilde{C}_2 = 0$.

Case 2.1: $\widetilde{A}_2 \neq 0, \widetilde{B}_2 \neq 0, \widetilde{C}_2 \neq 0$.

Solving (4.1.7) gives the roots

$$x_1^* = \frac{-\widetilde{B}_2 + \sqrt{\widetilde{B}_2^2 - 4\widetilde{A}_2\widetilde{C}_2}}{2\widetilde{A}_2}, \quad x_3^* = \frac{-\widetilde{B}_2 - \sqrt{\widetilde{B}_2^2 - 4\widetilde{A}_2\widetilde{C}_2}}{2\widetilde{A}_2}. \tag{4.1.9}$$

Hence, the two fixed points that are on $L_2 = 0$ (see (4.1.6)) take the form

$$\mathbf{E}_1^* = (x_1^*, y_1^*) \quad \text{and} \quad \mathbf{E}_3^* = (x_3^*, y_3^*), \quad \text{where} \quad y_i^* = -x_i^* - \tilde{k}_1, \quad \text{for } i = 1, 3.$$

From (4.1.8) and (4.1.5), we obtain

$$\widetilde{B}_2 = (1-\alpha)[d\mu + (1-\alpha)(\delta-1)] \quad \text{and} \quad \widetilde{A}_2\tilde{k}_1 = \widetilde{B}_2.$$

By Vieta's formulas for a quadratic,

$$x_3^* + x_1^* = -\frac{\widetilde{B}_2}{\widetilde{A}_2} = -\tilde{k}_1 \quad \text{and} \quad x_3^* x_1^* = \frac{\widetilde{C}_2}{\widetilde{A}_2},$$

Since $y_i^* = -x_i^* - \tilde{k}_1$, it follows that

$$y_3^* = x_1^*, \quad y_1^* = x_3^*, \quad \mathbf{E}_1^* = (x_1^*, x_3^*), \quad \mathbf{E}_3^* = (x_3^*, x_1^*), \tag{4.1.10}$$

i.e., $\mathbf{E}_1^*$ and $\mathbf{E}_3^*$ are symmetric about $y = x$. A necessary and sufficient condition for $x_3^*, x_1^* > 0$ to hold is

$$x_3^* + x_1^* > 0, \quad x_3^* x_1^* > 0, \quad \widetilde{\Delta}_2 = \widetilde{B}_2^2 - 4\widetilde{A}_2\widetilde{C}_2 \geqslant 0.$$

Equivalently,

$$\widetilde{A}_2\widetilde{B}_2 < 0, \quad \widetilde{A}_2\widetilde{C}_2 > 0, \quad \widetilde{B}_2^2 \geqslant 4\widetilde{A}_2\widetilde{C}_2.$$

Therefore, there are only two possible cases that can give new interior fixed points:

$$\textbf{Case 2.1(a)}: \quad \begin{cases} \widetilde{A}_2 > 0, \quad \widetilde{B}_2 < 0, \quad \widetilde{C}_2 > 0, \\ \widetilde{B}_2^2 \geqslant 4\widetilde{A}_2\widetilde{C}_2, \end{cases}$$

or

$$\textbf{Case 2.1(b)}: \quad \begin{cases} \widetilde{A}_2 < 0, \quad \widetilde{B}_2 > 0, \quad \widetilde{C}_2 < 0, \\ \widetilde{B}_2^2 \geqslant 4\widetilde{A}_2\widetilde{C}_2. \end{cases}$$

We analyze each case in turn.

Case 2.1(a): $\widetilde{A}_2 > 0$, $\widetilde{B}_2 < 0$, $\widetilde{C}_2 > 0$. A direct calculation shows that

$$\widetilde{A}_2 > 0, \quad \widetilde{B}_2 < 0 \iff 0 < \alpha, \delta < 1.$$

Hence **Case 2.1(a)** is the regime with $0 < \alpha, \delta < 1$. We now prove that no new interior fixed point exists in this regime.

Lemma 4.1.2. *Consider system* (3.1.3) *with* (4.0.1). *If*

$$0 < \alpha < 1, \quad 0 < \delta < 1,$$

the only interior fixed point is $\mathbf{E}_2^*$.

Proof. Since $\alpha, \delta < 1$, a direct calculation shows

$$\widetilde{C}_2 > 0 \iff d < -\frac{1 + \frac{\alpha(\delta-1)^2(1-\alpha)}{\mu}}{(1-\alpha)(1-\delta)} < 0,$$

contradicting $d > 0$. Hence, $\widetilde{C}_2 \leqslant 0$, and therefore

$$x_3^* x_1^* = \frac{\widetilde{C}_2}{\widetilde{A}_2} < 0, \quad x_3^* + x_1^* = -\frac{\widetilde{B}_2}{\widetilde{A}_2} > 0.$$

Finally, since $\widetilde{C}_2 \leqslant 0 < \widetilde{B}_2^2$,

$$\widetilde{\Delta}_2 = \widetilde{B}_2^2 - 4\widetilde{A}_2\widetilde{C}_2 > 0.$$

It follows that one root is negative and one positive, so neither $\mathbf{E}_3^*$ nor $\mathbf{E}_1^*$ lies in $\operatorname{int}\mathbb{R}_+^2$. □

Since one root is negative and other is positive, and $x_3^* < x_1^*$, it follows that $x_3^* < 0 < x_1^*$. Hence, $\mathbf{E}_3^* = (x_3^*, x_1^*)$ lies in the second quadrant and $\mathbf{E}_1^* = (x_1^*, x_3^*)$ lies in the fourth quadrant.

Case 2.1(b): $\widetilde{A}_2 < 0$, $\widetilde{B}_2 > 0$, $\widetilde{C}_2 < 0$. We show this case can admit two interior fixed points. Define

$$\begin{aligned} d_{\mathrm{tc}}^* &= \frac{\alpha(\delta-1)}{\mu} - \frac{1}{(\alpha-1)(\delta-1)}, \quad d_-^* = \frac{(\alpha+1)(\delta-1)}{\mu} - \frac{2}{\sqrt{(\alpha-1)\mu}}, \\ \mu_2^* &= (\alpha-1)(\delta-1)^2, \quad \mu_1^* = \alpha\,\mu_2^*, \quad \mu_3^* = \frac{(\alpha+1)^2\,\mu_2^*}{4}, \quad \mu_4^* = \frac{\mu_1^*}{1+d(\delta-1)(\alpha-1)}. \end{aligned} \tag{4.1.11}$$

A direct calculation shows

$\widetilde{A}_2 < 0 \iff \alpha > 1$, $\widetilde{B}_2 > 0 \iff d\mu < (\alpha-1)(\delta-1)$ and $\delta > 1$, $\widetilde{C}_2 < 0 \iff d > d_{\mathrm{tc}}^* \iff \mu > \mu_4^*$.

Hence, this case holds exactly when the following holds

$$\alpha > 1, \quad \delta > 1, \quad d\mu < (\alpha-1)(\delta-1), \quad d > d_{\mathrm{tc}}^* (\iff \mu > \mu_4^*). \tag{4.1.12}$$

Under $\alpha, \delta > 1$, we obtain

$$d_{\mathrm{tc}}^* > 0 \iff \mu < \mu_1^* \quad \text{and} \quad \mu_4^* > 0.$$

Hence, $d > d_{\mathrm{tc}}^*$ always hold if $\mu \geqslant \mu_1^*$. After simplifications, (4.1.12) gives the following non-empty sets:

$$\mathcal{C}_1 = \left\{ (\alpha, \delta, \mu, d) : \begin{array}{l} \alpha > 1, \quad \delta > 1, \\ \mu \geqslant \mu_1^*, \quad 0 < d < \frac{(\alpha-1)(\delta-1)}{\mu} \end{array} \right\}, \tag{4.1.13}$$

or

$$\mathcal{C}_2 = \left\{ (\alpha, \delta, \mu, d) : \begin{array}{l} \alpha > 1, \quad \delta > 1, \quad \mu_2^* < \mu < \mu_1^*, \\ d_{\mathrm{tc}}^* < d < \frac{(\alpha-1)(\delta-1)}{\mu} \end{array} \right\}. \tag{4.1.14}$$

Noting that both $\mathcal{C}_1$ and $\mathcal{C}_2$ must satisfy $\alpha > 1$ and $\delta > 1$. In that regime, we have

$$\mu_2^* < \mu_1^*, \quad \text{so that} \begin{cases} \mathcal{C}_1 \neq \varnothing & \text{by choosing } \mu \geqslant \mu_1^*,\ d > 0, \\ \mathcal{C}_2 \neq \varnothing & \text{by choosing } \mu \in (\mu_2^*, \mu_1^*),\ d \in \big(d_{\mathrm{tc}}^*,\, (\alpha-1)(\delta-1)/\mu\big). \end{cases}$$

Next, we check when $\widetilde{\Delta}_2 \geqslant 0$. Since $\alpha > 1$, a direct calculation shows $\widetilde{\Delta}_2 \geqslant 0 \iff \widetilde{M}_0(d) \leqslant 0$, where

$$\widetilde{M}_0(d) = [(1-\alpha)\mu^2]d^2 + [2(\alpha^2-1)(\delta-1)\mu]d + (1-\alpha)(1+\alpha)^2(\delta-1)^2 + 4\mu. \tag{4.1.15}$$

$\widetilde{M}_0(d)$ is a parabola that opens downward with two real roots

$$d^*_{\pm} = \frac{(\alpha+1)(\delta-1)}{\mu} \pm \frac{2}{\sqrt{(\alpha-1)\mu}}.$$

Hence, under $\alpha, \delta > 1$, we obtain

$$\widetilde{\Delta}_2 \geqslant 0 \iff (d \leqslant d^*_-) \quad \text{or} \quad (d \geqslant d^*_+). \tag{4.1.16}$$

A direct calculation shows

$$\begin{aligned} d \geqslant d^*_+ &\iff d\mu \geqslant (\alpha-1)(\delta-1) + 2(\delta-1) + 2\sqrt{\frac{\mu}{\alpha-1}} \\ &\Longrightarrow \quad d\mu > (\alpha-1)(\delta-1), \end{aligned}$$

contradicting $d\mu < (\alpha-1)(\delta-1)$. Hence, $d \geqslant d^*_+$ is impossible. For d^*_-, a direct calculation shows $d^*_- > 0 \iff \mu < \mu^*_3$. Hence, in Case 2.1(b), $\widetilde{\Delta}_2 \geqslant 0$ holds if and only if

$$\mathcal{D}_1 = \left\{ (\alpha,\delta,\mu,d) : \begin{array}{ll} \alpha > 1, & \delta > 1 \\ 0 < \mu < \mu^*_3, & 0 < d \leqslant d^*_- \end{array} \right\}. \tag{4.1.17}$$

Thus, in **Case 2.1**, two additional interior fixed points occur if and only if $\mathcal{C}_1 \cap \mathcal{D}_1 \neq \varnothing$ or $\mathcal{C}_2 \cap \mathcal{D}_1 \neq \varnothing$. In order to determine when they are non-empty, the following lemma will be used.

Lemma 4.1.3. *Assume $\alpha > 1$ and $\delta > 1$. Then, the following inequalities hold:*

(a) $\mu^*_2 < \mu^*_1 < \mu^*_3$ *and* $\mu^*_2 \leqslant \mu^*_4 < \mu^*_1$, *with* $\mu^*_2 = \mu^*_4$ *if and only if* $d = \frac{1}{\delta-1}$.

(b) $d^*_{\mathrm{tc}} \leqslant d^*_-$ *with equality if and only if* $\mu = \mu^*_2$ *and* $d^*_- \leqslant \frac{(\alpha-1)(\delta-1)}{\mu} \leqslant \frac{1}{\delta-1} \iff \mu \geqslant \mu^*_2$.

Proof. See Appendix A.2. □

Next, we consider when at least one of $\widetilde{A}_2, \widetilde{B}_2, \widetilde{C}_2$ defined in (4.1.8) is zero.

Case 2.2: $\widetilde{A}_2\widetilde{B}_2\widetilde{C}_2 = 0$. In the next Lemma we prove that if any one of $\widetilde{A}_2, \widetilde{B}_2, \widetilde{C}_2$ vanishes, then no new interior fixed points occur.

Lemma 4.1.4. *Consider system* (3.1.3) *with* (4.0.1). *If at least one of* $\widetilde{A}_2$, $\widetilde{B}_2$, $\widetilde{C}_2$ *in* (4.1.7) *is zero, then no interior fixed point can arise in* ***Case 2.2****.*

Proof. The proof is given in Appendix A.3. □

Thus, we have shown that except for $\mathbf{E}^*_2 = (x^*_2, x^*_2)$ determined in **Case 1**, and possibly $\mathbf{E}^*_1$ and $\mathbf{E}^*_3$ considered in **Case 2.1(b)**, there are no other parameter ranges for which interior fixed points can occur. The conditions when interior fixed points exist are given next.

Theorem 4.1.1. *Consider system* (3.1.3) *with* (4.0.1).

(a) There are three interior fixed points, $\mathbf{E}^*_1, \mathbf{E}^*_2, \mathbf{E}^*_3$, *if and only if*

$$(\alpha,\delta,\mu,d) \in \mathcal{C}_1 \cap \mathcal{D}_1, \quad \text{or} \quad (\alpha,\delta,\mu,d) \in \mathcal{C}_2 \cap \mathcal{D}_1.$$

(b) There is a unique interior fixed point, $\mathbf{E}^* = \mathbf{E}_2^*$, if and only if

$$0 < \delta < 1 + \frac{1}{d} \text{ and } \big[\alpha \leqslant 1 \text{ or } \delta \leqslant 1\big] \cup \big[\alpha > 1, \delta > 1, (\mu, d) \notin (\mathcal{C}_1 \cup \mathcal{C}_2) \cap \mathcal{D}_1\big], \tag{4.1.18}$$

where

$$\mathcal{C}_1 \cap \mathcal{D}_1 = \left\{(\alpha, \delta, \mu, d) : \begin{array}{ll} \alpha > 1, & \delta > 1 \\ \mu_1^* \leqslant \mu < \mu_3^*, & 0 < d < d_-^* \end{array} \right\}, \tag{4.1.19}$$

and

$$\mathcal{C}_2 \cap \mathcal{D}_1 = \left\{(\alpha, \delta, \mu, d) : \begin{array}{ll} \alpha > 1, & \delta > 1 \\ \mu_2^* < \mu < \mu_1^*, & d_{\mathrm{tc}}^* < d < d_-^* \end{array} \right\}. \tag{4.1.20}$$

Proof. (a) For $(\alpha, \delta, \mu, d) \in \mathcal{C}_1 \cap \mathcal{D}_1$, one has $\mu \geqslant \mu_1^*$ and $0 < \mu < \mu_3^*$. By Lemma 4.1.3,

$$\mu_1^* \leqslant \mu < \mu_3^*, \quad d \leqslant d_-^* < \frac{(\alpha-1)(\delta-1)}{\mu}.$$

This then yields (4.1.19). For $(\alpha, \delta, \mu, d) \in \mathcal{C}_2 \cap \mathcal{D}_1$, one has $\mu_2^* < \mu < \mu_1^*$. Lemma 4.1.3(b) gives $d_{\mathrm{tc}}^* < d_-^* < \frac{(\alpha-1)(\delta-1)}{\mu}$. Thus the condition $d_{\mathrm{tc}}^* < d < \frac{(\alpha-1)(\delta-1)}{\mu}$ in $\mathcal{C}_2$ and $0 < d \leqslant d_-^*$ from $\mathcal{D}_1$ reduces to $d_{\mathrm{tc}}^* < d \leqslant d_-^*$, which yields (4.1.20).

(b) By Lemma 4.1.1, $\mathbf{E}_2^*$ exists if and only if $0 < \delta < 1 + \frac{1}{d}$. Since $\mathcal{C}_1 \cap \mathcal{D}_1$ and $\mathcal{C}_2 \cap \mathcal{D}_1$ are subsets of $\big\{(\alpha, \delta, \mu, d) : 0 < \delta < 1 + \frac{1}{d}\big\}$, it follows that whenever $\mathbf{E}_1^*$ and $\mathbf{E}_3^*$ exist, so does $\mathbf{E}_2^*$. If $0 < \delta < 1 + \frac{1}{d}$ and $(\mu, d) \notin (\mathcal{C}_1 \cup \mathcal{C}_2) \cap \mathcal{D}_1$, the fixed point $\mathbf{E}_2^*$ is unique. □

In (4.1.19) and (4.1.20), we have excluded the case for which $d = d_-^*$, since in that case, $\mathbf{E}_1^*, \mathbf{E}_2^*$ and $\mathbf{E}_3^*$ coalesce. Hence, it will be treated as the case for unique interior fixed point.

The following results follow directly from Lemma 4.1.3.

Remark 4.1.1. If one of the following holds, then (4.1.18) holds:

(i) $0 < \alpha \leqslant 1$ and $0 < \delta < 1 + \frac{1}{d}$.

(ii) $0 < \delta \leqslant 1$.

(iii) $\alpha, \delta > 1$ and $d_-^* < d \leqslant \frac{1}{\delta - 1}$.

(iv) $\alpha, \delta > 1$, $\mu \geqslant \mu_3^*$, and $d < \frac{1}{\delta-1}$.

(v) $\alpha, \delta > 1$, $0 < \mu \leqslant \mu_2^*$, and $d < \frac{1}{\delta-1}$.

(vi) $\alpha, \delta > 1$, $\mu_2^* < \mu < \mu_1^*$, and $d \leqslant d_{\mathrm{tc}}^*$.

(vii) $\alpha, \delta > 1$, $\mu_2^* < \mu < \mu_1^*$, and $d = d_-^*$.

It will be shown in Chapter 5 that $d = d_{\mathrm{tc}}^*$ is a transcritical bifurcation point and $d = d_-^*$ is a pitchfork bifurcation point. Next, we show in **Case 2.2(c)**, $\mathbf{E}_1^*$ and $\mathbf{E}_3^*$ coalesce with $\mathbf{E}_x$ and $\mathbf{E}_y$.

Lemma 4.1.5. *Consider system* (3.1.3) *with* (4.0.1). $\mathbf{E}_1^* = (0, x_3^*)$ *becomes* $\mathbf{E}_y$ *and* $\mathbf{E}_3^* = (x_3^*, 0)$ *becomes* $\mathbf{E}_x$ *if and only if*

$$\alpha > 1, \quad 1 < \delta < 1 + \frac{1}{d}, \quad \text{and} \quad \mu = \mu_4^*,$$

This is equivalent to

$$\alpha > 1, \quad 1 < \delta < 1 + \frac{1}{d}, \quad \mu_2^* < \mu < \mu_1^*, \quad \textit{and} \quad d = d_{\mathrm{tc}}^*,$$

i.e., (vi) in Remark 4.1.1 with $d = d_{\mathrm{tc}}^*$.

Proof. In **Case 2.2(c)**, $\widetilde{C}_2 = 0$ and $\widetilde{A}_2, \widetilde{B}_2 \neq 0$. A direct calculation shows

$$\widetilde{C}_2 = 0 \iff d(\delta - 1) - 1 = \alpha(\delta - 1)\tilde{k}_1 \iff \mu = \mu_4^* \iff d = d_{\mathrm{tc}}^*$$

By calculation, the two fixed points that are on $L_2 = 0$ take the form

$$x_3^* = -\frac{\widetilde{B}_2}{\widetilde{A}_2} = -\tilde{k}_1, \quad y_3^* = 0, \quad y_1^* = x_3^*.$$

Correspondingly, $\mathbf{E}_1^*$ becomes $(0, -\tilde{k}_1)$ and $\mathbf{E}_3^*$ becomes $(-\tilde{k}_1, 0)$. Next, the necessary and sufficient condition for both $-\tilde{k}_1$ and μ_4^* to be positive is

$$-\tilde{k}_1, \mu_4^* > 0 \iff \alpha > 1 \quad \text{and} \quad 1 < \delta < 1 + \frac{1}{d}.$$

This is equivalent to

$$-\tilde{k}_1, d_{\mathrm{tc}}^* > 0 \iff \alpha > 1, \quad 1 < \delta < 1 + \frac{1}{d}, \quad \text{and} \quad \mu_2^* < \mu < \mu_1^*.$$

By Proposition 3.2.1(b), $\mathbf{E}_x = (\overline{x}, 0)$ and $\mathbf{E}_y = (0, \overline{x})$ with $\overline{x} > 0$ if and only if $0 < \delta < 1 + \frac{1}{d}$. Substituting $d(\delta - 1) - 1 = \alpha(\delta - 1)\tilde{k}_1$ into $\overline{x}$ yields

$$\overline{x} = \frac{-[\mu\tilde{k}_1 + \alpha(\delta - 1)] + |\mu\tilde{k}_1 - \alpha(\delta - 1)|}{2\mu}.$$

Suppose for contradiction that $\mu\tilde{k}_1 - \alpha(\delta - 1) \geqslant 0$, then

$$|\mu\tilde{k}_1 - \alpha(\delta - 1)| = \mu\tilde{k}_1 - \alpha(\delta - 1) \implies \overline{x} = -\frac{\alpha(\delta - 1)}{\mu} < 0,$$

a contradiction. Thus $\mu\tilde{k}_1 - \alpha(\delta - 1) < 0$. This shows

$$|\mu\tilde{k}_1 - \alpha(\delta - 1)| = \alpha(\delta - 1) - \mu\tilde{k}_1 \implies \overline{x} = -\tilde{k}_1 = x_3^*,$$

completing the proof. ∎

We next identify how all the fixed points are arranged with respect to $\leqslant_K$.

Proposition 4.1.1. *Consider system* (3.1.3) *with* (4.0.1). *The following statements hold.*

(a) *If* $0 < \delta < 1 + \frac{1}{d}$, *then* $\mathbf{E}_y \ll_K \mathbf{E}_2^* \ll_K \mathbf{E}_x$.

(b) *If* $(\alpha, \delta, \mu, d) \in (\mathcal{C}_1 \cup \mathcal{C}_2) \cap \mathcal{D}_1$, *then* $\mathbf{E}_y \ll_K \mathbf{E}_1^* \ll_K \mathbf{E}_2^* \ll_K \mathbf{E}_3^* \ll_K \mathbf{E}_x$.

(c) *If* $\alpha, \delta > 1$ *and either* $\mu_1^* \leqslant \mu < \mu_3^*, d = d_-^*$ *or* $\mu_2^* < \mu < \mu_1^*, d = d_-^*$, *then* $\mathbf{E}_1^* = \mathbf{E}_2^* = \mathbf{E}_3^*$.

Proof. *(a)* follows directly from Lemma 3.2.11 and Lemma 4.1.1.

(b) By (4.1.9), a direct calculation shows

$$x_1^* - x_3^* = \frac{\sqrt{\widetilde{\Delta}_2}}{2\,\widetilde{A}_2} < 0 \implies 0 < x_1^* < x_3^*.$$

Next, set $h_1(x) = \ell_1(x) - x$. By (3.2.3),

$$\ell_1'(x) < 0, \quad \forall x \geqslant 0 \implies h_1'(x) = \ell_1'(x) - 1 < 0.$$

This is strictly decreasing in the first quadrant. Since x_3^* and x_1^* are on both $y = -x - \tilde{k}_1$ and $y = \ell_1(x)$, we have

$$\ell_1(x_1^*) = -x_1^* - \tilde{k}_1, \quad \ell_1(x_3^*) = -x_3^* - \tilde{k}_1.$$

From(4.1.10), we obtain

$$-x_1^* - \tilde{k}_1 = x_3^*, \quad -x_3^* - \tilde{k}_1 = x_1^*.$$

Hence,

$$\ell_1(x_1^*) = x_3^*, \quad \ell_1(x_3^*) = x_1^* \implies h_1(x_1^*) = x_3^* - x_1^* > 0, \quad h_1(x_3^*) = x_1^* - x_3^* < 0.$$

The Intermediate Value Theorem implies,

$$0 < x_1^* < x_2^* < x_3^*,$$

and Lemma 3.2.11 yields

$$\mathbf{E}_y \ll_K \mathbf{E}_1^* \ll_K \mathbf{E}_2^* \ll_K \mathbf{E}_3^* \ll_K \mathbf{E}_x.$$

(c) Letting $d = d_-^*$ yields

$$\ell_1(x_1^*) = x_3^* = x_1^* = \ell_1(x_3^*).$$

This shows $x_2^* = x_1^* = x_3^*$. Equivalently, $\mathbf{E}_1^* = \mathbf{E}_2^* = \mathbf{E}_3^*$. □

4.2 Global Dynamics and Stability

In order to determine the basins of attraction of $\mathbf{E}_1^*, \mathbf{E}_3^*$, $\mathbf{E}_x$, and $\mathbf{E}_y$, in the symmetric case, we first need to determine the invariant regions.

Define the regions

$$\mathcal{R}^- := \{(x, y) : 0 < y < x\}, \quad \mathcal{R}^+ := \{(x, y) : 0 < x < y\}, \quad \mathcal{R}^0 := \{(x, x) : x > 0\}.$$

Proposition 4.2.1. *Consider system* (3.1.3) *with* (4.0.1). *If* $0 < \delta < 1 + \frac{1}{d}$, *every interior orbit on* $\mathcal{R}^0$ *converges to* $\mathbf{E}_2^*$ *and* $\mathcal{R}^-$ *and* $\mathcal{R}^+$ *are forward invariant under* $\mathbf{T}$.

Proof. That every interior orbit converges to $\mathcal{R}^0$ if $0 < \delta < 1 + \frac{1}{d}$ follows from Theorem 2.5.1 and the fact that $\mathbf{E}_0$ is unstable.

Now, we prove the forward invariance of $\mathcal{R}^-$ and $\mathcal{R}^+$. By Lemma 3.2.7, $\mathbf{T}$ is strongly competitive in $\text{int}\mathbb{R}_+^2$. Hence, for any initial point (x_0, y_0) with $0 < y_0 < x_0$, we have

$$\mathbf{T}(y_0, y_0) = (q, q) \ll_K \mathbf{T}(x_0, y_0) = (x_1, y_1), \quad \text{for some } \ q > 0.$$

Note that

$$(q,q) \ll_K (x_1,y_1) \iff 0<q<x_1,\ q>y_1>0 \implies 0<y_1<q<x_1.$$

Therefore, $0<y_1<x_1$. Since the same argument applies at each step,

$$(x_t,y_t)\in\mathcal{R}^- \implies (x_{t+1},y_{t+1})\in\mathcal{R}^-,\quad \forall t\in\mathbb{N}.$$

A similar argument then shows

$$(x_t,y_t)\in\mathcal{R}^+ \implies (x_{t+1},y_{t+1})\in\mathcal{R}^+,\quad \forall t\in\mathbb{N}.$$

□

In order to determine the local stability of $\mathbf{E}_x$ and $\mathbf{E}_y$, when there is a unique interior fixed point, we require several algebraic relations among the parameter thresholds which are summarized in the following lemma. Define

$$\alpha^* := \frac{(\mu d+\delta-1)+\sqrt{[\mu d-(\delta-1)]^2+4\mu}}{2(\delta-1)},\quad \alpha_* := \frac{1+\sqrt{1+\frac{4\mu}{(\delta-1)^2}}}{2}. \tag{4.2.1}$$

Lemma 4.2.1. *The following statements hold.*

(a) If $1<\delta<1+\frac{1}{d}$, then $\alpha^*>1$.

(b) If $\alpha,\delta>1$, then $\mu\geqslant\mu_1^* \iff \alpha\leqslant\alpha_*$ and $\alpha_*>1$.

(c) If $\alpha,\delta>1, 0<d<\frac{1}{\delta-1}$, and $\mu<\mu_1^*$, then $d>d_{\mathrm{tc}}^* \iff 1<\alpha<\alpha^*$.

(d) If $\alpha,\delta>1$ and $0<d<\frac{1}{\delta-1}$, then $1<\alpha_*<\alpha^*$.

Proof. The proof is given in Appendix A.4. □

In the next Lemma, we consider the stability of the boundary fixed points under the symmetry condition (4.0.1).

Lemma 4.2.2. *Consider system* (3.1.3) *with* (4.0.1)*. If $\mathbf{E}_x$ and $\mathbf{E}_y$ are hyperbolic, then they are locally asymptotically stable if and only if*

$$1<\delta<1+\frac{1}{d}\quad \textit{and}\quad \alpha>\alpha^*, \tag{4.2.2}$$

where α^* is given by (4.2.1)*. Condition* (4.2.2) *is equivalent to each of the following conditions:*

(i) $\alpha>1$, $\delta>1$, $0<\mu<\mu_4^*$, and $0<d<\frac{1}{\delta-1}$,

(ii) $\alpha>1$, $\delta>1$, $0<d<d_{\mathrm{tc}}^*$ and $d<\frac{1}{\delta-1}$.

Proof. Under (4.0.1), α_1^*, and α_2^* in (3.2.25) coincide, and both simplify to (4.2.1). The conditions in Proposition 3.2.3 simplify to (4.2.2). By Lemma 4.2.1, $\alpha^*>1$. Under $\delta>1$, a direct calculation shows

$$\alpha>\alpha^* \iff 4(\delta-1)^2\alpha^2-4\alpha(\delta-1)[\mu d+\delta-1]+4\mu d(\delta-1)-4\mu>0 \iff \mu<\mu_4^* \iff d<d_{\mathrm{tc}}^*.$$

□

Using Lemma 4.2.2 and Remark 4.1.1, we summarize the local stability of the fixed points when there is a unique interior fixed point. Recall, $\mathbf{E}_0$ is always unstable in this case.

Proposition 4.2.2. *Consider system* (3.1.3) *with* (4.0.1). *There is a unique interior fixed point, $\mathbf{E}^* = \mathbf{E}_2^*$, if and only if the parameters are in one of the regions given in Remark 4.1.1. In the regions listed in (a), $\mathbf{E}^*$ is locally asymptotically stable and in the regions listed in (b), $\mathbf{E}^*$ is a saddle. In case (b)(vii) with $d = d_{\mathrm{tc}}^*$, $\mathbf{E}_x, \mathbf{E}_y$ are both non-hyperbolic, but locally asymptotically stable. The stability of $\mathbf{E}_x$ and $\mathbf{E}_y$ in all parameter regimes is summarized below.*

(a) $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable when at least one of the following holds:

(i) $0 < \delta \leqslant 1$;

(ii) $0 < \alpha \leqslant 1$ *and* $0 < \delta < 1 + \frac{1}{d}$;

(iii) $\alpha, \delta > 1$, $d_-^* \leqslant d < \frac{1}{\delta - 1}$;

(iv) $\alpha, \delta > 1$, $\mu \geqslant \mu_3^*$, *and* $0 < d < \frac{1}{\delta - 1}$;

(v) $\alpha, \delta > 1$, $\mu_2^* < \mu < \mu_1^*$, *and* $d = d_-^*$.

(b) $\mathbf{E}_x$ and $\mathbf{E}_y$ are locally asymptotically stable when one of the following holds:

(vi) $\alpha, \delta > 1$, $0 < \mu \leqslant \mu_2^*$, *and* $0 < d < \frac{1}{\delta - 1}$;

(vii) $\alpha, \delta > 1$, $\mu_2^* < \mu < \mu_1^*$, *and* $0 < d \leqslant d_{\mathrm{tc}}^*$.

Proof. (a) In cases *(i)-(v)*, one of the hypotheses of Lemma 4.2.2 fails, so both $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable. In *(i)*, $\alpha \leqslant 1$ contradicts $\alpha^* > 1$. In *(ii)*, $0 < \delta \leqslant 1$ contradicts $\delta > 1$. In *(iii)*, $d_-^* \leqslant d > \frac{1}{\delta - 1}$, which implies $\mu > \mu_2^*$. But $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable since $d_-^* > d_{\mathrm{tc}}^*$ whenever $\mu \neq \mu_2^*$. In *(iv)*, Lemma 4.1.3(a) gives $\mu_4^* < \mu_3^*$, so $\mu > \mu_3^* > \mu_4^*$ contradicting $\mu < \mu_4^*$. Hence, $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable. In *(v)*, $d = d_-^*$ and $d_-^* > d_{\mathrm{tc}}^*$ whenever $\mu \neq \mu_2^*$ (Lemma 4.1.3) and hence $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable.

(b) In cases *(vi)-(vii)*, all conditions in Lemma 4.2.2 hold except at $d = d_{\mathrm{tc}}^*$. By Lemma 4.1.5, $\mathbf{E}_x$ and $\mathbf{E}_y$ coalesce with $\mathbf{E}_3^*$ and $\mathbf{E}_1^*$, respectively. Hence, we must analyze the local stability of $\mathbf{E}_2^* = (x_2^*, x_2^*)$.

Let

$$g_1 = 1 + d + (1 + \alpha)x_2^*, \quad g_2 = \delta + \mu x_2^*,$$

where x_2^* is the positive root of (4.1.4). By (3.2.23) and (3.2.24), a direct computation shows that $D\mathbf{T}(\mathbf{E}_2^*)$ is a symmetric matrix with eigenvalues

$$\lambda_1(\mathbf{E}_2^*) = \frac{1 + d}{(g_1)^2} + \frac{\delta}{(g_2)^2} = 1 - \frac{\alpha x_2^*}{(g_1)^2} - \frac{x_2^*}{(g_2)^2}, \quad \lambda_2(\mathbf{E}_2^*) = \frac{1 + d + 2\alpha x_2^*}{(g_1)^2} + \frac{\delta}{(g_2)^2}.$$

By Lemma 4.1.1, $x_2^* > 0 \iff 0 < \delta < 1 + \frac{1}{d}$. This shows $\lambda_1(\mathbf{E}_2^*) < 1$ whenever it exists

$$0 < \lambda_1(\mathbf{E}_2^*) < 1 \iff 0 < \delta < 1 + \frac{1}{d}.$$

By $f_1(x_2^*, y_2^*) = 1$, we obtain

$$\frac{1}{g_1} + \frac{1}{g_2} = 1. \tag{4.2.3}$$

Next, we show $\lambda_2(\mathbf{E}_2^*) > 1$. Define

$$S(x) := s_0 + s_1 x + s_2 x^2, \tag{4.2.4}$$

with

$$s_0 = (\alpha - 1) - \mu(d_{\mathrm{tc}}^*)^2, \quad s_1 = 2\mu(1+\alpha) - 2\mu\big(1 + d_{\mathrm{tc}}^*\big)(1+\alpha), \quad s_2 = -\mu(1+\alpha)^2.$$

From $\frac{1}{(g_2)^2} = 1 - \frac{2}{g_1} + \frac{1}{(g_1)^2}$ and $\lambda_2(\mathbf{E}_2^*) - 1 = x_2^* \left[\frac{\alpha-1}{(g_1)^2} - \frac{\mu}{(g_2)^2}\right]$, we obtain

$$\lambda_2(\mathbf{E}_2^*) - 1 = x_2^* \left[\frac{\alpha - 1 - \mu}{(g_1)^2} + \frac{2\mu}{g_1} - \mu\right]. \tag{4.2.5}$$

Multiplying both sides of (4.2.5) by $\frac{(g_1)^2}{x_2^*}$ gives

$$S(x_2^*) = \frac{(g_1)^2[\lambda_2(\mathbf{E}_2^*) - 1]}{x_2^*}.$$

Since $S(x)$ opens downward, the only positive root to $S(x) = 0$ is

$$x_* = \frac{\sqrt{\alpha - 1}}{\sqrt{\mu}(1+\alpha)} - \frac{d_{\mathrm{tc}}^*}{1+\alpha}.$$

Hence, we obtain

$$\lambda_2(\mathbf{E}_2^*) > 1 \iff S(x_2^*) > 0 \iff x_2^* < x_*.$$

Let $\zeta = \frac{\mu}{\mu_2^*} \in (1, \alpha)$. A direct computation shows

$$x_2^* - x_* = \frac{\delta - 1}{2\mu(1+\alpha)}\Phi(\zeta),$$

where

$$\Phi(\zeta) = -(\zeta+1) + \sqrt{(\zeta+1)^2 + 4\zeta(\alpha^2 - 1)} - 2\sqrt{\zeta}(\alpha - 1).$$

Since $\delta > 1$,

$$x_2^* < x_* \iff \Phi(\zeta) < 0.$$

For any $\alpha > 1$ and $\zeta \in (1, \alpha)$, a direct calculation shows

$$\begin{aligned}
\Phi(\zeta) < 0 &\iff (\zeta+1)^2 + 4\zeta(\alpha^2 - 1) < \big[(\zeta+1) + 2\sqrt{\zeta}(\alpha-1)\big]^2 \\
&\iff (\zeta+1)^2 + 4\zeta(\alpha^2 - 1) < \underbrace{(\zeta+1)^2 + 4(\zeta+1)\sqrt{\zeta}(\alpha-1) + 4\zeta(\alpha-1)^2}_{\left[(\zeta+1)+2\sqrt{\zeta}(\alpha-1)\right]^2} \\
&\iff \underbrace{4\zeta\big[(\alpha^2-1) - (\alpha-1)^2\big]}_{=4\zeta\cdot 2(\alpha-1)} < 4(\zeta+1)\sqrt{\zeta}(\alpha-1) \\
&\iff 2\zeta < (\zeta+1)\sqrt{\zeta} \iff (\sqrt{\zeta} - 1)^2 > 0 \quad (\zeta > 1).
\end{aligned}$$

Hence, $\Phi(\zeta) < 0$ and $\lambda_2(\mathbf{E}_2^*) > 1$. so $\mathbf{E}_2^*$ is an unstable saddle point. □

Biologically, Proposition 4.2.2*(a)* lists all parameter regimes where both species survive, whereas *(b)* lists all regimes in which one species excludes the other.

Remark 4.2.1. In Proposition 4.2.2*(a)(i)*, both nullcline asymptotes lie in the first quadrant and so $\tilde{x}$ and $\tilde{y}$ are irrelevant (see Figure 5.2*(a)*). In *(a)(iii-v)* , $\tilde{x} > \overline{x}$ (see Figure 3.2*(c)*). In *(a)(ii)*, both configurations can occur. In *(b)(vi-vii)*, $\tilde{x} < \overline{x}$ (see Figure 3.2*(d)*).

Combining the preceding lemmas, we obtain the complete global dynamics in the symmetric case.

Theorem 4.2.1. *Consider system* (3.1.3) *assuming symmetry condition* (4.0.1) *with expressions of* $\alpha^*, \cdots, d^*_-$ *listed in Table B.2.*

(a) The interior fixed point $\mathbf{E}_2^*$ *is globally asymptotically stable with respect to* $\mathrm{int}\mathbb{R}^2_+$ *if either*

1. $0 < \delta \leqslant 1$ *or* $\left[0 < \alpha \leqslant 1 \quad \text{and} \quad 0 < \delta < 1 + \frac{1}{d}\right]$,
or
2. $\alpha, \delta > 1$ *and one of the following holds:*
   i. $d^*_- \leqslant d < \frac{1}{\delta - 1}$, *or*
   ii. $\mu \geqslant \mu^*_3,\ 0 < d < \frac{1}{\delta-1}$,
   iii. $\mu^*_2 < \mu < \mu^*_1, \quad d = d^*_-$.

(b) If $(\alpha, \delta, \mu, d) \in (\mathcal{C}_1 \cup \mathcal{C}_2) \cap \mathcal{D}_1$,
then $\mathbf{E}_3^*$ *is globally asymptotically stable with respect to* $\mathcal{R}^-$ *and* $\mathbf{E}_1^*$ *is globally asymptotically stable with respect to* $\mathcal{R}^+$*.* $\mathbf{E}_2^*$ *is a saddle.*

(c) If $\alpha, \delta > 1$ *and*

$$\left[0 < \mu \leqslant \mu^*_2,\ 0 < d < \tfrac{1}{\delta-1}\right] \quad \text{or} \quad \left[\mu^*_2 < \mu < \mu^*_1,\ 0 < d \leqslant d^*_{\mathrm{tc}}\right],$$

then $\mathbf{E}_x$ *is globally asymptotically stable with respect to* $\mathcal{R}^- \cup \{(x,0) : x > 0\}$ *and* $\mathbf{E}_y$ *is globally asymptotically stable with respect to* $\mathcal{R}^+ \cup \{(0,y) : y > 0\}$*.*

(d) If none of the above is satisfied, then $\mathbf{E}_0$ *is globally asymptotically stable in the entire first quadrant.*

Proof. (a) In either parameter regime, Proposition 4.2.2 implies that $\mathbf{E}_x, \mathbf{E}_y$ is unstable and leaves a unique interior fixed point $\mathbf{E}_2^*$. Exactly the same argument in Theorem 3.2.6(a) applies and the conclusion follows.

(b) Theorem 3.2.6(c) shows that the boundary points $\mathbf{E}_x$ and $\mathbf{E}_y$ are necessarily unstable whenever $\mathbf{E}_2^*$, $\mathbf{E}_3^*$, and $\mathbf{E}_1^*$ exist. By Proposition 4.1.1(b),

$$\mathbf{E}_y \ll_K \mathbf{E}_1^* \ll_K \mathbf{E}_2^* \ll_K \mathbf{E}_3^* \ll_K \mathbf{E}_x.$$

The proof that $\mathbf{E}_1^*, \mathbf{E}_3^*$ are stable and $\mathbf{E}_2^*$ unstable follows by exactly the same argument as in Theorem 3.2.6(c)(ii). Since $\mathcal{R}^-$ and $\mathcal{R}^+$ are invariant (Proposition 4.2.1) and each contains one attractor, Theorem 3.2.1 implies that every interior orbit in $\mathcal{R}^-$ converges to $\mathbf{E}_3^*$, and every interior orbit in $\mathcal{R}^+$ converges to $\mathbf{E}_1^*$.

(c) By Proposition 4.2.2, $\mathbf{E}_x$ and $\mathbf{E}_y$ are stable, and $\mathbf{E}_2^*$ is the unique interior fixed point. Combining Theorem 3.2.1 with Proposition 4.2.1, we conclude that $\mathbf{E}_x$ (respectively, $\mathbf{E}_y$) is globally asymptotically stable with respect to $\mathcal{R}^- \cup \{(x,0) : x > 0\}$ (respectively, $\mathcal{R}^+ \cup \{(0,y) : y > 0\}$).

(d) If the parameters do not lie in any of the above regimes, then $\mathbf{E}_0$ is the only fixed point in the first quadrant. Convergence of orbits to $\mathbf{E}_0$ follows from Theorems 3.2.1 and 3.2.3. $\square$

4.2.1 Continuum of Fixed Points

In this section only, we assume $\mu = 0$ and $\alpha = 1$. Biologically, for each species, $\mu = 0$ eliminates intra-specific competition among newborns, and $\alpha = 1$ implies that the inter-specific competition coefficient among adults of each species is equal to their intra-specific competition coefficient.

Define

$$K_0 := \frac{\delta}{\delta - 1} - (1 + d).$$

Proposition 4.2.3. *Consider system* (3.1.3) *with* (4.0.1). *If* $\mu = 0, \alpha = 1$ *and* $1 < \delta < 1 + \frac{1}{d}$, *then every orbit, except the one starting from the origin, converges to a point on* $x + y = K_0$.

Proof. Under the given conditions, system (3.1.3) reduces to

$$x_{t+1} = T_1(x_t, y_t) = x_t\, f(x_t, y_t), \tag{4.2.6}$$
$$y_{t+1} = T_2(x_t, y_t) = y_t\, f(x_t, y_t). \tag{4.2.7}$$

with

$$f(x, y) = \frac{1}{1 + d + x + y} + \frac{1}{\delta}.$$

The nontrivial x- and y-nullclines are the same, yielding a continuum of fixed points. If $\delta \leqslant 1$, no positive solution exists. Otherwise,

$$f(x, y) = 1 \iff x + y = K_0.$$

Hence, every (x, y) with $x + y = K_0$ is a fixed point. A direct calculation shows $x + y = K_0 > 0$ if and only if $1 < \delta < 1 + \frac{1}{d}$. Letting

$$h_0(x) = K_0 - x, \quad k_0(y) = K_0 - y,$$

the next-iterate operators (see definition in [26]) become

$$\mathcal{L}_{h_0}(x, y) = T_2(x, y) - h_0(T_1(x, y)) = yf(x, y) - (K_0 - xf(x, y)) = (x + y)f(x, y) - K_0,$$
$$\mathcal{L}_{k_0}(x, y) = T_2(x, y) - k_0(T_1(x, y)) = (x + y)f(x, y) - K_0 = \mathcal{L}_{h_0}(x, y).$$

Let $u = x + y$ and $g(u) = uf(u)$. A direct calculation shows

$$g'(u) = \frac{1 + d}{(1 + d + u)^2} + \frac{1}{\delta} > 0, \quad \forall\ u \geqslant 0.$$

So $g(u)$ is strictly increasing in u. At $u = K_0$,

$$1 + d + K_0 = \frac{\delta}{\delta - 1} \implies g(K_0) = K_0.$$

Thus whenever $0 < u < K_0$, strict monotonicity gives

$$g(u) < g(K_0) = K_0 \implies uf(u) < K_0 \implies \mathcal{L}_{h_0}(x, y) < 0,$$

and if $u > K_0 > 0$, then $\mathcal{L}_{h_0}(x, y) > 0$. By Lemma 3.4 and Theorem 3.5 from [26], the conclusion follows.

□

Chapter 5

Numerical Results and Bifurcation Analysis

First, we provide phase portraits to demonstrate all the possible dynamical outcomes in model (3.1.3) in both the symmetric and general cases, and then, we provide bifurcation diagrams to illustrate the saddle-node and pitchfork bifurcations that can occur.

5.1 Phase Portraits

5.1.1 Symmetric Case

In the symmetric case, Theorem 4.2.1 partitions the parameter space into regions where all the different dynamical outcomes occur. Figures 5.1 and 5.2 show schematic phase portraits demonstrating each possible case. Figure 5.1 illustrates that there is an entire line given by $x + y = K_0$ of interior fixed points that are stable, but not asymptotically stable, and all solutions converge to one of the fixed points on the line, depending on the initial conditions.

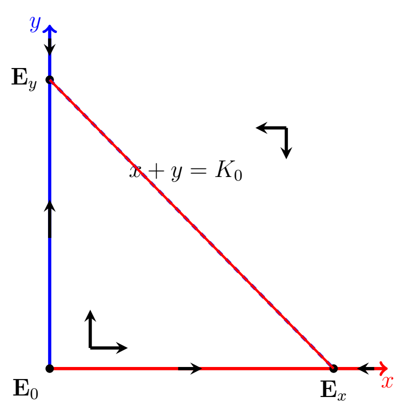


Figure 5.1: Phase portrait illustrating the continuum of stable interior fixed points when $\mu = 0, \alpha = 1$, and $1 < \delta < 1 + \frac{1}{d}$. The blue curve on the y axis is the trivial x-nullcline and the red curve on the y-axis is the trivial y-nullcline. The diagonal line, $x + y = K_0$, shown by a dashed red-blue line, shows that the nontrivial nullclines for both species are the same.

The next figure illustrates the remaining possible cases under the symmetry assumption (3.1.6). Under this assumption, there is at least one interior fixed point.

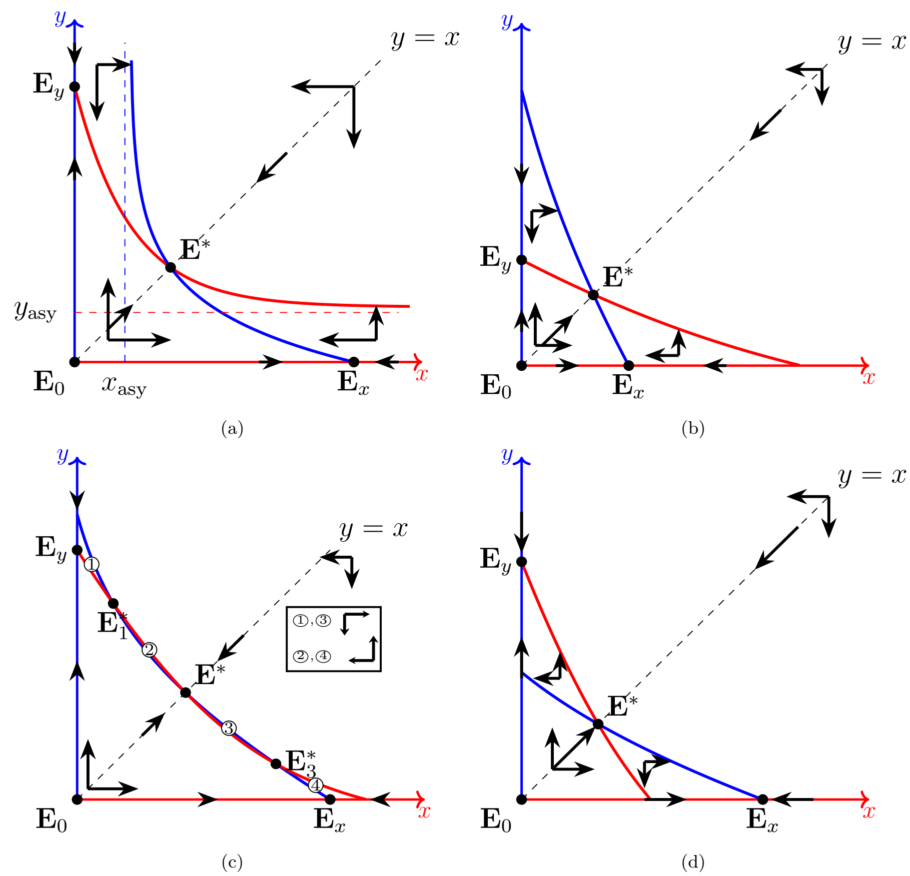


Figure 5.2: Phase portraits illustrating all the remaining possible cases in Theorem 4.2.1 (excluding the case in which $\mathbf{E}_0$ is globally asymptotically stable with respect to $\mathbb{R}_+^2$). The blue curves are the x-nullclines and the red curves are the y-nullclines. Every interior orbit on the diagonal converges to $\mathbf{E}^*$. By Theorem 3.2.1, every orbit starting in each region converges monotonically to a locally asymptotically stable fixed point in that region. In (a),(b), all interior orbits converge to $\mathbf{E}^*$. In (c), orbits in $\mathcal{R}^-$ converge to $\mathbf{E}_3^*$ and those in $\mathcal{R}^+$ to $\mathbf{E}_1^*$. In (d), orbits in $\mathcal{R}^-$ converge to $\mathbf{E}_x$ and those in $\mathcal{R}^+$ to $\mathbf{E}_y$.

Note that Figure 5.2(c) illustrates the case in which there are three interior fixed points. This case has not been observed in other two-species competition models [4, 7, 21].

5.1.2 General Case

Here, we illustrate the remaining phase portraits that can occur for model (3.1.3) that do not occur under the symmetry assumption. Figure 5.3 illustrate schematic phase portraits where one of the species drives the other to extinction, shown to be possible in Theorem 3.2.4.

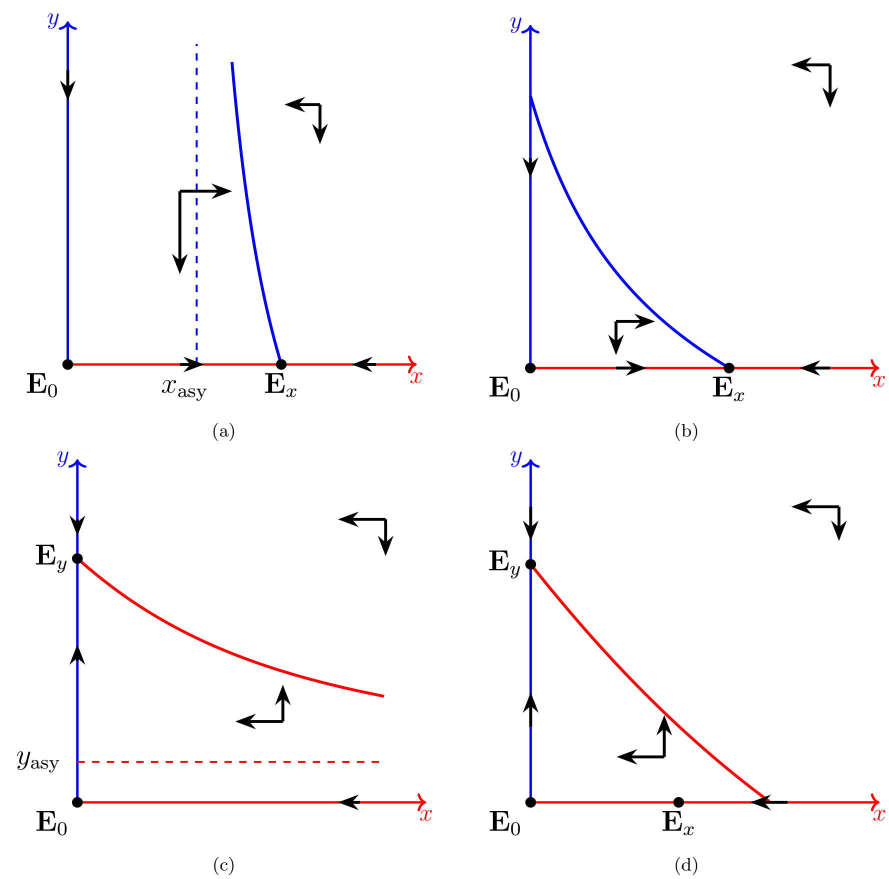


Figure 5.3: Phase portraits illustrating Theorem 3.2.4. Blue curves are the x-nullclines and red curves are the y-nullclines. By Theorem 3.2.1, every orbit starting in each region converges monotonically to a locally asymptotically stable fixed point in that region. (a)–(b) show regimes in which only the non-trivial x-nullcline exists and all interior orbits converge to the boundary fixed point $\mathbf{E}_x$. (c)–(d) show regimes in which only the non-trivial y-nullcline exists and all interior orbits converge to the boundary fixed point $\mathbf{E}_y$.

Theorem 3.2.5 covers the rest of the possible dynamical outcomes, i.e., there are no interior fixed points or there are two. Figure 5.4 illustrates each of these possibilities.

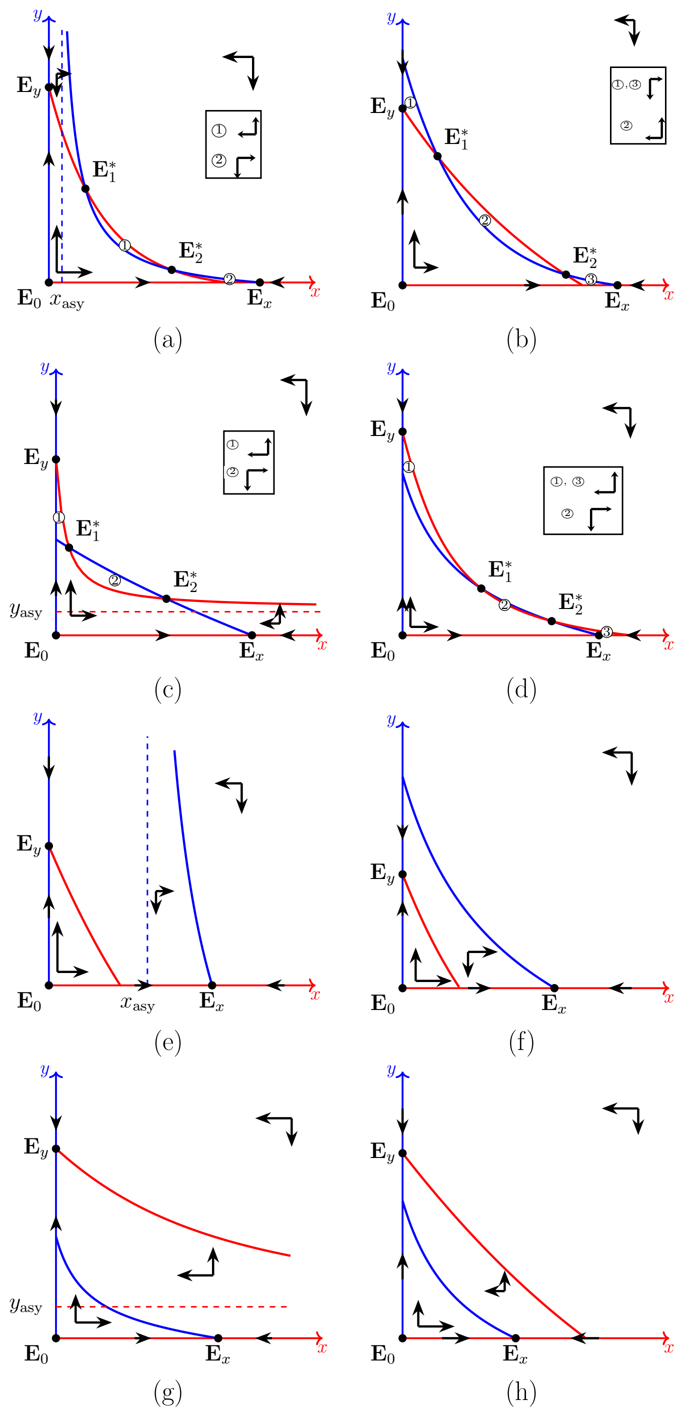


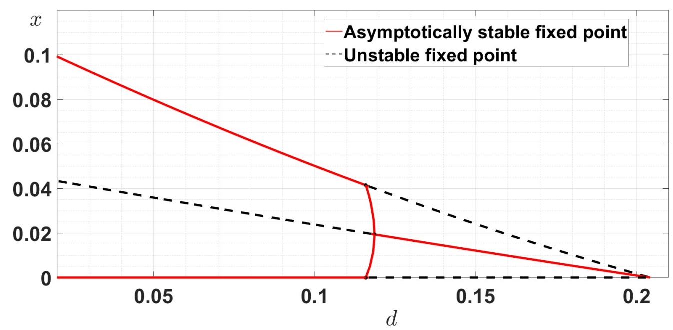
Figure 5.4: Phase portraits illustrating Theorem 3.2.5. Parameter values are summarized in Table B.1. The blue curves are the x-nullclines and the red curves are the y-nullclines. In the graphs on the right, the dashed curves represent the horizontal and vertical asymptotes that lie in the first quadrant. By Theorem 3.2.1, every orbit starting in each region converges monotonically to a locally asymptotically stable fixed point in that region. In (a–b), there are two interior fixed points. Orbits converge to $\mathbf{E}_1^*$ or $\mathbf{E}_x$. In (c–d), there are two fixed points. Orbits converge to $\mathbf{E}_2^*$ or $\mathbf{E}_y$. In (e–f), there are no interior fixed points. All orbits converge to $\mathbf{E}_x$. In (g–h), there are no there are no interior fixed points. All orbits converge to $\mathbf{E}_y$.

5.2 Sequences of Bifurcations

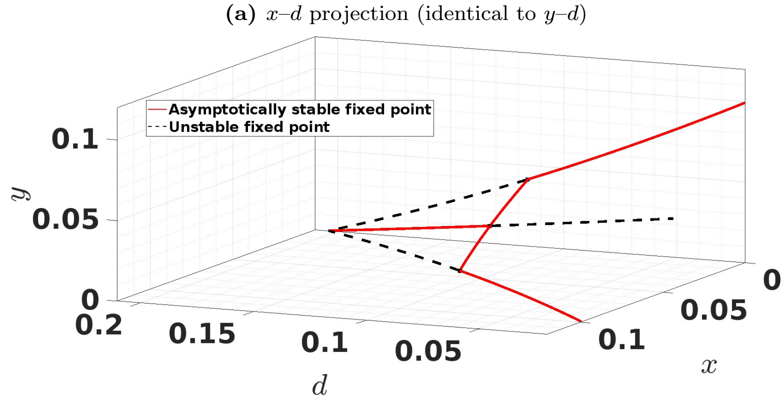
All bifurcation diagrams were generated using MatContM [12].

5.2.1 Sequences of Bifurcations Including a Pitchfork Bifurcation

In the symmetric case (see Theorem 4.2.1), varying the natural mortality coefficient d of adults can produce a pitchfork bifurcation. Reducing d allows more adults to survive each breeding cycle, which increases the adult populations and thus strengthens both inter- and intra- specific competition among adults. Once d crosses the threshold d_-^*, the coexistence state on the diagonal loses stability and two coexistence states that are symmetric about the diagonal appear. Figure 5.5 illustrates how three interior fixed points merge before coalescing with the origin as d.



(a) x–d projection (identical to y–d)

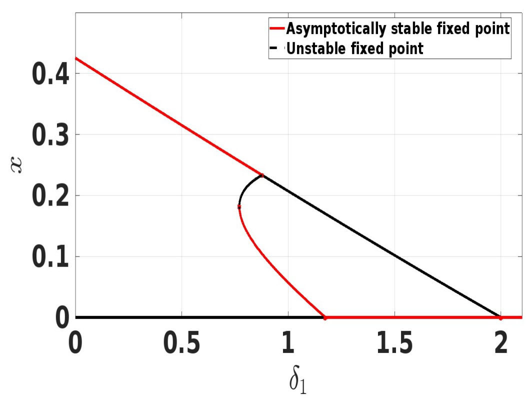


(b) 3-D view

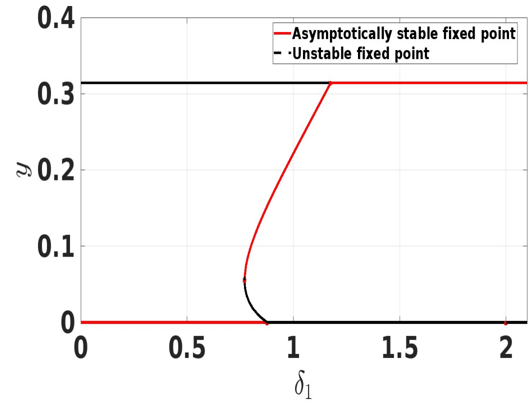
Figure 5.5: Sequence of bifurcations including a pitchfork bifurcation for the symmetric parameter set ($\alpha = 2.13$, $\mu = 35.2$, $\delta = 5.9$) as d increases from zero to 0.21. (a) shows the two dimensional projection of (b), a three dimensional bifurcation diagram . At d close to zero, the boundary fixed points $\mathbf{E}_x$ and $\mathbf{E}_y$ are both locally asymptotically stable, there is a unique interior fixed point $\mathbf{E}_2^*$ that is unstable, and the origin $\mathbf{E}_0$ is also unstable. When $d \approx 0.1159$, two new interior fixed points $\mathbf{E}_3^*$ and $\mathbf{E}_1^*$ appear from transcritical bifurcations with $\mathbf{E}_x$ and $\mathbf{E}_y$, respectively. At $d \approx 0.1186$ all three interior fixed points $\mathbf{E}_1^*$, $\mathbf{E}_2^*$, and $\mathbf{E}_3^*$ collide in a pitchfork bifurcation, leaving $\mathbf{E}_2^*$ globally asymptotically stable. At $d \approx 0.204$, $\mathbf{E}_x$ and $\mathbf{E}_y$ together with $\mathbf{E}_2^*$ coalesce with $\mathbf{E}_0$ and leave the first quadrant, leaving $\mathbf{E}_0$ globally asymptotically stable.

5.2.2 Sequences of Bifurcations Including a Saddle-Node Bifurcation

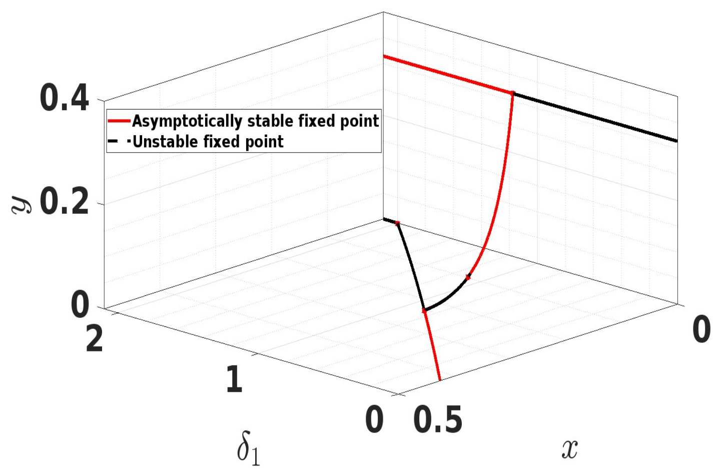
Next, in the general case we fix all other parameters and vary species X's newborn cohort mortality to adult reproduction coefficient, $\delta_1 = \frac{1+D_1}{r_1}$. Figure 5.6 illustrates the saddle–node bifurcation and subsequent transcritical bifurcations of $\mathbf{E}_x$ and $\mathbf{E}_y$, as described in Theorem 3.2.5.



(a) x–δ_1 projection



(b) y–δ_1 projection

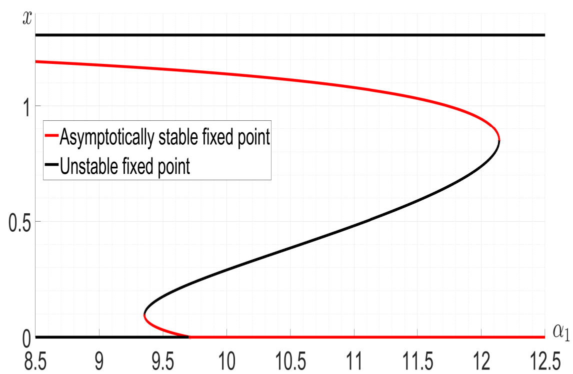


(c) 3-D view

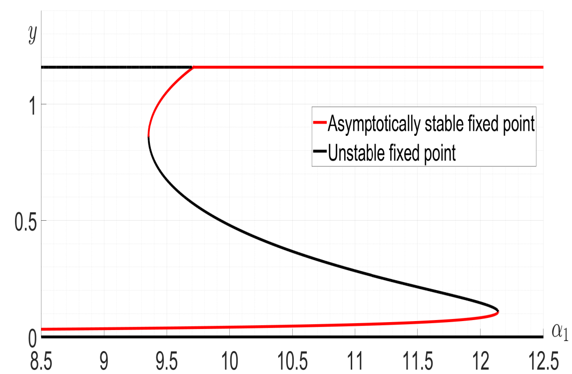
Figure 5.6: Sequence of bifurcations including a saddle–node bifurcation in the general case. (a) and (b) show the 2-D projections, and (c) shows the 3-D view. Parameter values are given by $\alpha_1 = 15$, $\alpha_2 = 3$, $\delta_2 = 2$, $d_1 = 1$, $d_2 = 0.3$, $\mu_1 = 4$, $\mu_2 = 2$ and δ_1 increases from zero to 2.1. For δ_1 near zero, $\mathbf{E}_x$ is locally asymptotically stable and $\mathbf{E}_y$ and $\mathbf{E}_0$ are both unstable. At $\delta_1 \approx 0.7704$, two interior fixed points (ordered as $\mathbf{E}_y \ll_K \mathbf{E}_1^* \ll_K \mathbf{E}_2^* \ll_K \mathbf{E}_x$) are born via a saddle–node bifurcation, where $\mathbf{E}_1^*$ is locally asymptotically stable and $\mathbf{E}_2^*$ is unstable. The unstable interior fixed point $\mathbf{E}_2^*$ leaves the first quadrant through a transcritical bifurcation with $\mathbf{E}_x$ at $\delta_1 \approx 0.8776$. The stable interior fixed point $\mathbf{E}_2^*$ leaves the first quadrant through a subsequent transcritical bifurcation with $\mathbf{E}_y$ at $\delta_1 \approx 1.175$. At $\delta_1 \approx 2.0$, the boundary fixed point $\mathbf{E}_x$ undergoes a transcritical bifurcation with $\mathbf{E}_0$ leaving $\mathbf{E}_y$ globally asymptotically stable.

5.2.3 Sequences of Bifurcations Including Two Saddle-Node Bifurcations

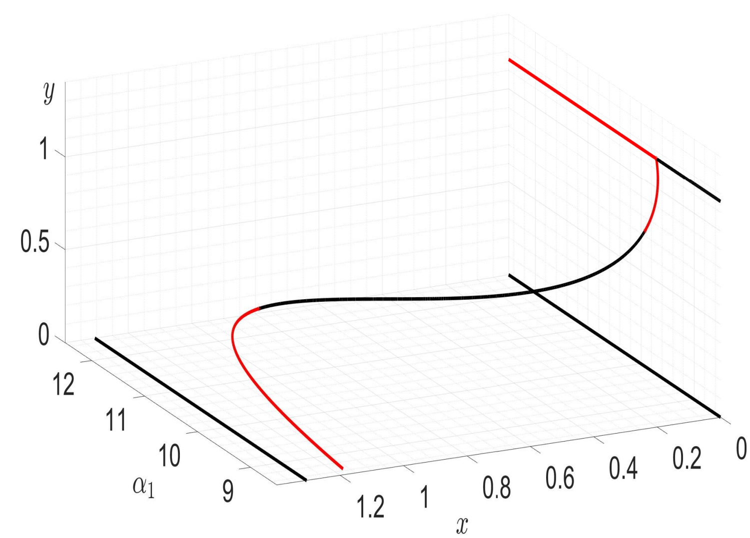
Finally, we give an example, in the general case, that illustrates that there can be zero, one, two, or three interior fixed points caused by two saddle-node bifurcations and a transcritical bifurcation. We fix all other parameters and vary $\alpha_1 = \frac{C_{12}}{C_{22}}$, species Y's inter- to intra-specific adult competition ratio. The bifurcations are summarized below.



(a) x–α_1 projection



(b) y–α_1 projection



(c) 3-D view

Figure 5.7: Sequence of bifurcations including two saddle–node bifurcations in the general case. (a) and (b) show the 2-D projections, and (c) shows the 3-D view. Parameter values are given by $\alpha_2 = 6.9$, $\delta_1 = 1.083$, $\delta_2 = 1.1$, $d_1 = 0.8$, $d_2 = 0.1$, $\mu_1 = 0.3$, $\mu_2 = 0.6$ and α_1 increases from 8.5 to 12.5. For α_1 near 8.5, there is a unique interior fixed point $\mathbf{E}_3^*$ that is globally asymptotically stable, whereas both $\mathbf{E}_x$ and $\mathbf{E}_y$ are unstable. As $\alpha_1 \approx 9.35$, the first saddle-node bifurcation occurs, creating two interior fixed points that can be ordered as $\mathbf{E}_1^* \ll_K \mathbf{E}_2^*$. Here, $\mathbf{E}_1^*$ is locally asymptotically stable, $\mathbf{E}_2^*$ is unstable, and $\mathbf{E}_3^*$ remains locally asymptotically stable but loses its global attractivity. At $\alpha_1 \approx 9.71$, $\mathbf{E}_1^*$ coalesces with $\mathbf{E}_y$ in a transcritical bifurcation and then leaves the first quadrant, leaving $\mathbf{E}_y$ locally asymptotically stable. Finally, as $\alpha_1 \approx 12.14$, the second saddle-node bifurcation annihilates $\mathbf{E}_2^*$ and $\mathbf{E}_3^*$, leaving $\mathbf{E}_y$ globally asymptotically stable. Throughout, $\mathbf{E}_0$ and $\mathbf{E}_x$ remain unstable.

Chapter 6

Conclusions and Future Directions

This thesis analyzes a two-species, discrete-time, single-cycle maturation competition model obtained by adapting the single-species framework in [27] to two species with reproduction delay τ to be zero. Therefore, we are assuming that the cohort of newborns takes exactly one cycle before they are able to contribute to the growth of the population. The associated map $\mathbf{T}$ is proven competitive, globally injective and it satisfies Condition $(O+)$ as in Lemma 2.5.2, which ensures that every interior orbit converges to a fixed point by Theorem 2.5.1. Sufficient conditions are obtained for global convergence to the origin, to the boundary fixed point, and to a unique interior fixed point, and are also obtained for two new types of bistability regimes. The first bistability regime contains one stable and one unstable interior fixed point together with one stable and one unstable boundary fixed points. The second bistability regime has three interior fixed points, two are attractors and they are separated by the third, a saddle. Both boundary fixed points are unstable.

More specifically, in the general case, Theorem 3.2.3 shows that if a species' newborn cohort mortality to adult reproduction ratio ($\frac{1+D_i}{r_i}$) is larger than its survival threshold $1+\frac{1}{d_i}$, then that species dies out. This is one of the classical outcomes discovered in the discrete Leslie–Gower competition model (see [5]). Theorem 3.2.4 shows that if one species satisfies $\frac{1+D_i}{r_i} > 1+\frac{1}{d_i}$ while the other species' newborn cohort mortality to adult reproduction ratio is below the survival ratio, then only the latter species survives and approaches its carrying capacity. In this case, the carrying capacity is exactly the x or y coordinate of the boundary fixed point for this species. Theorem 3.2.6(i) shows that when both species' newborn cohort mortality to adult reproduction ratio are sufficiently small ($\frac{1+D_i}{r_i} \leqslant 1$), and the combined inter- to intra-specific adult competition ratio ($\frac{C_{12}C_{21}}{C_{22}C_{11}}$) is weak enough, then coexistence between the two species is possible. Theorem 3.2.6(b) shows that there is an adult competition threshold for each species such that if both species' inter- to intra-specific adult competition ratios are larger than their threshold defined in (3.2.25), there is a unique coexistence fixed point that is a saddle and the only species that survives is determined by the initial conditions. Thus the model (3.1.3) recovers all the classical outcomes. The model can also have up to three interior fixed points and the two bistability regimes already described. We give an example in which there are two interior fixed points. This occurs via a saddle-node bifurcation. Each of these fixed points eventually disappears by transcritical bifurcations involving an interior fixed point and a fixed point on one of the axes.

In the symmetric case, certain ratios of the corresponding parameters are identical for the two species. Unlike in the general case, there can only be zero, one, or three interior fixed points, not two. A saddle-node bifurcation cannot occur. If $\frac{1+D}{r} \geqslant 1+\frac{1}{d}$, then both species die out. If instead, $\frac{1+D}{r} < 1+\frac{1}{d}$, then there can be either one or three interior fixed points. One of them is always on the diagonal and the other two are symmetric about the diagonal. When there is a unique interior fixed point, it can be a saddle or globally asymptotically stable. When it is globally asymptotically stable, both species coexist regardless of the initial populations. When it is a saddle, the boundary fixed points are attractive and their basins of attraction are separated by the diagonal. This agrees with Theorem 3.2 of [4]. It is shown that when the unique symmetric fixed point on the diagonal exists, there can be simultaneous transcritical bifurcations with the fixed points on the axes giving birth to two more interior fixed points that are asymptotically stable that then eventually disappear through a pitchfork bifurcation. When the three interior fixed points all exist, the interior fixed point on the diagonal and both boundary fixed points are unstable. The basins of attraction of the two asymptotically stable interior fixed points that are symmetric about the diagonal are still separated by the diagonal.

Next, we compare the dynamics of our model with other existing models. Because our model can have more than one interior fixed point, our model captures richer dynamics than the classical two-species competition models [4, 7, 21]. Besides the four classical outcomes, the four-dimensional juvenile–adult competition model in [6] admits stable or unstable two-cycles and the six-dimensional three-stage, competition model in [32] can undergo period-doubling bifurcations and chaos, not possible in our model. However, again neither one of their high dimensional models can exhibit the multiple interior fixed points, and related dynamics possible in our two dimensional model. Our model also exhibits different dynamics compared to the stage-structured competition models in [6, 32], while remaining only two-dimensional.

Although our model reveals richer dynamics than the two-species competition models in [4, 7, 21], our analysis remains incomplete in several aspects. First, we have proved that there are at most three interior fixed points in the general case. In the symmetric case, we proved there can be zero, one, or three interior fixed points. Unlike in the symmetric case, in the general case, we were only able to determine sufficient conditions for the precise number of interior fixed points as a function of parameters. Next, our analysis is restricted to the case where the newborn cohort becomes mature at the end of only one cycle. This is not biologically realistic for many species. In order to capture more realistic maturation steps, we could introduce reproduction delays $\tau_1, \tau_2 \in \mathbb{N}$ following the single-species framework for immature cohorts as in [27]. This modification yields a $\tau_1 + \tau_2 + 2$ dimensional model,

$$X_{t+1} = \frac{X_t}{1 + d_1 + C_{11}X_t + C_{12}Y_t} + \frac{D_1 r_1 X_{t-\tau_1}}{D_1\beta_1 + (\beta_1 - 1)C_1 r_1 X_{t-\tau_1}}, \tag{6.0.1a}$$

$$Y_{t+1} = \frac{Y_t}{1 + d_2 + C_{22}Y_t + C_{21}X_t} + \frac{D_2 r_2 Y_{t-\tau_2}}{D_2\beta_2 + (\beta_2 - 1)C_2 r_2 Y_{t-\tau_2}}, \tag{6.0.1b}$$

where $\beta_i = (1 + D_i)^{\tau_i+1}$ for $i \in \{1, 2\}$. Since the model is no longer planar, Theorem 2.5.1 in [25] no longer applies. Note that the Order Interval Trichotomy (Theorem 2.5.2) still holds in higher dimensional cases so it remains a useful tool once we can verify hypothesis 2.5.1. At the same time, we expect the presence of delays can introduce richer dynamics than the non-delayed case and we reserve this direction for future work.

In summary, this thesis shows that a planar competition model with single-cycle maturation not only recovers all the outcomes of the classical planar competition models, but also admits two new bistable regimes involving multiple interior fixed points. Hence, this thesis provides a bridge between the classical planar competition models [4, 7, 21] and the higher dimensional stage-structured competition models ([6, 32]). The most important next step is to reintroduce explicit maturation delays in the model. This will raise the dimension of the model and likely produce new types of bifurcations that cannot occur in the non-delayed model.

Appendix A

Auxiliary Proofs

A.1 Coefficients of the Quartic Equation

The coefficients for

$$\widetilde{Q}(x) = \eta_4 x^4 + \eta_3 x^3 + \eta_2 x^2 + \eta_1 x + \eta_0,$$

are

$$\begin{aligned}
\eta_4 &= (1-\alpha_1\alpha_2)\mu_1^2\mu_2, \\
\eta_3 &= -\mu_1\left[2\alpha_1\alpha_2\mu_2(-1+\delta_1) - 2\mu_2(-1+d_1\mu_1+\delta_1)\right. \\
&\qquad \left. -\alpha_1^2\alpha_2\mu_1(-1+\delta_2) + \alpha_1\mu_1(-1+d_2\mu_2+d_1\alpha_2\mu_2+\delta_2)\right], \\
\eta_2 &= \mu_2\left[d_1^2\mu_1^2 + \mu_1(-2+4d_1(-1+\delta_1)) + (-1+\delta_1)^2\right] \\
&\quad + \alpha_1^2\mu_1\left[\mu_1(-1+d_2(-1+\delta_2)) + 2\alpha_2(-1+\delta_1)(-1+\delta_2)\right] \\
&\quad - \alpha_1\left[\alpha_2\mu_2(-1+\delta_1)^2 + \mu_1\left(\alpha_2\mu_2(-1+2d_1(-1+\delta_1))\right.\right. \\
&\qquad \left.\left. +2d_2\mu_2(-1+\delta_1) + 2(-1+\delta_1)(-1+\delta_2)\right) + d_1\mu_1^2(-1+d_2\mu_2+\delta_2)\right], \qquad \text{(A.1.1)} \\
\eta_1 &= 2\mu_2(-1+d_1(-1+\delta_1))(-1+d_1\mu_1+\delta_1) \\
&\quad + \alpha_1^2(-1+\delta_1)\left(2\mu_1(-1+d_2(-1+\delta_2)) + \alpha_2(-1+\delta_1)(-1+\delta_2)\right) \\
&\quad - \alpha_1\left[(-1+\delta_1)\left(\alpha_2\mu_2(-1+d_1(-1+\delta_1)) + d_2\mu_2(-1+\delta_1)\right.\right. \\
&\qquad \left.\left. +(-1+\delta_1)(-1+\delta_2)\right) + \mu_1(-1+2d_1(-1+\delta_1))(-1+d_2\mu_2+\delta_2)\right], \\
\eta_0 &= \mu_2(1+d_1-d_1\delta_1)^2 + \alpha_1^2(-1+\delta_1)^2(-1+d_2(-1+\delta_2)) \\
&\quad - \alpha_1(-1+d_1(-1+\delta_1))(-1+\delta_1)(-1+d_2\mu_2+\delta_2).
\end{aligned}$$

A.2 Proof of Lemma 4.1.3

Proof of Lemma 4.1.3. (a) Since

$$\frac{\mu_1^*}{\mu_2^*} = \alpha > 1, \quad \frac{\mu_3^*}{\mu_1^*} = \frac{(\alpha-1)^2+4\alpha}{4\alpha} > 1,$$

we have $\mu_2^* < \mu_1^* < \mu_3^*$. A direct calculation shows

$$\mu_4^* = \frac{\mu_1^*}{1 + d(\delta-1)(\alpha-1)} < \mu_1^*, \quad \mu_4^* \geqslant \mu_2^* \iff d \leqslant \frac{1}{\delta-1}.$$

(b) A direct expansion shows

$$d_-^* - d_{\mathrm{tc}}^* = \frac{\delta-1}{\mu} + \frac{1}{(\alpha-1)(\delta-1)} - \frac{2}{\sqrt{(\alpha-1)\mu}} = A + B - 2\sqrt{AB},$$

where

$$A = \frac{\delta-1}{\mu}, \quad B = \frac{1}{(\alpha-1)(\delta-1)}.$$

By the arithmetic mean-geometric mean inequality (i.e., for any $A, B \geqslant 0$, $A + B \geqslant 2\sqrt{AB}$), $d_{\mathrm{tc}}^* \leqslant d_-^*$ with equality if and only if $\mu = \mu_2^*$. Next, a direct calculation shows

$$d_-^* \leqslant \frac{(\alpha-1)(\delta-1)}{\mu} \iff 2\frac{\delta-1}{\mu} \leqslant \frac{2}{\sqrt{(\alpha-1)\mu}} \iff \mu \geqslant (\alpha-1)(\delta-1)^2 = \mu_2^*,$$

and one checks easily that

$$\frac{(\alpha-1)(\delta-1)}{\mu} \leqslant \frac{1}{\delta-1} \iff \mu \geqslant (\alpha-1)(\delta-1)^2 = \mu_2^*.$$

This completes the proof. □

A.3 Proof of Lemma 4.1.4

Proof of Lemma 4.1.4. We check the three cases *(a)* $\widetilde{A}_2 = 0$, *(b)* $\widetilde{B}_2 = 0$, and $\widetilde{A}_2 \neq 0$, and *(c)* $\widetilde{C}_2 = 0$ and $\widetilde{A}_2, \widetilde{B}_2 \neq 0$.

(a) $\widetilde{A}_2 = 0$. Since $\widetilde{A}_2 = 0$, $\alpha = 1$. This shows

$$\widetilde{B}_2 = (1-\alpha)\big[d\mu + (1-\alpha)(\delta-1)\big] = 0,$$

forcing $\widetilde{C}_2 = 0$. But when $\alpha = 1$, we obtain $\widetilde{C}_2 = -1 \neq 0$, which yields a contradiction.

(b) Since $\widetilde{B}_2 = 0$ and $\widetilde{A}_2 \neq 0$, $d\mu = (\alpha-1)(\delta-1)$. This implies

$$\widetilde{k}_1 = 0, \quad \widetilde{C}_2 = d(\delta-1) - 1.$$

The quadratic equation yields two roots

$$\widetilde{A}_2 x^2 + \widetilde{C}_2 = 0 \implies x_1^* = -\sqrt{\frac{-\widetilde{C}_2}{\widetilde{A}_2}}, \quad x_3^* = \sqrt{\frac{-\widetilde{C}_2}{\widetilde{A}_2}}.$$

If $\alpha, \delta > 1$, then $\widetilde{A}_2, \widetilde{C}_2 < 0$, and no real roots can exist. If instead $0 < \alpha, \delta < 1$, then $\widetilde{A}_2 > 0, \widetilde{C}_2 < 0$ giving two real roots $x_1^* < 0 < x_3^*$. But then $y_3^* = -x_3^* < 0$. So no interior fixed point can arise.

(c) The quadratic equation yields two roots

$$\widetilde{A}_2 x^2 + \widetilde{B}_2 x = 0 \implies x_1^* = 0, \quad x_3^* = \frac{-\widetilde{B}_2}{\widetilde{A}_2} - \tilde{k}_1.$$

Hence, both fixed points are on the axes and no interior fixed points can exist. □

A.4 Proof of Lemma 4.2.1

Proof of Lemma 4.2.1. *(a)* Let $\theta = \mu d - (\delta - 1)$. Assume for contradiction that $\alpha^* \leqslant 1$, then

$$\alpha^* \leqslant 1 \implies \sqrt{\theta^2 + 4\mu} + \theta \leqslant 0. \tag{A.4.1}$$

However, for any real θ and $\mu > 0$,

$$\sqrt{\theta^2 + 4\mu} + \theta > |\theta| + \theta \geqslant 0,$$

a contradiction. Hence, $\alpha^* > 1$.

(b) A direct calculation shows

$$\mu \geqslant \mu_1^* \iff P_1(\alpha) \leqslant 0,$$

where

$$P_1(\alpha) = \widetilde{A}_5 \alpha^2 + \widetilde{B}_5 \alpha + \widetilde{C}_5,$$

with

$$\widetilde{A}_5 = (\delta - 1)^2 > 0, \quad \widetilde{B}_5 = -(\delta - 1)^2 < 0, \quad \widetilde{C}_5 = -\mu < 0.$$

Hence, $P_1(\alpha)$ opens upward with two real roots

$$\alpha_- = \frac{1 - \sqrt{1 + \frac{4\mu}{(\delta-1)^2}}}{2}, \quad \alpha_* = \frac{1 + \sqrt{1 + \frac{4\mu}{(\delta-1)^2}}}{2}.$$

Since $\alpha_* > 1$ and $\alpha_- < 0$,

$$P_1(\alpha) \leqslant 0 \iff \alpha \in [\alpha_-, \alpha_*].$$

This implies

$$\mu \geqslant \mu_1^* \iff P_1(\alpha) \leqslant 0 \iff 1 < \alpha \leqslant \alpha_*.$$

(c) Rearranging shows

$$d > d_{\mathrm{tc}}^* \iff d > \frac{\alpha(\delta - 1)}{\mu} - \frac{1}{(\alpha - 1)(\delta - 1)} \iff P_2(\alpha) < 0,$$

where

$$P_2(\alpha) = \widetilde{A}_6 \alpha^2 + \widetilde{B}_6 \alpha + \widetilde{C}_6,$$

with

$$\widetilde{A}_6 = (\delta - 1)^2 > 0, \quad \widetilde{B}_6 = -[(\delta - 1)^2 + d\mu(\delta - 1)] < 0, \quad \widetilde{C}_6 = \mu[d(\delta - 1) - 1] < 0.$$

So $P_2(\alpha)$ opens upward and has two real roots of opposite sign:

$$\tilde{\alpha}_- = \frac{(\mu d + \delta - 1) - \sqrt{[\mu d - (\delta - 1)]^2 + 4\mu}}{2(\delta - 1)}, \quad \alpha^* = \frac{(\mu d + \delta - 1) + \sqrt{[\mu d - (\delta - 1)]^2 + 4\mu}}{2(\delta - 1)}.$$

Since

$$\mu d + \delta - 1 < \sqrt{(\mu d - (\delta - 1))^2 + 4\mu},$$

$\tilde{\alpha}_-$ is negative, and from *(a)*, $\alpha^* > 1$. Hence, $P_2(\alpha) < 0$ if and only if $\tilde{\alpha}_- < \alpha < \alpha^*$. Restricting to $\alpha > 1$ yields

$$d > d^*_{\mathrm{tc}} \iff P_2(\alpha) < 0 \iff 1 < \alpha < \alpha^*.$$

(d) From *(b)*, $\alpha = \alpha_*$ is a root of $P_1(\alpha) = 0$. Rearranging $P_1(\alpha_*) = 0$ leads to

$$P_1(\alpha_*) = 0 \iff \alpha_*^2(\delta - 1)^2 = (\delta - 1)^2\alpha_* + \mu. \tag{A.4.2}$$

Evaluating $P_2(\alpha)$ at $\alpha = \alpha_*$ yields

$$P_2(\alpha_*) = (\delta - 1)^2\alpha_*^2 - [(\delta - 1)^2 + d\mu(\delta - 1)]\alpha_* + \mu[d(\delta - 1) - 1]. \tag{A.4.3}$$

Substituting (A.4.2) into (A.4.3) and simplifying, we obtain

$$P_2(\alpha_*) = d\mu(\delta - 1)(1 - \alpha_*).$$

It follows from $\delta > 1$ and $\alpha_* > 1$ that $P_2(\alpha_*)$ is negative. From *(c)*, $P_2(\alpha) < 0$ if and only if $\tilde{\alpha}_- < \alpha < \alpha^*$. The fact that $P_2(\alpha_*) < 0$ implies

$$\tilde{\alpha}_- < 1 < \alpha_* < \alpha^*,$$

which completes the proof. $\square$

Appendix B

Tables

Case	α_1	μ_1	δ_1	d_1	α_2	μ_2	δ_2	d_2
(a)	15.0	4.00	0.80	1.00	3.00	2.00	2.00	0.30
(b)	6.90	0.60	1.10	0.10	9.50	0.30	1.10	0.80
(c)	5.20	0.63	1.65	0.27	34.00	2.96	0.80	0.44
(d)	9.50	0.30	1.10	0.85	6.90	0.60	1.10	0.01
(e)	4.00	4.00	0.20	1.00	3.00	2.00	2.00	0.50
(f)	4.00	2.20	1.30	1.00	8.00	2.00	2.00	0.30
(g)	10.00	4.00	1.30	0.10	3.00	2.00	0.90	0.30
(h)	10.00	4.00	1.30	1.00	3.00	2.00	2.00	0.30

Table B.1: Parameter values used in each of the eight phase portraits (a)–(h).

Threshold	**Expression**
α^*	$\dfrac{(\mu d + \delta - 1) + \sqrt{[\mu d - (\delta - 1)]^2 + 4\mu}}{2(\delta - 1)}$
α_*	$\dfrac{1 + \sqrt{1 + \frac{4\mu}{(\delta-1)^2}}}{2}$
μ_1^*	$\alpha(\alpha - 1)(\delta - 1)^2$
μ_2^*	$(\alpha - 1)(\delta - 1)^2$
μ_3^*	$\dfrac{(\alpha - 1)(\alpha + 1)^2(\delta - 1)^2}{4}$
μ_4^*	$\dfrac{\alpha(\alpha - 1)(\delta - 1)^2}{1 + d(\delta - 1)(\alpha - 1)}$
d_{tc}^*	$\dfrac{\alpha(\delta - 1)}{\mu} - \dfrac{1}{(\alpha - 1)(\delta - 1)}$
d_-^*	$\dfrac{(\alpha + 1)(\delta - 1)}{\mu} - \dfrac{2}{\sqrt{(\alpha - 1)\mu}}$
d_+^*	$\dfrac{(\alpha + 1)(\delta - 1)}{\mu} + \dfrac{2}{\sqrt{(\alpha - 1)\mu}}$

Table B.2: Key parameter thresholds under the symmetry condition. d_{tc}^* denotes the transcritical bifurcation and d_-^* denotes the pitchfork bifurcation.

Bibliography

[1] D. G. Ainley and D. P. DeMaster. Survival and mortality in a population of Adélie penguins. Ecology, 61(3):522–530, 1980.

[2] C. D. Aliprantis and R. Tourky. Cones and Duality, volume 84. American Mathematical Soc., 2007.

[3] E. J. Bertrand. Global Dynamics of some Competitive and Cooperative Discrete Dynamical Systems. University of Rhode Island, 2018.

[4] D. Clark, M. R. S. Kulenović, and J. F. Selgrade. Global asymptotic behavior of a two-dimensional difference equation modelling competition. Nonlinear Analysis: Theory, Methods & Applications, 52(7):1765–1776, 2003.

[5] J. M. Cushing. A discrete model for competing stage-structured species. Theoretical Population Biology, 41(3):372–387, 1992.

[6] J. M. Cushing, S. M. Henson, and L.-I. Roeger. Coexistence of competing juvenile–adult structured populations. Journal of Biological Dynamics, 1(2):201–231, 2007.

[7] J. M. Cushing, S. Levarge, N. Chitnis, and S. M. Henson. Some discrete competition models and the competitive exclusion principle. Journal of Difference Equations and Applications, 10(13-15):1139–1151, 2004.

[8] E. N. Dancer and P. Hess. Stability of fixed points for order-preserving discrete-time dynamical systems. Journal für die Reine und Angewandte Mathematik, 419:125–140, 1991.

[9] L. S. Davis and F. T. McCaffrey. Survival analysis of eggs and chicks of Adélie penguins (*Pygoscelis adeliae*). The Auk, 103(2):379–388, 1986.

[10] P. De Mottoni and A. Schiaffino. Competition systems with periodic coefficients: a geometric approach. Journal of Mathematical Biology, 11(3):319–335, 1981.

[11] R. L. Devaney. An Introduction to Chaotic Dynamical Systems. CRC Press, second edition, 2003.

[12] A. Dhooge, W. Govaerts, and Y. A. Kuznetsov. MatContM: A continuation toolbox in MATLAB for dynamical systems. `https://sourceforge.net/projects/matcont/`, 2008.

[13] K. Fukumori, N. Okuda, and Y. Yanagisawa. Female territoriality in a paternal mouthbrooding cardinalfish to avoid predation against spawned eggs. Canadian Journal of Zoology, 87(6):508–514, 2009.

[14] D. Gale and H. Nikaido. The Jacobian matrix and global univalence of mappings. Mathematische Annalen, 159(2):81–93, 1965.

[15] M. W. Hirsch and H. Smith. Monotone dynamical systems. Handbook of differential equations: ordinary differential equations, 2:239–357, 2006.

[16] S.-B. Hsu, H. Smith, and P. Waltman. Competitive exclusion and coexistence for competitive systems on ordered Banach spaces. Transactions of the American Mathematical Society, 348(10):4083–4094, 1996.

[17] M. R S. Kulenović and O. Merino. Competitive-exclusion versus competitive-coexistence for systems in the plane. Discrete and Continuous Dynamical Systems Series B, 6(5):1141, 2006.

[18] M R. S. Kulenović and O. Merino. Global bifurcation for discrete competitive systems in the plane. Discrete and Continuous Dynamical Systems B, 12(1):133–149, 2009.

[19] M. R. S. Kulenović and O. Merino. Invariant manifolds for competitive discrete systems in the plane. International Journal of Bifurcation and Chaos, 20(08):2471–2486, 2010.

[20] P. H. Leslie and J. C. Gower. The properties of a stochastic model for two competing species. Biometrika, 45(3/4):316–330, 1958.

[21] P. Liu and S. N. Elaydi. Discrete competitive and cooperative models of Lotka–Volterra type. Journal of Computational Analysis and Applications, 3:53–73, 2001.

[22] A. J. Lotka. The growth of mixed populations: two species competing for a common food supply. Journal of the Washington academy of Sciences, 22(16/17):461–469, 1932.

[23] C. Robinson. Dynamical Systems: Stability, Symbolic Dynamics, and Chaos, volume 28 of Studies in Advanced Mathematics. CRC Press, 2 edition, 1999.

[24] H. L. Smith. Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems. Number 41. American Mathematical Soc., 1995.

[25] H. L. Smith. Planar competitive and cooperative difference equations. J. Diff. Eq. Appl., 3:335–357, 1998.

[26] S. H. Streipert and G. S. K. Wolkowicz. An augmented phase plane approach for discrete planar maps: Introducing next-iterate operators. Mathematical Biosciences, 355:108924, January 2023.

[27] S. H. Streipert and G. S. K. Wolkowicz. Technique to derive discrete population models with delayed growth. Journal of Biological Dynamics, 17(1):2244987, 2023.

[28] J. J. A. van Iersel. An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* l.). Behaviour Supplement, (3):III–159, 1953.

[29] M. N. Vrahatis. Generalization of the Bolzano theorem for simplices. Topology and its Applications, 202:40–46, 2016.

[30] Y. Wang and J. Jiang. The general properties of discrete-time competitive dynamical systems. Journal of Differential Equations, 176(2):470–493, 2001.

[31] S. Wiggins. Introduction to Applied Nonlinear Dynamical Systems and Chaos, volume 2 of Texts in Applied Mathematics. Springer, 2 edition, 2003.

[32] Pei Z. and Azmy S. A. A discrete stage-structured two-species competition model with sexual and clonal reproduction. Journal of Biological Dynamics, 6(2):2–16, 2012.