INVADING A STRUCTURED POPULATION:
A BIFURCATION APPROACH

by

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Abstract

Matrix population models are discrete in both time and state-space, where a matrix with density-dependent entries is used to project a population vector of a stage-structured population from one time to the next. Such models are useful for modeling populations with discrete categorizations (e.g. developmental cycles, communities of multiple species, differing sizes, etc.). We present a general matrix model of two interacting populations where one (the resident) has a stable cycle, and we analyze when the other population (the invader) can successfully invade. Specifically, we study the local bifurcations of coexistence cycles as the resident cycle destabilizes, where a cycle of length 1 corresponds to an equilibrium.

We make no assumptions on the types of interactions between the populations or on the population structure of the resident; we consider when the invader's projection matrix is primitive or imprimitive and 2×2. The simplest biological scenarios for such structures are an iteroparous invader and a two-stage semelparous invader. When the invader has a primitive projection matrix, coexistence cycles (of the same period as the resident cycle) bifurcate from the resident-cycle. When the invader has an imprimitive two-stage projection matrix, two types of coexistence cycles bifurcate from the resident-cycle: cycles of the same period and cycles of double the period. In both the primitive and imprimitive cases, we provide diagnostic quantities to determine the direction of bifurcation and the stability of the bifurcating cycles. Because we only perform a local stability analysis, the only successful invasion provided by our results is through stable coexistence cycles. As we show in some simple examples, however, the invader may persist when the coexistence cycles are unstable through competitive exclusion where the branch of bifurcating cycles connects to a branch of invader attractors and creates a multi-attractor scenario known as a *strong Allee effect*.

Chapter 1

Introduction

In population dynamics, epidemiology, and genetics, a population — whether it be a community, species, or a genotype — may be under threat of invasion by some invading population, mutation, or disease. In this context, it is useful to know when the resident population is actually in danger. On the other hand, from the invader's perspective it is useful to know when they will be able to establish a foothold and successfully invade. We present and analyze a mathematical model to address when invasion is possible in the context of structured populations, making no assumptions on the types of interactions between the populations.

The analysis of invasion into a stable state lends itself to a bifurcation theoretic perspective. When analyzing the dynamics of a population model, often a bifurcation parameter is varied to see when survival or extinction occur — or in the case of multi-species interactions, when coexistence or competitive exclusion occur. We utilize this approach and specialize our analysis to a discrete-time model of structured populations, known as a matrix model. Such models are easy to construct and simulate and are used to model populations which can be split into classes based on developmental cycles, size, spatial location, etc.

Motivated by the scenario of two competing species, we begin this chapter by presenting the well-known Lotka-Volterra competition model and its discrete counterpart, the Leslie-Gower competition model, to illustrate the dynamics present in the simplest multi-species competition model. We then introduce the concept of a structured population and the matrix models used to model them along with the corresponding terminology; we also present the simplest nontrivial matrix model of a single species — a juvenile-adult model — and discuss how the matrix structure (primitive or imprimitive) can affect its dynamics. Combining the concepts of multi-species interactions and matrix models, we wrap-up the chapter with a discussion of a simple multi-species matrix model. In Chapter 2, we introduce a general matrix model of two interacting species where the resident species has a stable cycle or equilibrium. We also include preliminary notation, definitions, and assumptions to be used throughout the dissertation. In Chapter 3, we prove some preliminary theorems essential to the methods used in our later analysis. In Chapter 4, we assume a specific form of the invader's structure — specifically that it is modeled with a primitive matrix — and obtain a theorem describing the invasion into the resident population. In Chapter 5, we assume that the invader is instead modeled with an imprimitive matrix and obtain theorems describing the invasion into the resident population, the dynamics of which are dependent on the parity of the period of the resident cycle. Finally, in Chapter 6 we conclude with a summary of our results and remark on potential future extensions.

1.1 Multi-species competition

We begin by introducing the simplest and most well-known two-species competition model: the Lotka-Volterra competition model and its discrete equivalent, the Leslie-Gower competition model. We present a bifurcation-theoretic perspective of these, showing the dynamic scenarios present while introducing bifurcation terminology.

1.1.1 Lotka-Volterra competition model

The most classical and famous competitive two-species model is the Lotka-Volterra competition model, a system of two coupled differential equations formulated independently by both Lotka [33] and Volterra [39]. It can be written as

$$\begin{aligned} \frac{dx}{dt} &= x\left(b_1 - c_{11}x - c_{12}y\right) \\ \frac{dy}{dt} &= x\left(b_2 - c_{21}x - c_{22}y\right) \end{aligned} \tag{1.1}$$

with positive coefficients b_i, c_{ij}. The b_i coefficients represent the inherent (i.e. density-free) birth rates. The coefficients c_{11}, c_{22} measure the intensity of within-species (intraspecific) competition, and c_{12}, c_{21} measure the intensity of between-species (interspecific) competition. To measure the levels of competition, we define

$\alpha_x = c_{21}/c_{11}$	ratio of inter- vs. intraspecific competition against species x,
$\alpha_y = c_{22}/c_{12}$	ratio of intra- vs. interspecific competition against species y,
$\Delta = c_{11}c_{22} - c_{12}c_{21}$	measure of intra- vs. interspecific competition intensities.

Model 1.1 has four equilibria:

$E_0 = (0, 0)$	extinction equilibrium,
$E_x = \left(\frac{b_1}{c_{11}}, 0\right)$	species x equilibrium,
$E_y = \left(0, \frac{b_2}{c_{22}}\right)$	species y equilibrium,
$E_c = \frac{1}{\Delta}\Big(b_1c_{22} - b_2c_{12},\, b_2c_{11} - b_1c_{21}\Big)$	coexistence equilibrium.

The coexistence equilibrium is only biologically relevant when its components are positive. By the Hartman-Grobman Theorem, we can determine the stability of the fixed points when they are hyperbolic, i.e. when the Jacobian at the fixed point has eigenvalues with nonzero real part. When all of the eigenvalues of the Jacobian evaluated at the fixed point have negative real part, the fixed point is *stable*; if any of the eigenvalues have a positive real part, the fixed point is *unstable* [19]. Model (1.1) has four possible dynamic scenarios, whose mathematical conditions are based on such a stability analysis [6] and where global attractiveness is proved in [38]:

1. The coexistence equilibrium E_c is positive, stable, and globally attracting for positive initial conditions if

   $$b_1\alpha_x < b_2 < b_1\alpha_y.$$

   This implies $\Delta > 0$, meaning the between-species competition is weak compared to the within-species competition.

2. Species x's equilibrium, E_x, is stable and globally attracting for positive initial conditions if

   $$b_2 < b_1\alpha_x \text{ and } b_2 < b_1\alpha_y,$$

i.e. species x has a high enough birthrate to overcome competitive factors while species y does not.

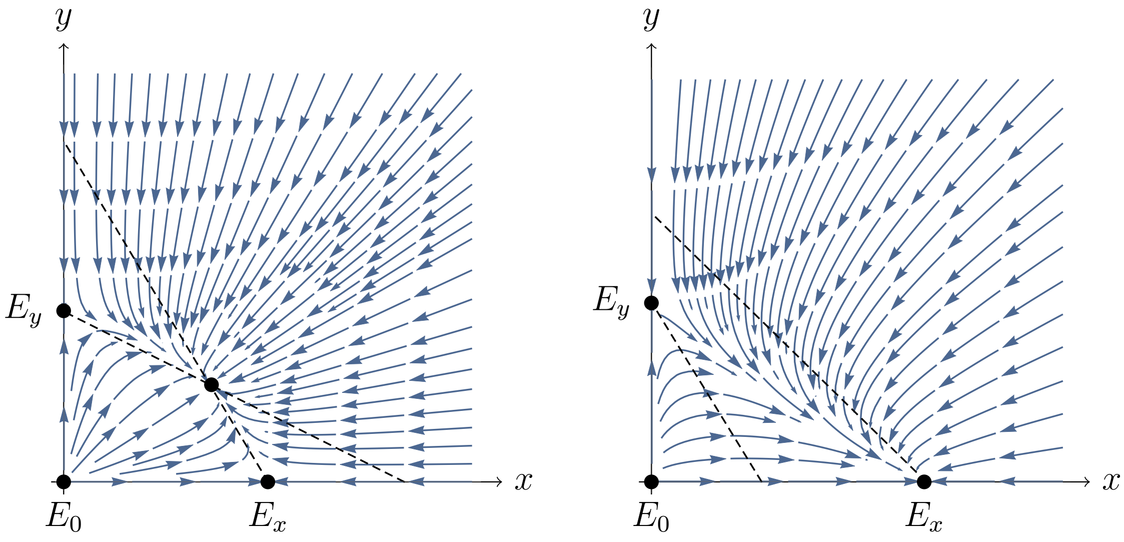
3. Species y's equilibrium, E_y, is stable and globally attracting for positive initial conditions if
$$b_1\alpha_x < b_2 \text{ and } b_1\alpha_y < b_2,$$
i.e. species y has a high enough birthrate to overcome competitive factors while species x does not.

4. The coexistence equilibrium, E_c, is positive and is an unstable saddle whose unstable manifold separates the basins of attraction for species x's and species y's equilibria, both of which are stable. Orbits may go to either, depending upon the initial conditions. This occurs when
$$b_1\alpha_y < b_2 < b_1\alpha_x,$$
which implies $\Delta < 0$, i.e. the within-species competition is weak compared to the between-species competition.

In all four cases, orbits go towards one of the three non-extinction equilibria and the extinction equilibrium is always unstable. If one species is absent in the initial conditions, then the orbit goes towards the other species' equilibrium. See Figure 1.1 for phase portraits of the four scenarios. In scenario 4, the competition provides a *strong Allee effect* for both populations because there are initial conditions which lead to the extinction or survival of either species.

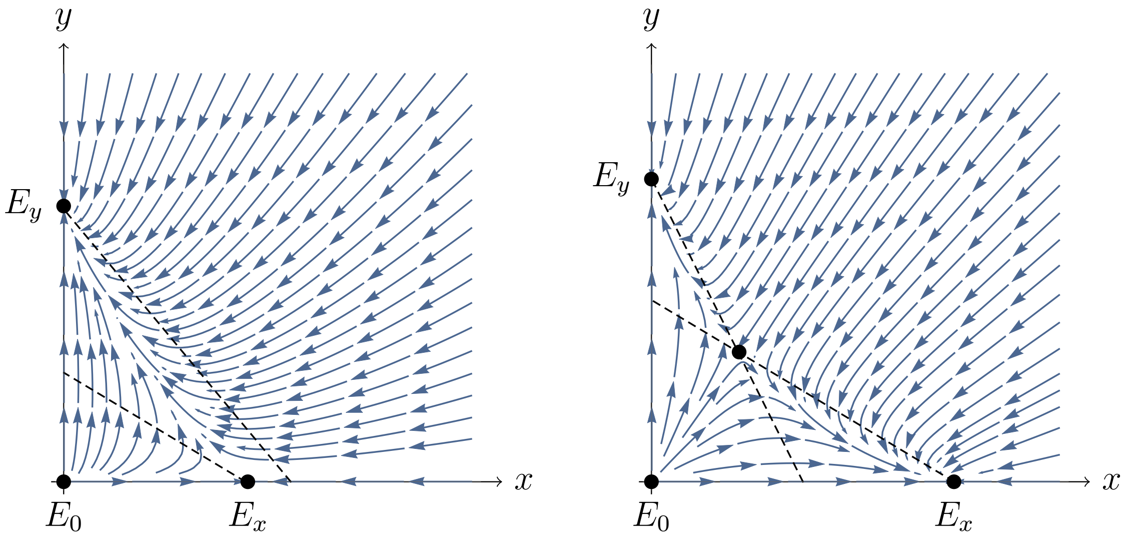
Notice that if one alters the value of b_2 while holding all other coefficients constant, then the dynamics of the model will change. In such a treatment, b_2 is called a *bifurcation parameter*. Caswell [4] describes a *bifurcation* in the following way:

> A *bifurcation* is said to occur when a small change in a parameter causes a qualitative change in dynamics. The simplest bifurcations involve the loss of stability of an equilibrium. When an equilibrium is stable, nearby trajectories converge to it. When it becomes unstable, those trajectories do not converge, and hence do something qualitatively different.



(a) Scenario 1

(b) Scenario 2



(c) Scenario 3

(d) Scenario 4

Figure 1.1: Phase portraits of the four dynamic scenarios of model (1.1). Solid dots indicate the biologically feasible (i.e. nonnegative) equilibria. Dashed lines indicate the nullclines for $dx/dt = 0$ (which connects to E_x) and $dy/dt = 0$ (which connects to E_y). The x- and y-axes are also nullclines for $dy/dt = 0$ and $dx/dt = 0$ respectively.

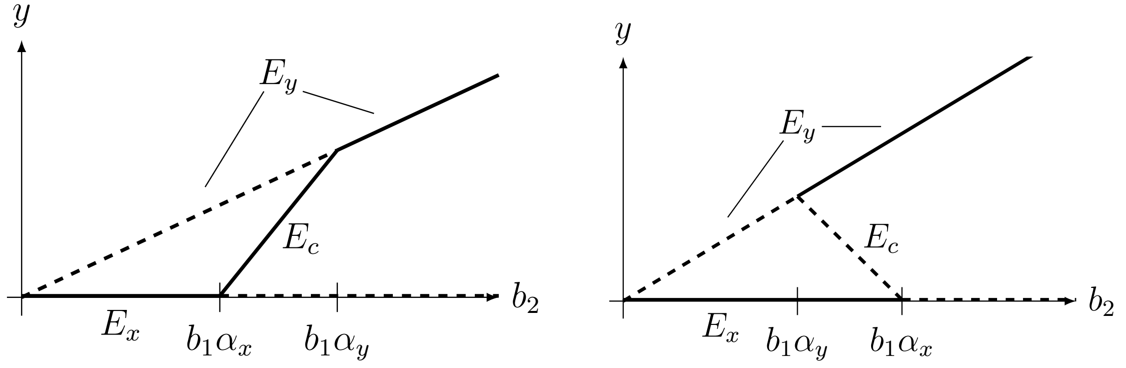
In the Lotka-Volterra setting, E_x loses stability when $b_2 - b_1\alpha_x$ becomes positive, and E_y loses stability when $b_1\alpha_y - b_2$ becomes positive. Therefore, bifurcations occurs at $b_2 = b_1\alpha_x$ and $b_2 = b_1\alpha_y$.

When using b_2 as a bifurcation parameter, E_x is stationary and is therefore — in some sense — a "trivial" equilibrium. When b_2 is small, E_x is stable (scenario 2); and when $b_2 - b_1\alpha_x$ becomes positive, E_x loses stability (scenario 1 or 3). Looking at the *bifurcation diagrams* in Figure 1.2, we see that the positive coexistence equilibria of scenarios 1 and 4 bifurcate from E_x to either the right or the left of $b_2 = b_1\alpha_x$. We call a bifurcation to the right a *forward bifurcation* and a bifurcation to the left a *backward bifurcation*, and name these the *direction of bifurcation.* In actuality, in Figure 1.2 the coexistence equilibria contain a negative component (which are not biologically feasible) when b_2 is not between $b_1\alpha_x$ and $b_1\alpha_y$, and the line of coexistence equilibria intersects with the line of species x's equilibria. Such a bifurcation, where two lines of equilibria intersect, is known as a *transcritical bifurcation.* The Principle of Exchange of Stability [26, Theorem I.7.4] states that at the intersection, the two branches of equilibria exchange stability types.

In summary, the Lotka-Volterra world view has purely equilibrium dynamics. High within-species competition and weak between-species competition allows for coexistence. High between-species competition and weak within-species competition leads to competitive exclusion, where only one species may exist at a given time with the surviving species dependent on the initial conditions. When a parameter beneficial to the survival of species y is chosen as the bifurcation parameter, increasing it leads to a bifurcation of positive coexistence equilibria from species x's equilibrium. If the bifurcation is forward, they are stable; if it is backward, they are unstable and orbits instead go to one of the two competitive exclusion equilibria. Because our study involves discrete-time models for structured populations, in the next section we present a classic discrete-time model which maintains the same dynamics as the Lotka-Volterra competition model.

1.1.2 Leslie-Gower competition model

The discrete analogue to system (1.1) is known as the Leslie-Gower competition model. In discrete models, the population values are projected from time t to time $t+1$. For compactness, we use LaSalle's notation $x = x(t)$ and $x' = x(t+1)$. The



(a) Bifurcation diagram when $\alpha_x < \alpha_y$. (b) Bifurcation diagram when $\alpha_y < \alpha_x$.

Figure 1.2: Bifurcation diagrams for model (1.1) which plot the y components of the equilibria against the bifurcation parameter b_2. Solid lines indicate stability of the corresponding equilibria, while dashed lines indicate instability. Species x's equilibrium, E_x, is stable for $b_2 \in (0, b_1\alpha_x)$. Species y's equilibrium, E_y, is stable for $b_2 \in (b_1\alpha_y, \infty)$. The coexistence equilibrium, E_c, is biologically relevant for b_2 between $b_1\alpha_x$ and $b_1\alpha_y$ and is stable if $\alpha_x < \alpha_y$ and unstable if $\alpha_y < \alpha_x$. The E_c equilibria which extend beyond the lines of the E_x and E_y equilibria are not biologically feasible.

Leslie-Gower competition model can be written as

$$\begin{aligned} x' &= \frac{b_1 x}{1 + c_{11}x + c_{12}y} \\ y' &= \frac{b_2 y}{1 + c_{21}x + c_{22}y} \end{aligned} \tag{1.2}$$

with positive coefficients $b_i > 1$ and c_{ij}. The coefficients play similar roles as in the differential equation model (1.1). In particular, b_1, b_2 are density-free birth rates, c_{11}, c_{22} are within-species (intraspecific) competition coefficients, and c_{12}, c_{21} are between-species (interspecific) competition coefficients. The requirement $b_i > 1$ allows each species to exist on their own and is equivalent to $b_i > 0$ in model (1.1). We again define variables to measure the levels of competition:

$\alpha_x = c_{21}/c_{11}$	ratio of inter- vs. intraspecific competition against species x,
$\alpha_y = c_{22}/c_{12}$	ratio of intra- vs. interspecific competition against species y,
$\Delta = c_{11}c_{22} - c_{12}c_{21}$	measure of intra- vs. interspecific competition intensities.

Model 1.2 has four equilibria:

$$\begin{aligned}
&E_0 = (0,0) && \text{extinction equilibrium,}\\
&E_x = \left(\frac{b_1-1}{c_{11}}, 0\right) && \text{species } x \text{ equilibrium,}\\
&E_y = \left(0, \frac{b_2-1}{c_{22}}\right) && \text{species } y \text{ equilibrium,}\\
&E_c = \frac{1}{\Delta}\Big(c_{22}(b_1-1) - c_{12}(b_2-1), c_{11}(b_2-1) - c_{21}(b_1-1)\Big) && \text{coexistence equilibrium.}
\end{aligned}$$

Each equilibrium is only biologically relevant when its components are nonnegative. The Linearization Principle for maps allows us to determine the stability of the fixed points when they are hyperbolic, i.e. when the Jacobian at the fixed point has no eigenvalues with absolute value equal to 1. When all of the eigenvalues of the Jacobian evaluated at the fixed point are within the complex unit circle (i.e. have absolute value less than 1), the fixed point is *stable*; if any of the eigenvalues are outside the unit circle, the fixed point is *unstable* [16, Theorem 5.15].

Model 1.2 has the same dynamic scenarios and corresponding biological interpretations as the Lotka-Volterra competition model (1.1) [11] (regarding global stability, see [11] and [29]):

1. The coexistence equilibrium E_c is positive, stable, and globally attracting for positive initial conditions if
$$0 < (b_1-1)\alpha_x < b_2 - 1 < (b_1-1)\alpha_y.$$
2. Species x's equilibrium, E_x, is stable and globally attracting for positive initial conditions if
$$0 < (b_1-1)\alpha_x \text{ and } b_2 - 1 < (b_1-1)\alpha_x \text{ and } b_2 - 1 < (b_1-1)\alpha_y.$$
3. Species y's equilibrium, E_y, is stable and globally attracting for positive initial conditions if
$$0 < b_2 - 1 \text{ and } (b_1-1)\alpha_x < b_2 - 1 \text{ and } (b_1-1)\alpha_y < b_2 - 1.$$

4. The coexistence equilibrium, E_c, is positive and is an unstable saddle whose unstable manifold separates the basins of attraction for species x's and species y's equilibria, both of which are stable. Orbits may go to either, depending upon the initial conditions. This occurs when

$$(b_1 - 1)\alpha_y < b_2 - 1 < (b_1 - 1)\alpha_x.$$

These scenarios are again exhaustive and distinct, where all orbits go towards one of the four equilibria.

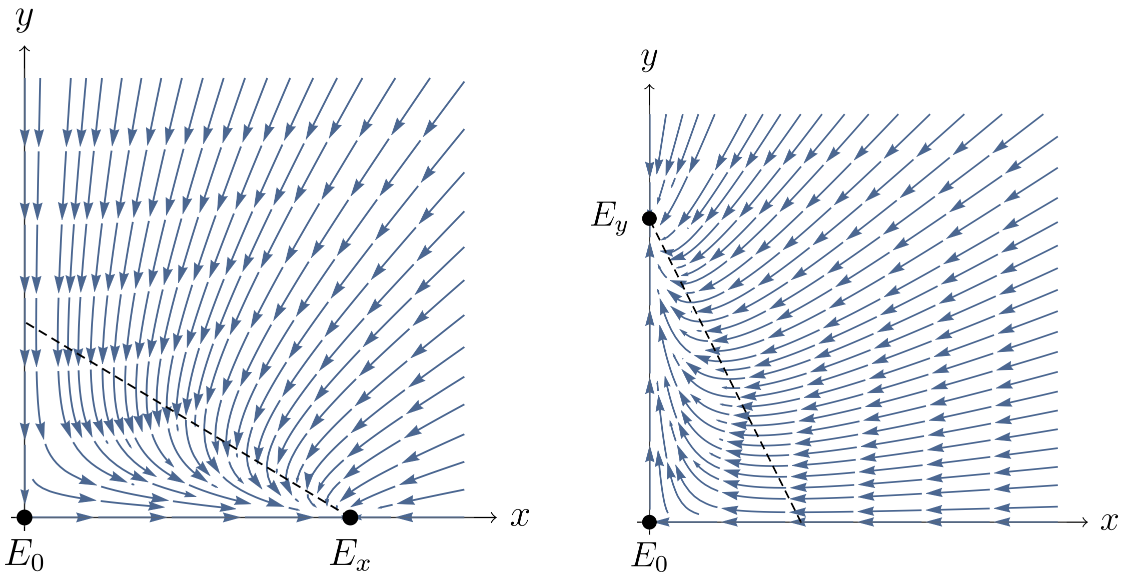
If one allows $b_i \leq 1$, then there is an additional scenario where both species may go extinct. Specifically,

5. The extinction equilibrium is globally asymptotically stable if

$$b_1 < 1 \text{ and } b_2 < 1.$$

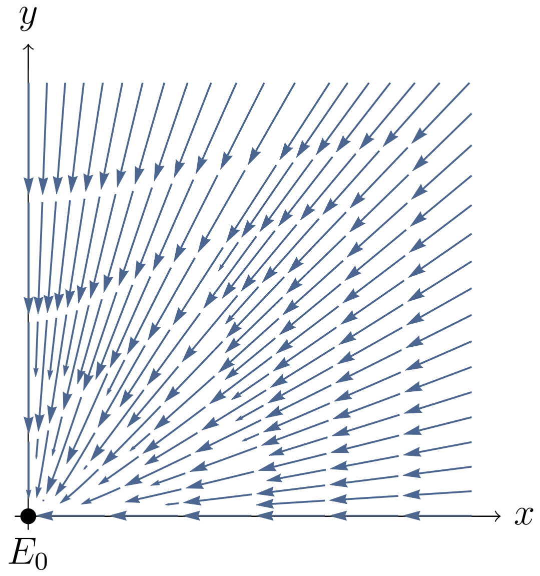
In this case, neither species is fit enough to survive on its own (see the phase portrait in Figure 1.3). When $b_1 < 1$, the inequalities in scenarios 1, 2, and 4 correspond to scenario 5; when $b_2 < 1$, scenarios 1, 3, and 4 correspond to scenario 5. Thus, if either $b_i < 1$, coexistence is not possible. The dynamics on the axes in scenarios 2 and 3 are also dependent on whether $b_2 > 1$ and $b_1 > 1$ respectively. If species x is absent in the initial conditions of scenario 3 (or y in scenario 2) and $b_2 < 1$ ($b_1 < 1$), then the orbit goes towards the extinction equilibrium (see Figure (1.3)); if species x is absent in the initial conditions of scenario 3 (or y in scenario 2) and $b_2 > 1$ ($b_1 > 1$), then the orbit goes towards E_y (E_x) (see Figure (1.1)). Similar dynamics occur in model (1.1) when $b_i < 0$.

When b_2 is viewed as a bifurcation parameter, the bifurcation diagrams in Figure 1.2 apply (see Figure 1.4 for a bifurcation diagram when $b_1 < 1$ — in this case, E_y bifurcates from E_0 as b_2 passes through 1). The takeaways from this model are the same as those summarized for the Lotka-Volterra competition model. In both models, each species is represented by a single state variable. In the next section, we introduce the concept of a structured population model, where a population may be split into categories — based on age, size, or another classification — and thus be represented by a vector of state variables. We will show that this allows for non-equilibrium



(a) Scenario 2 with $b_2 < 1$

(b) Scenario 3 with $b_1 < 1$



(c) Scenario 5, where $b_1, b_2 < 1$

Figure 1.3: Phase portraits for model (1.2) when $b_i < 1$ is allowed. Solid dots indicate the biologically feasible (i.e. nonnegative) equilibria. Dashed lines indicate the lines where $x' - x = 0$ (which connects to E_x) and $y' - y = 0$ (which connects to E_y). The x- and y-axes also satisfy $x' - x = 0$ and $y' - y = 0$ respectively. Figure 1.1 shows phase portraits for when $b_1 > 1$ and $b_2 > 1$.

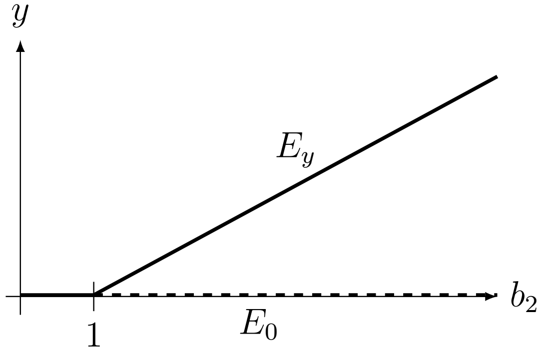


Figure 1.4: Bifurcation diagram for model (1.2) with bifurcation parameter b_2 when $b_1 < 1$. Solid lines indicate stability of the corresponding equilibria, while dashed lines indicate instability. The extinction equilibrium, E_0, is stable for $b_2 < 1$. Species y's equilibrium, E_y, is stable for $b_2 > 1$. This diagram plus those in Figure 1.2, for the case when $b_1 > 1$, represent the bifurcation diagrams for model (1.2).

dynamics, even in the case of a single species — a divergence from the Lotka-Volterra world view.

1.2 Matrix population models

If the vital rates of a population differ based on some (discretizable) classification — such as age, size, developmental stage, physiological condition, location, genetic makeup, or any other biologically relevant partition — it is often inappropriate to model its dynamics via a single state variable. Instead, using the most relevant biological factor, a population may be divided up into discrete classes and represented in time by a *population vector* $x(t)$ with either the number of individuals in each class or the density of each class at time t. When time is also discretized, the resulting model is a matrix model where a nonnegative *projection matrix*[1] $P(x(t), t)$ projects the population vector from t to $t + 1$ using the map

$$x(t+1) = P(x(t), t)x(t). \tag{1.3}$$

---

[1] Note $P(x(t), t)$ is a projection matrix in the sense that it projects $x(t)$ forward in time and not in the sense that $P^2 = P$. Its nonnegativity implies that $x(t) \geq 0$ for all $t > 0$ if $x(0) \geq 0$.

In particular, p_{ij} is the contribution from class i to class j at time t; such contributions are generally transitions or births, whose rates may be density dependent. When there is no density dependence, i.e. when P is a constant matrix, the total population either grows or decays exponentially[2] [7]; however, realistically no population grows unhindered, motivating the use of density dependent terms. The density effects may be in the form of cannibalism, competition, or cooperation, and the flexibility of structured population models allows for different types of interactions to occur both within and between different classes. See [7] for a variety of examples involving the different types of intraspecific interactions.

The timestep in (1.3) is taken to be the unit of time which it takes an individual to move from one class to another, which is generally taken to be the maturation period. Given an initial population vector, the *orbit* or *trajectory* produced by (1.3) is the sequence of resulting $x(t)$ vectors for $t = 0, 1, 2, \ldots$.

We ignore explicit time dependence in (1.3), instead considering the resulting autonomous system with $P(x(t))$. We can therefore rewrite (1.3) using LaSalle's notation as

$$x' = P(x)x. \tag{1.4}$$

Given the generality of system (1.4), it has the potential for complex steady-state dynamics — e.g. cycles, invariant loops, and chaos [4, 7]. Even a one-dimensional map can produce cycles and chaos, e.g. the discrete logistic map [17]. Thus complex dynamics of a matrix model may be a result of the nonlinearities chosen or the structure of the projection matrix. A variety of these dynamics can even be seen in the same model for different parameter values, for example by choosing and varying a bifurcation parameter. Take, for example, the three-stage model with Leslie-Gower nonlinearities presented in [8] which has equilibria, cycles, and invariant loops.

Synchronous orbits, where at least one class is missing at any given time (i.e. that lie on the boundary of the nonnegative cone), are an example of behavior resulting from the structure of the model. Kon [27] proved that synchronous orbits only occur if the projection matrix is *imprimitive*. To introduce the concept of primitivity, we must first define irreducibility. A projection matrix is *reducible* if it is possible to

---

[2] except in degenerate cases where the dominant eigenvalue of P is on the complex unit circle

renumber the stages to obtain a projection matrix with the block form

$$\begin{pmatrix} A & 0 \\ B & C \end{pmatrix}.$$

If it is not reducible, or equivalently if there are paths from every class to every other class through transitions and births, then it is irreducible. A projection matrix for a single species is irreducible unless there exists an absorbing class (such as a post-reproduction class) where individuals can no longer contribute to the population through transitions or births; on the other hand, a projection matrix for multiple species is reducible since individuals cannot cross into classes of other species. Nonnegative irreducible matrices are then either *primitive* or *imprimitive*, where a matrix is *primitive* it has a strictly dominant eigenvalue. For sufficient conditions and equivalent definitions of irreducibility and primitivity see [3] and [4].

The eigenvalue structures, and hence the possible dynamics of the system, differ between primitive and imprimitive matrices. The Perron-Frobenius Theorem, provided below, states that primitive matrices have a strictly dominant eigenvalue that is algebraically simple and positive and has a corresponding positive eigenvector. On the other hand, imprimitive matrices have multiple dominant eigenvalues, where one such eigenvalue is positive with an associated positive eigenvector [4, pg. 84]. When studying the stability of a fixed point of a primitive matrix using bifurcation theory, a single eigenvalue leaving the complex unit circle through 1 corresponds to a bifurcation of equilibria. For a fixed point of an imprimitive matrix, multiple eigenvalues leave simultaneously through the roots of unity, which may correspond to the creation of two-cycles (if an eigenvalue leaves through -1) and/or invariant loops (if a complex-conjugate pair of eigenvalues leave) [4, pg. 528–533].

Perron-Frobenius Theorem. *A primitive matrix has a strictly dominant eigenvalue that is algebraically simple and positive with corresponding positive right and left eigenvectors. No other eigenvectors associated with any other eigenvalues are nonnegative.*

Imprimitive matrices and synchronous cycles arise when studying *semelparous* populations, which give birth once before dying. For example, the 3-stage Leslie matrix where only the oldest age-class gives birth,

$$\begin{pmatrix} 0 & 0 & \phi(x) \\ \sigma_1(x) & 0 & 0 \\ 0 & \sigma_2(x) & 0 \end{pmatrix}.$$

Because of the matrix structure, the boundary of $\mathbb{R}^3$ is invariant, meaning that if any of the classes are initially 0, then the classes will forever cycle being zero:

$$\begin{pmatrix} + \\ + \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ + \\ + \end{pmatrix} \to \begin{pmatrix} + \\ 0 \\ + \end{pmatrix} \to \begin{pmatrix} + \\ + \\ 0 \end{pmatrix} \to \cdots .$$

For an example comparing primitivity and imprimitivity, we present a juvenile-adult model with and without adult survival.

1.2.1 A juvenile-adult model

The juvenile-adult model is the simplest example of a matrix population model:

$$x' = \begin{pmatrix} 0 & \phi(x) \\ \sigma_1(x) & \sigma_2(x) \end{pmatrix} x. \tag{1.5}$$

The values $\phi(0)$, $\sigma_1(0)$, and $\sigma_2(0)$ are known as the *inherent vital rates*, where $\phi(0) > 0$ is the inherent fecundity, $0 < \sigma_1(0) < 1$ the inherent juvenile survival, and $0 < \sigma_2(0) < 1$ the inherent adult survival. The functions $\phi(x)$, $\sigma_1(x)$, and $\sigma_2(x)$ are the density-dependent fecundity and survival functions. Although the dynamics of the model depend on the nonlinearities used, we can say something general about the dynamics near as the extinction equilibrium loses stability. When

$$\phi(0)\sigma_1(0)/(1 - \sigma_2(0))$$

is less than 1 the extinction equilibrium is stable. As this quantity increases through 1, the extinction equilibrium destabilizes and a bifurcation occurs, creating a branch of positive equilibria. With the positive left and right eigenvectors of $P(0)$ denoted by w and v, the direction of bifurcation can be determined by the quantity

$$\kappa = -\frac{w(\nabla_x p_{ij}(0) \cdot v)v}{wv}.$$

The bifurcation is forward and stable when $\kappa > 0$ and is backward and unstable when $\kappa < 0$ [9].

Setting $\sigma_2(x) = 0$ in (1.5) gives what is known as Ebenman's model (see [13]),

$$x' = \begin{pmatrix} 0 & \phi(x) \\ \sigma_1(x) & 0 \end{pmatrix} x,$$

which describes a *semelparous* population in which an individual produces offspring only once before death. In this case, when $\phi(0)\sigma_1(0)$ increases through 1, the extinction equilibrium loses stability as both eigenvalues of $P(0)$ exit the complex unit circle (through 1 and -1), and branches of positive equilibria and synchronous two-cycles simultaneously bifurcate. The branches may each bifurcate forward or backward. A backward bifurcating branch is unstable. A forward bifurcating branch may be stable or unstable. If both branches bifurcate forward, then exactly one contains stable attractors; this alternative is known as the *dynamic dichotomy* [12].

Even without specifying the nonlinearities, it is clear that structure can affect the dynamics of the model. Extending to a matrix model for multiple species further complicates the possible dynamics. While the projection matrix of the system can no longer be primitive — individuals cannot cross between species — each species has a projection matrix, dependent on the densities of the classes of both species, which may be primitive or imprimitive.

1.3 Multi-species matrix models

Structured population models may be extended to model multiple interacting species. While there is a rich literature analyzing interacting species with discrete-time models, most such models are similar to the Leslie-Gower competition model of Section 1.1.2 in that the populations are unstructured and are each represented by a single state-variable. For example, some recent papers include [1, 2, 5, 21, 22, 23, 30, 31, 32, 36]. The few discrete-time multi-species models allowing structured populations, i.e.

multi-species matrix models, often assume specific nonlinearities and interspecific interactions (for example, see [10, 14, 15]); many of the references in the previous sentence also assume specific interactions and nonlinearities.

In a structured two-species matrix model, $x(t)$ represents the $(m+n)$-dimensional population vector of both species, where the first m entries represent the first population's m classes and the final n entries represent the second population's n classes. The projection matrix is block-diagonal,

$$P(x) = \begin{pmatrix} P_1(x) & 0_{m\times n} \\ 0_{n\times m} & P_2(x) \end{pmatrix},$$

because individuals cannot transition to (or give birth to individuals of) classes of the other population. Interspecific interactions can include predator-prey, competition, and mutualism and may be class-dependent. See [40] for examples of interacting structured species with mixed-type interactions. This general two-species model can possess more complicated dynamics than the single-species models, although often the primary concern is analyzing the survival and extinction of the populations. Such survival may be through coexistence or competitive exclusion.

When a bifurcation parameter is chosen which is only present in $P_2(x)$, the first population may be thought of as a resident and the second population as an invader whose fitness changes with the bifurcation parameter. Labeling the chosen bifurcation parameter as γ, we then write the projection matrix as

$$P(\gamma, x) = \begin{pmatrix} P_R(x) & 0_{m\times n} \\ 0_{n\times m} & P_I(\gamma, x) \end{pmatrix}$$

where $P_R(x)$ is the resident's projection matrix and $P_I(\gamma, x)$ is the invader's projection matrix. In the following chapters, we study this general two-species model, specifically analyzing when the invading population can exist either through coexistence or competitive exclusion. While our initial motivation was based on competitive interactions, such as those in the Lotka-Volterra and Leslie-Gower competition models, we make no assumptions on the types of intraspecific or interspecific interactions. We also make no assumptions on the structure of the resident's projection matrix; for example, it may be a community of species, wherein its projection matrix would be reducible.

Chapter 2

The Model

We consider a matrix model of two species, a resident population with m stages and an invader population with n stages, with general nonlinearities. The population vector $x(t) \in \mathbb{R}^{m+n}$ holds the population levels or densities for both species. The model is given by

$$x' = \begin{pmatrix} P_R(x) & 0_{m\times n} \\ 0_{n\times m} & P_I(\gamma, x) \end{pmatrix} x, \tag{2.1}$$

where $P_R(x) \in \mathbb{R}^{m\times m}$ and $P_I(\gamma, x) \in \mathbb{R}^{n\times n}$ are the resident and invader projection matrices respectively, and where γ is a scalar parameter appearing in $P_I(\gamma, x)$. We use LaSalle's notation of x' to denote the next iterate of the map. The projection matrix for the system,

$$P(\gamma, x) = \begin{pmatrix} P_R(x) & 0_{m\times n} \\ 0_{n\times m} & P_I(\gamma, x) \end{pmatrix}, \tag{2.2}$$

has a block diagonal structure which prevents births or transitions from one population to the other. When the resident is in isolation, its dynamics depend crucially on the nonlinearities in $P_R(x)$. We consider the case where the resident has a stable equilibrium or periodic cycle, and we analyze when invasion is possible into such a state using γ as a bifurcation parameter. We make no assumptions on the structure of the resident (in fact, it may be a community of multiple species), the appearance of the bifurcation parameter, or the types of interactions between the two populations.

2.1 Notation

We start by defining some notation used throughout the dissertation.

With the exception of left eigenvectors and left nullvectors (which are row vectors), vectors are column vectors. For a vector $y \in \mathbb{R}^{m+n}$, we define the resident and invader components $y_R \in \mathbb{R}^m$ and $y_I \in \mathbb{R}^n$ such that $y = \mathrm{col}(y_R, y_I)$. For a matrix $A \in \mathbb{R}^{(m+n)\times(m+n)}$, we define the A_R as the upper-left $m \times m$ block and A_I as the bottom-right $n \times n$ block. In matrices or vectors, we use a $\star$ to indicate entries irrelevant to the calculations. A superscript ^{0} indicates evaluation at a specified bifurcation point (γ^0, x^0), e.g. $f^0 = f(\gamma^0, x^0)$. To clarify the order of differentiation and evaluation, for a function $g(\gamma, x)$ we define $g^0_\gamma = \partial^0_\gamma g = g_\gamma(\gamma, x)|_{(\gamma^0,x^0)}$ and $\nabla^0_x g = \nabla_x g(\gamma, x)|_{(\gamma^0,x^0)}$.

If we iterate map (2.1) $\theta - 1$ times, we arrive at a map $q^{(\theta)}(\gamma, x)$ which we call the *θ-composite map* or the *θ-composite system*. It can be written as a matrix-vector product $q^{(\theta)}(\gamma, x) = P^{(\theta)}(\gamma, x)x$, where we call $P^{(\theta)}(\gamma, x)$ the *θ-composite projection matrix*. To clarify, $q^{(1)}(\gamma, x) = q(\gamma, x)$, $P^{(1)}(\gamma, x) = P(\gamma, x)$, and $P^{(2)}(\gamma, x) = P(\gamma, P(\gamma, x)x)P(\gamma, x)$. Let $\mathcal{J}(\gamma, x)$ denote the Jacobian of $q(\gamma, x)$ with respect to x; $\mathcal{J}^{(\theta)}(\gamma, x)$ the Jacobian of the θ-composite system $q^{(\theta)}(\gamma, x)$; $J_R(x)$ the Jacobian of the resident's system in isolation, i.e. of $P_R(\text{col}(x_R, 0_{n\times 1}))x_R$; and $J^{(\theta)}_R(x)$ the Jacobian of the resident's θ-composite system in isolation, i.e. of $P^{(\theta)}_R(\text{col}(x_R, 0_{n\times 1}))x_R$.

2.2 Terminology

For clarity, we define some terminology used throughout the dissertation.

Branch A *branch* is a curve of points (γ, x), i.e a continuous mapping from a one-dimensional domain into $(m+n+1)$-dimensional space.

Coexistence The two populations are said to *coexist* at a fixed point if the population vector x is nonnegative and contains at least one positive entry for each population, i.e. there exist integers $i \in [1, m]$ and $j \in [m + 1, n]$ such that $x_i, x_j > 0$.

Cycle A set of points $\{\tau^{(i)}\}_{i=1}^n$ is a *cycle* of the system $x' = P(x)x$ if $\tau^{(i+1)} = P(\tau^{(i)})\tau^{(i)}$ and $\tau^{(1)} = P(\tau^{(n)})\tau^{(n)}$.

Direction of bifurcation Given a bifurcation point (γ^0, x^0) and a branch of fixed points $(\gamma, x(\gamma))$ bifurcating from (γ^0, x^0), the direction of bifurcation is *forward* (*backward*) if $\gamma > \gamma^0$ ($\gamma < \gamma^0$) for the fixed points in a neighborhood of the bifurcation point.

Dominant eigenvalue The *dominant eigenvalue* of a matrix is the eigenvalue with the largest absolute value (may not be unique).

Imprimitive A matrix P is *imprimitive* if it is nonnegative, irreducible, and does not have a strictly dominant eigenvalue.

Invasion We say *invasion* is possible when there exists a stable attractor in which the invader is present.

Irreducible A matrix is *irreducible* if it is not reducible.

Projection matrix The *projection matrix* projects the population vector from one time to the next, e.g. see (2.1).

Primitive A matrix P is *primitive* if it is nonnegative, irreducible, and has a strictly dominant eigenvalue.

Reducible A matrix is *reducible* if it is possible to achieve a block triangular projection matrix of the form

$$\begin{pmatrix} A & 0 \\ B & C \end{pmatrix},$$

where A and C are square matrices, via conjugation by a permutation matrix, i.e. through a reordering of the classes.

Stable A fixed point (γ^0, x^0) of system (2.1) is *stable* if the following two properties hold:

1. For every $\epsilon > 0$, there exists a $\delta > 0$ such that $\|x(0) - x^0\| < \delta$ implies $\|x(t) - x^0\| < \epsilon$ for all $t > 0$.
2. There exists a $\delta > 0$ such that $\|x(0) - x^0\| < \delta$ implies $\lim_{t\to\infty} \left\|x(t) - x^0\right\| = 0$.

Strong Allee effect A population is said to undergo a *strong Allee effect* if it has a critical population threshold below which it goes extinct and above which it persists.

Synchronous An orbit/trajectory is *synchronous* if at least one (but not every) of the invader's classes is absent at every timestep, i.e. x_I always contains at least one zero entry.

Unstable A fixed point is *unstable* if property 1 of *stable* does not hold.

A few of the definitions have been modified from their typical usage in the literature to better suit our application. In general, *synchronous* orbits allow for the zero to appear in any class (including those belonging to the resident). Also, property 1 of *stable* is the usual definition of a *stable* fixed point (also sometimes referred to as *Lyapunov stable*) while property 2 defines an *attracting* fixed point. A fixed point with both properties is usually referred to as *asymptotically stable.* Because our arguments of stability always imply asymptotic stability, we have adopted *stable* as a shorthand with the above definition, and write out *asymptotically stable* in the theorems for clarity.

2.3 Assumptions

We now present two basic assumptions which will be used throughout the dissertation. The remainder of the assumptions are section-specific and will be introduced as needed.

Let $\mathcal{C}^k(\mathcal{D})$ denote the set of all k-times continuously differentiable real-valued functions defined on the domain $\mathcal{D}$. With $\mathbb{R}^k$ denoting standard k-dimensional Euclidean space, define the space of k-dimensional *positive vectors* as

$$\mathbb{R}^k_+ = \{x \in \mathbb{R}^k : x_i > 0 \text{ for } i = 1, 2, ..., k\}$$

and the space of k-dimensional *nonnegative vectors* as

$$\overline{\mathbb{R}^k_+} = \{x \in \mathbb{R}^k : x_i \geq 0 \text{ for } i = 1, 2, ..., k\}.$$

Positive and nonnegative matrices are defined similarly. We require the entries of the projection matrix to be nonnegative and sufficiently smooth for our calculations.

Assumption A1. *The entries of P in (2.2) are in $\mathcal{C}^2(\Gamma \times \Omega)$, where $\Gamma \subset \mathbb{R}$ is an open interval and $\Omega \supset \overline{\mathbb{R}^{m+n}_+}$ is an open set, and are nonnegative for $\gamma \in \Gamma$ and $x \in \overline{\mathbb{R}^{m+n}_+}$.*[1]

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[1] Technically our analysis only requires smoothness in an open set containing the cycle points $\{(\gamma^0, \tau^{(i)})\}_{i=1}^n$ which are defined in Assumptions A2 and A3. Similarly, nonnegativity is only required for nonnegative x in neighborhoods of the cycle points.

Our goal is to study when it is possible for a species to successfully invade a resident species which has a stable attractor. Specifically, we assume the resident has a stable cycle of period θ, which we refer to as the *resident θ-cycle* or the *resident cycle*, where $\theta = 1$ corresponds to an equilibrium state. The resident cycle is a cycle of the resident subsystem

$$x_R' = P_R(\text{col}(x_R, 0_{n\times 1}))x_R. \tag{2.3}$$

Assumption A2. *There exists a nonnegative (and nonzero) cycle of period $\theta \geq 1$ of (2.3) with x_R values $\tau_R \to \tau_R^{(2)} \to \cdots \to \tau_R^{(\theta)} \to \tau_R$ such that the absolute value of the dominant eigenvalue of $J_R^{(\theta)}(\tau_R)$ is less than 1.*

We label the points of the corresponding solution x of equation (2.1) as $\tau^{(i)} = \text{col}(\tau_R^{(i)}, 0_{n\times 1})$, which we also refer to as the *resident cycle*. These points form a cycle of (2.1) and are each fixed points of the θ-composite system

$$x' = P^{(\theta)}(\gamma, x)x. \tag{2.4}$$

When the absolute value of the dominant eigenvalue of $J_R^{(\theta)}(\tau_R)$ is less than 1, the m eigenvalues of $J_R^{(\theta)}(\tau_R)$ are within the complex unit circle and the θ-cycle is locally stable as a periodic cycle of the resident system $x_R' = P_R(\text{col}(x_R, 0_{n\times 1}))x_R$. Successful invasion becomes possible when an eigenvalue of Jacobian of the full system moves outside the unit circle, the occurrence of which is guaranteed by our next assumption.

Assumption A3. *There exists a $\gamma^0 \in \Gamma$ where the absolute value of the (not necessarily strictly) dominant eigenvalue of $P_I^{(\theta)}(\gamma^0, \tau)$ equals 1 and the corresponding right eigenvector v_I and left eigenvector w_I satisfy $w_I \partial_\gamma^0 P_I^{(\theta)} v_I \neq 0$.*

We will see the usefulness of Assumption A3 in the next chapter for the specific case when the value of a dominant eigenvalue of $P_I^{(\theta)}(\gamma^0, \tau)$ equals 1.

Chapter 3

Preliminary Theorems

Before delving into the analysis of our problem, we introduce some necessary theorems. The theorem in Section 3.1 establishes the existence of a bifurcation when the Jacobian of the system has an eigenvalue equal to 1 (when a nondegeneracy condition holds). The two theorems in Section 3.2 provide smoothness of eigenvalues and eigenvectors of a matrix, which will later be applied to the Jacobian of our system.

3.1 Solution branches of an algebraic system

Consider the algebraic system

$$x = K(\gamma, x)x \tag{3.1}$$

where the entries of K satisfy Assumption A1, with Jacobian $\mathcal{J}(\gamma, x)$ of the right-hand side. We give conditions under which two branches of solutions transversely intersect, i.e. a transcritical bifurcation occurs. The theorem presented here is slightly more general than that found in [7, Appendix B.2] but the proof follows the same general arguments known collectively as the Lyapunov-Schmidt Reduction, which invokes the Implicit Function Theorem and the Fredholm Alternative. We reproduce the Implicit Function Theorem (see [35, Theorem 9.2]) and the Fredholm Alternative (see [20, Section 0.6.6]) below, followed by the theorem and proof of the algebraic problem specified.

Implicit Function Theorem [35]. *Let $U \subseteq \mathbb{R}^{k+n}$ be open and $f : U \to \mathbb{R}^n$ be $\mathcal{C}^r$ (r-times continuously differentiable). Let $x \in \mathbb{R}^k$ and $y \in \mathbb{R}^n$ to write $f(x, y)$. If there exists some $(a, b) \in U$ such that $f(a, b) = 0$ and*

$$det \frac{\partial f}{\partial y}(a, b) \neq 0$$

(i.e. the Jacobian at (a, b) is invertible), then there exists a neighborhood $A \subseteq \mathbb{R}^k$ of a and C^r function $g : A \to \mathbb{R}^n$ such that $g(a) = b$ and $f(x, g(x)) = 0$ for every $x \in A$.

Fredholm Alternative (with real numbers) [20]. *The linear system* $Ax = b$ *has a solution (not necessarily unique) if and only if* $b^T z = 0$ *for every vector* z *such that* $z^T A = 0$.

Theorem 1. *Assume the entries of* $K(\gamma, x)$ *in (3.1) satisfy Assumption A1 and that* x^0 *is a nonzero fixed point of the system so that* $x^0 = K(\gamma, x^0)x^0$ *for all* $\gamma \in \Gamma$. *Assume* $\mathcal{J}(\gamma, x^0)$ *has an algebraically simple eigenvalue* 1 *at some* γ^0 *with right eigenvector* v *and left eigenvector* w *such that* $w\partial_\gamma^0 \mathcal{J} v \neq 0$. *Then in a neighborhood of* $(\gamma, x) = (\gamma, x^0)$ *there exists a branch of solutions to (3.1) of the form*

$$\gamma(\epsilon) = \gamma^0 + \kappa\epsilon + o(\epsilon), \quad x(\epsilon) = x^0 + v\epsilon + u\epsilon^2 + o(\epsilon^2)$$

where $\gamma(\epsilon)$ *is continuously differentiable and* $x(\epsilon)$ *is twice continuously differentiable.*

Proof. The equation $x = K(\gamma, x)x$ near $x = x^0$ takes the form

$$x = x^0 + \mathcal{J}(\gamma, x^0)(x - x^0) + h(\gamma, x) \tag{3.2}$$

where $h(\gamma, x) = o(|x - x^0|)$ uniformly on compact intervals of γ and h is twice continuously differentiable in (γ, x). We recenter the problem around (γ^0, x^0) using $y = x - x^0$, $\lambda = \gamma - \gamma^0$. Then (3.2) becomes

$$\left(I - \mathcal{J}(\gamma^0, x^0)\right) y = B(\lambda)y + \hat{h}(\lambda, y) \tag{3.3}$$

where $B(\lambda) = \mathcal{J}(\lambda + \gamma^0, x^0) - \mathcal{J}(\gamma^0, x^0)$ and $\hat{h}(\lambda, y) = o(|y|)$. Note $\hat{h}(\lambda, 0) = 0$ and $B(0) = \mathcal{J}(\gamma^0, x^0) - \mathcal{J}(\gamma^0, x^0) = 0$. Denote $g(\lambda, y) = B(\lambda)y + \hat{h}(\lambda, y)$.

By the Fredholm Alternative, there exists a solution y to (3.3) if and only if $wg(\lambda, y) = 0$, where w is a left eigenvector of $\mathcal{J}(\gamma^0, x^0)$ corresponding to eigenvalue 1. With v as a right eigenvector of $\mathcal{J}(\gamma^0, x^0)$ corresponding to eigenvalue 1, define $V = \operatorname{span}(v)$ and $V^\perp = \{u \in \mathbb{R}^{m+n} : u^T v = 0\}$. Because $V \oplus V^\perp = \mathbb{R}^{m+n}$, we can decompose a solution y into components from V and $V^\perp$. Write $y = \epsilon v + z$ where $z \in V^\perp$ and $\epsilon \in \mathbb{R}$, and let G be the linear map from $g(\lambda, y)$ to z so that $Gg(\lambda, y) = z$. Then finding a pair (λ, y) that satisfies (3.3) is equivalent to finding a triple (ϵ, λ, z)

that satisfies

$$0 = w\left[B(\lambda)\epsilon v + B(\lambda)z + \hat{h}(\lambda, \epsilon v + z)\right] \tag{3.4}$$

$$0 = z - G\left[B(\lambda)\epsilon v + B(\lambda)z + \hat{h}(\lambda, \epsilon v + z)\right]. \tag{3.5}$$

Note that $G0 = 0$ because $(I - \mathcal{J}(\gamma^0, x^0))\, y = 0$ implies $y \in V$.

We would now like to apply the Implicit Function Theorem to equations (3.4) and (3.5) to obtain nontrivial (i.e. not identically zero) functions $z(\epsilon)$ and $\lambda(\epsilon)$; we cannot, however, because the Jacobian of this system of equations with respect to λ and z at $\epsilon = \lambda = z = 0$ is singular (the derivative with respect to λ of both equations is zero), or intuitively because we expect two solutions (the trivial and nontrivial solutions). The derivative with respect to λ of (3.4) gives

$$w\left[B_\lambda(\lambda)\epsilon v + B_\lambda(\lambda)z + \hat{h}_\lambda(\lambda, \epsilon v + z)\right]\Bigg|_{\epsilon=0,\lambda=0,z=0} = w\hat{h}_\lambda(0,0) = 0$$

because $\hat{h}(\lambda, y) = o(|y|)$. Similarly, the derivative with respect to λ of (3.5) gives

$$-G\left[B_\lambda(\lambda)\epsilon v + B_\lambda(\lambda)z + \hat{h}_\lambda(\lambda, \epsilon v + z)\right]\Bigg|_{\epsilon=0,\lambda=0,z=0} = -G\hat{h}_\lambda(0,0) = 0.$$

Instead, we start by applying the Implicit Function Theorem to equation (3.5) to get a solution for $z = z(\epsilon, \lambda)$. Note that $\epsilon = \lambda = 0$ and $z = 0$ is a solution to (3.5). At this point, the Jacobian of the right-hand side with respect to z is equal to the identity and is thus invertible. We can thus apply the Implicit Function Theorem to solve (3.5) for $z = z(\epsilon, \lambda)$ where $z(\epsilon, \lambda)$ is twice continuously differentiable in (ϵ, λ).

Next, note that $z(0, \lambda) = 0$ is a solution to (3.5), and with uniqueness given by the Implicit Function Theorem it follows that $z(0, \lambda) = 0$ in a neighborhood of $\lambda = 0$. Thus, by Taylor's Theorem we can write $z(\epsilon, \lambda) = \epsilon\zeta(\epsilon, \lambda)$ where $\zeta(\epsilon, \lambda)$ is continuously differentiable in (ϵ, λ). Equation (3.5), after a cancellation of ϵ, becomes

$$0 = \zeta(\epsilon, \lambda) - G\left[B(\lambda)v + B(\lambda)\zeta(\epsilon, \lambda) + \epsilon^{-1}\hat{h}(\lambda, \epsilon v + \epsilon\zeta(\epsilon, \lambda))\right]$$

from which we find $\zeta(0,0) = 0$ (because $\hat{h}(\lambda, y) = o(|y|)$). Equation (3.4) becomes

$$0 = w\left[B(\lambda)v + B(\lambda)\zeta(\epsilon, \lambda) + \epsilon^{-1}\hat{h}(\lambda, \epsilon v + \epsilon\zeta(\epsilon, \lambda))\right] \tag{3.6}$$

which has a solution of $\lambda = \epsilon = 0$, and the Jacobian at this point of the right-hand side with respect to λ is $wB_\lambda(0)v$. Assuming $wB_\lambda(0)v \neq 0$, we can apply the Implicit Function Theorem to (3.6) to get a unique solution $\lambda(\epsilon)$ that is continuously differentiable and where $\lambda(0) = 0$.

Thus, as long as $w\partial_\gamma^0 \mathcal{J} v \neq 0$, we have acquired nonzero functions $z(\epsilon) = \epsilon\zeta(\epsilon, \lambda(\epsilon))$ and $\lambda(\epsilon)$ and thus a branch of nontrivial solutions

$$\gamma(\epsilon) = \gamma^0 + \lambda(\epsilon), \quad x(\epsilon) = x^0 + \epsilon v + \epsilon\zeta(\epsilon)$$

to $x = K(\gamma, x)x$, where $\zeta(\epsilon) = \zeta(\epsilon, \lambda(\epsilon))$. Because $\lambda(0) = 0$ and $\zeta(0) = 0$ and both λ, ζ are continuously differentiable, through another application of Taylor's Theorem we can write

$$\gamma(\epsilon) = \gamma^0 + \kappa\epsilon + o(\epsilon), \quad x(\epsilon) = x^0 + v\epsilon + u\epsilon^2 + o(\epsilon^2)$$

where κ and u are constants. ■

3.2 Continuous differentiability of eigenvalues and eigenvectors

Given matrix at least twice-continuously differentiable $A(\epsilon) = A_0 + A_1\epsilon + A_2\epsilon^2 + o(\epsilon^2)$, we present and extend theorems by Kato in [24] and [25] on the continuous differentiability of its eigenvalues and eigenvectors. At what Kato refers to as *exceptional points*, where two eigenvalues cross in value, differentiability of the eigenvalues and eigenvectors is not guaranteed. For example, [37] gives

$$A(\epsilon) = \begin{pmatrix} 0 & 1 \\ \epsilon & 0 \end{pmatrix}.$$

This matrix has eigenvalues $\pm\sqrt{\epsilon}$ which lack differentiability at $\epsilon = 0$. Continuity of the eigenvalues, on the other hand, is guaranteed — because eigenvalues are the roots of the characteristic polynomial of $A(\epsilon)$ and the roots of a polynomial depend continuously on its coefficients [34], the eigenvalues depend continuously on the entries of $A(\epsilon)$. Further, an application of Theorem 5.13a in [25] gives that simple eigenvalues and their corresponding eigenvector are as smooth as the matrix entries.

Specifically, Theorem 5.13a in [25] gives the smoothness of the eigenprojection, which can be applied to give smoothness of an eigenvector with arbitrary choice of normalization. To see this, let $S(\epsilon)$ denote the eigenprojection, which is an idempotent matrix that projects onto the line of eigenvectors corresponding to the simple eigenvalue in consideration. Then $S(\epsilon)u$ is a nonzero eigenvector of $A(\epsilon)$ for any non-orthogonal vector u. Further, note that if u is a constant vector non-orthogonal to $S(\epsilon)$, then the image of $S(\epsilon)u$ is as smooth as $S(\epsilon)$ and u acts as a normalization choice of the eigenvector. For our purposes, we reproduce the theorem specialized to a second-order series expansion of $A(\epsilon)$, though the theorem in [25] provides an arbitrary level of differentiability.

Theorem 2. *Consider a matrix* $A(\epsilon) = A_0 + A_1\epsilon + o(\epsilon)$ *near* $\epsilon = 0$ *such that* A_0 *has an algebraically simple eigenvalue* λ *with eigenvector* ξ. *Then* $A(\epsilon)$ *has an eigenvalue* $\mu(\epsilon) = \lambda + \mu_1\epsilon + o(\epsilon)$ *with corresponding eigenvector (unique up to scalar multiple)* $\xi(\epsilon) = \xi + \xi_1\epsilon + o(\epsilon)$.

In general, such expansions are not guaranteed to exist when the eigenvalue λ is not simple; however, they are attainable for *semisimple* eigenvalues, where the algebraic multiplicity is equal to the geometric multiplicity. For semisimple eigenvalues, there is no loss of dimension of the eigenspace at $\epsilon = 0$, and Theorem 5.11 in [24] provides us with expansions of the eigenvalues and the corresponding eigenprojections. We provide a modified version of Theorem 5.11 from [24] for a semisimple eigenvalue λ of multiplicity 2.

Theorem 3. *Consider a matrix* $A(\epsilon) = A_0 + A_1\epsilon + A_2\epsilon^2 + o(\epsilon^2)$ *near* $\epsilon = 0$ *where* A_0 *has an eigenvalue* λ *of multiplicity* 2 *with a two-dimensional corresponding eigenspace. The eigenvalues of* $A(\epsilon)$ *can be written as* $\mu(\epsilon) = \lambda + \mu_1\epsilon + o(\epsilon)$ *and* $\widetilde{\mu}(\epsilon) = \lambda + \widetilde{\mu}_1\epsilon + o(\epsilon)$.

If $\mu_1 = \widetilde{\mu}_1$, *then their eigenprojections are continuously differentiable and equal up to order* ϵ, *i.e.* $S(\epsilon) = S_0 + S_1\epsilon + o(\epsilon)$ *and* $\widetilde{S}(\epsilon) = S_0 + S_1\epsilon + o(\epsilon)$.

If $\mu_1 \neq \widetilde{\mu}_1$*, then each has a continuously differentiable eigenprojection,* $S(\epsilon) = S_0 + S_1\epsilon + o(\epsilon)$ *and* $\widetilde{S}(\epsilon) = \widetilde{S}_0 + \widetilde{S}_1\epsilon + o(\epsilon)$*, such that* $\dim(S(\epsilon)) = \dim(\widetilde{S}(\epsilon)) = 1$*. Thus each has a continuously differentiable (linearly independent) eigenvector (unique up to scalar multiple),* $\xi(\epsilon) = \xi_0 + \xi_1\epsilon + o(\epsilon)$ *and* $\widetilde{\xi}(\epsilon) = \widetilde{\xi}_0 + \widetilde{\xi}_1\epsilon + o(\epsilon)$ *respectively.*

In the case of $\mu_1 \neq \widetilde{\mu}_1$, the existence of the eigenvector expansions follows from the eigenprojection expansions and the argument used before in the simple case. Further, although Kato's theorem only specifies $\dim(S_0) = \dim(\widetilde{S}_0) = 1$, it follows that $\dim(S(\epsilon)) = \dim(\widetilde{S}(\epsilon)) = 1$ due to the fact that the eigenvalues are distinct away from $\epsilon = 0$. In the case of $\mu_1 = \widetilde{\mu}_1$, the eigenprojection projects onto a two-dimensional eigenspace. Although the choice of eigenvectors is not unique, $S(\epsilon)u$ is still continuously differentiable for any constant non-orthogonal vector u. Thus, with two appropriate choices of u, one can still obtain two linearly independent vectors in the two-dimensional eigenspace.

CHAPTER 4

INVADING THE RESIDENT CYCLE: PRIMITIVE CASE

We look to determine when successful invasion into the resident θ-cycle is possible. This requires a destabilization of the resident θ-cycle, which occurs when an eigenvalue of $\mathcal{J}^{(\theta)}(\gamma, \tau)$ leaves the interior of the complex unit circle. As may be seen in the next section, Assumption A3 provides the existence of such an occurrence. If $P_I^{(\theta)}(\gamma^0, \tau)$ is primitive, the Perron-Frobenius Theorem states that it has a positive, simple, and strictly dominant eigenvalue, and so we are guaranteed that if the dominant eigenvalue leaves the unit circle then it does so alone and through 1. Addressing this case, we use Theorem 1 from Chapter 3 to prove existence of bifurcating θ-cycles and then analyze their stability and direction of bifurcation. We conclude the chapter by looking at a simple example to illustrate our results.

Assumption A4. $P_I^{(\theta)}(\gamma^0, \tau)$ *is primitive.*

4.1 Destabilization of the resident cycle

We examine the Jacobian of the θ-composite system and its relevant eigenvalues and eigenvectors. When an eigenvalue leaves the complex unit circle, we apply Theorem 1 to prove the existence of bifurcating θ-cycles.

4.1.1 Eigenvectors of the composite Jacobian

The Jacobian of the θ-composite system at τ,

$$\mathcal{J}^{(\theta)}(\gamma, \tau) = P^{(\theta)}(\gamma, \tau) + \left(\sum_{k=1}^{m+n} \tau_k \partial_{x_j}^0 p_{ik}^{(\theta)} \right), \tag{4.1}$$

can be written as a product of the Jacobian of the base system evaluated at each of the different cycle points:

$$\begin{aligned}\mathcal{J}^{(\theta)}(\gamma,\tau) &= \prod_{i=\theta}^{1} \mathcal{J}(\gamma,\tau^{(i)}) \\ &= \mathcal{J}(\gamma,\tau^{(\theta)})\mathcal{J}(\gamma,\tau^{(\theta-1)})\ldots\mathcal{J}(\gamma,\tau^{(2)})\mathcal{J}(\gamma,\tau)\end{aligned}$$

where

$$\mathcal{J}(\gamma,\tau^{(i)}) = \left(\begin{array}{c:c} J_R(\tau_R^{(i)}) & \star_{m\times n} \\ \hdashline 0_{n\times m} & P_I(\gamma,\tau^{(i)}) \end{array}\right).$$

Using this property, one can see that $\mathcal{J}^{(\theta)}(\gamma,\tau)$ has the form

$$\mathcal{J}^{(\theta)}(\gamma,\tau) = \left(\begin{array}{c:c} J_R^{(\theta)}(\tau_R) & \star_{m\times n} \\ \hdashline 0_{n\times m} & \prod_{i=\theta}^{1} P_I(\gamma,\tau^{(i)}) \end{array}\right). \tag{4.2}$$

It follows from (4.1) and (4.2) that

$$P_I^{(\theta)}(\gamma,\tau) = \prod_{i=\theta}^{1} P_I(\gamma,\tau^{(i)}). \tag{4.3}$$

Under Assumption A4, $P_I^{(\theta)}(\gamma^0,\tau)$ is primitive[1] and thus has a positive, strictly dominant eigenvalue by the Perron-Frobenius Theorem. By Assumption A3, that dominant eigenvalue is equal to 1 at $\gamma=\gamma^0$. Because the eigenvalues of $J_R^{(\theta)}(\tau_R)$ are assumed to be within the unit circle (Assumption A2), $\mathcal{J}^{(\theta)}(\gamma^0,\tau)$ then also has a unique dominant eigenvalue of 1 with a one-dimensional eigenspace. From the block form of $\mathcal{J}^{(\theta)}(\gamma,\tau)$, the right eigenvector of $\mathcal{J}^{(\theta)}(\gamma^0,\tau)$ corresponding to eigenvalue 1

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[1] Primitivity of each factor matrix $P_I(\gamma^0,\tau^{(i)})$ does not guarantee primitivity of $P_I^{(\theta)}(\gamma^0,\tau)$. For an example of this, and for a sufficient condition for the primitivity of $P_I^{(\theta)}(\gamma^0,\tau)$, see Appendix A.

has the form

$$v = \begin{pmatrix} \star_{m\times 1} \\ \hdashline v_I \end{pmatrix}$$

where v_I is the positive eigenvector of $P_I^{(\theta)}(\gamma,\tau)$ guaranteed by the Perron-Frobenius Theorem. The left eigenvector is $w = (0_{1\times m}, w_I)$ where $w_I \in \mathbb{R}_+^n$ is the positive left eigenvector of $P_I^{(\theta)}(\gamma,\tau)$.

4.1.2 Existence of bifurcating cycles

We obtain sufficient conditions for the bifurcation of θ-cycles by applying Theorem 1 to the algebraic equation $x = P^{(\theta)}(\gamma,x)x$ to find fixed points of the θ-composite system. The Jacobian of the right-hand side of this equation is $\mathcal{J}^{(\theta)}(\gamma,x)$.

As mentioned in Section 4.1.1, under Assumption A4 the strictly dominant eigenvalue of $P_I^{(\theta)}(\gamma,\tau)$ is also the dominant eigenvalue of $\mathcal{J}^{(\theta)}(\gamma,\tau)$ near γ^0. At γ^0, $P_I^{(\theta)}(\gamma^0,\tau)$ — and hence $\mathcal{J}^{(\theta)}(\gamma^0,\tau)$ — has a simple, strictly dominant eigenvalue of 1. If $w\partial_\gamma^0\mathcal{J}^{(\theta)}v \neq 0$, where v and w are right and left eigenvectors of $\mathcal{J}^{(\theta)}(\gamma^0,\tau)$ corresponding to eigenvalue 1, then we can apply Theorem 1 with $x^0 = \tau$ to obtain the existence of a branch of solutions of $x = P^{(\theta)}(\gamma,x)x$ which bifurcates from (γ^0,τ). Using v and w from Section 4.1.1, (4.2), (4.3), and the fact that the bottom-left $n\times m$ block of $\partial_\gamma^0\mathcal{J}^{(\theta)}$ is zero,[2] we see that

$$w\partial_\gamma^0\mathcal{J}^{(\theta)}v = w_I\partial_\gamma^0 P_I^{(\theta)}v_I. \tag{4.4}$$

Thus $w\partial_\gamma^0\mathcal{J}^{(\theta)}v \neq 0$ is equivalent to $w_I\partial_\gamma^0 P_I^{(\theta)}v_I \neq 0$, which is contained in Assumption A3. Theorem 1 then gives the form of the branch of fixed points of (2.4) which, together with the fact that $v_I \in \mathbb{R}_+^n$, shows that they are coexistence fixed points for $\epsilon > 0$. These coexistence fixed points of the θ-composite map correspond to coexistence θ-cycles of the original map, $x' = P(\gamma,x)x$.

Theorem 4. *Under Assumptions A1–A4, a branch of coexistence θ-cycles of system (2.1) bifurcates from (γ^0,τ). The corresponding fixed points of system (2.4) have the*

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[2] To see this, we must show that $(p_{ij}^{(\theta)})_\gamma^0 + \sum_k x_k^0 (p_{ik}^{(\theta)})_{\gamma x_j}^0 = 0$ when $i > m$ and $j < m$ are both true (see (4.1)). First, $p_{ij}^{(\theta)} = 0$ when $i > m$ and $j < m$, and thus $\partial_\gamma p_{ij}^{(\theta)} = 0$. Then, for $k > m$ note $x_k^0 = 0$ and for $k < m$ again $p_{ik}^{(\theta)} = 0$ when $i > m$, so that $\sum_k x_k^0 (p_{ik}^{(\theta)})_{\gamma x_j}^0 = 0$.

form

$$\gamma(\epsilon) = \gamma^0 + \kappa\epsilon + o(\epsilon),\ \ x(\epsilon) = \tau + v\epsilon + u\epsilon^2 + o(\epsilon^2)$$

near $\epsilon = 0$ *where* v *is the right eigenvector of* $\mathcal{J}^{(\theta)}(\gamma^0, \tau)$ *corresponding to eigenvalue* 1 *and* $\epsilon > 0$ *corresponds to coexistence.*

4.2 Direction of bifurcation and stability of the coexistence θ-cycles

In this section we determine the direction of bifurcation and stability of the bifurcating coexistence θ-cycles, established in Theorem 4, as the resident θ-cycle loses stability. To this end, and using the fact that τ is a fixed point of the θ-composite system, we parameterize the variables of the θ-composite map in ϵ along the branch of bifurcating fixed points. The relevant expansions include the state variables $x(\epsilon)$, the bifurcation parameter $\gamma(\epsilon)$, the Jacobian of the θ-composite map $\mathcal{J}^{(\theta)}(\gamma(\epsilon), x(\epsilon))$, and the eigenvalue $\mu(\epsilon)$ of said Jacobian which leaves the unit circle through 1:

$$\begin{aligned}
\gamma(\epsilon) &= \gamma^0 + \kappa\epsilon + o(\epsilon)\\
x(\epsilon) &= \tau + v\epsilon + u\epsilon^2 + o(\epsilon^2)\\
\mu(\epsilon) &= 1 + \mu_1\epsilon + o(\epsilon)\\
\mathcal{J}^{(\theta)}(\gamma(\epsilon), x(\epsilon)) &= \mathcal{J}_0^{(\theta)} + \mathcal{J}_1^{(\theta)}\epsilon + o(\epsilon).
\end{aligned} \tag{4.5}$$

The expansions of $x(\epsilon)$ and $\gamma(\epsilon)$ are provided by Theorem 4, the eigenvalue expansion is guaranteed by Theorem 2, and the expansion of $\mathcal{J}^{(\theta)}(\gamma(\epsilon), x(\epsilon))$ is guaranteed by the smoothness provided by Assumption A1. Because we are interested in biologically feasible points, i.e. $x(\epsilon) \in \overline{\mathbb{R}_+^{m+n}}$, we restrict our attention to $\epsilon > 0$. Then κ determines the direction of bifurcation in terms of the bifurcation parameter; namely, $\kappa > 0$ indicates a forward bifurcation and $\kappa < 0$ a backward bifurcation. If $\mu_1 < 0$, then the dominant eigenvalue is contained in the unit circle and the fixed points are stable; conversely, if $\mu_1 > 0$ then the fixed points are unstable.

4.2.1 Direction of bifurcation

To derive a formula for κ, we Taylor expand the θ-composite map, substitute the ϵ-expansions of $x(\epsilon)$ and $\gamma(\epsilon)$ from (4.5) into the Taylor expansion, and equate orders of ϵ.

Step 1: Taylor expand $P^{(\theta)}(\gamma, x)x$.
We compute the Taylor expansion of the right-hand side of $x_i = \sum_j x_j p_{ij}^{(\theta)}(\gamma, x)$ in terms of x and γ near (γ^0, τ). Recall a superscript of ^{0} denotes evaluation at (γ^0, τ).

$$\begin{aligned}
x_i = \tau_i &+ (\gamma - \gamma^0) \sum_j \tau_j \left(p_{ij}^{(\theta)}\right)_\gamma^0 + \sum_j (x_j - \tau_j) \left[\left(p_{ij}^{(\theta)}\right)^0 + \sum_k \tau_k (p_{ik}^{(\theta)})_{x_j}^0\right] \\
&+ \frac{1}{2}(\gamma - \gamma^0)^2 \sum_j \tau_j \left(p_{ij}^{(\theta)}\right)_{\gamma\gamma}^0 + (\gamma - \gamma^0) \sum_j (x_j - \tau_j) \left[(p_{ij}^{(\theta)})_\gamma^0 + \sum_k \tau_k (p_{ik}^{(\theta)})_{\gamma x_j}^0\right] \\
&+ \frac{1}{2} \sum_j (x_j - \tau_j) \sum_k (x_k - \tau_k) \left[2(p_{ik}^{(\theta)})_{x_j}^0 + \sum_r \tau_r (p_{ir}^{(\theta)})_{x_k x_j}^0\right] \\
&+ o_2
\end{aligned}$$

where o_2 contains all terms of order higher than two in combinations of x and $\gamma - \gamma^0$.

Terms 2 and 4 on the right-hand side evaluate to zero due to the structure of 0's in $\tau = \mathrm{col}(\tau_R, 0_{n\times 1})$ and $\partial_\gamma^0 P^{(\theta)}$ — note $P^{(\theta)}(\gamma, \tau)$ has the same block structure as $P(\gamma, \tau)$ (see (2.1)) and in its upper-left block γ can only appear in internal arguments attached to x_I terms, making the upper-left block of $\partial_\gamma^0 P^{(\theta)}$ zero.

Step 2: Substitute in the ϵ expansions and equate orders of ϵ.
We substitute the expansions of $x(\epsilon)$ and $\gamma(\epsilon)$ from (4.5) into the Taylor expansion and equate orders of ϵ.

At order ϵ^0, we see $\tau_i = \tau_i$.

At order ϵ^1, we see

$$\begin{aligned}
v_i &= \sum_j v_j \left[\left(p_{ij}^{(\theta)}\right)^0 + \sum_k \tau_k (p_{ik}^{(\theta)})_{x_j}^0\right] \\
&= (P^{(\theta)}(\gamma^0, \tau)v)_i + \sum_j v_j \sum_k \tau_k (p_{ik}^{(\theta)})_{x_j}^0 .
\end{aligned}$$

This is true because v is a right eigenvector of $\mathcal{J}^{(\theta)}(\gamma^0, x^0)$ corresponding to eigenvalue 1 (see 4.1).

At order ϵ^2, we see

$$\begin{aligned}
u_i &= \sum_j u_j \left[\left(p_{ij}^{(\theta)}\right)^0 + \sum_k \tau_k (p_{ik}^{(\theta)})^0_{x_j} \right] + \kappa \sum_j v_j \left[(p_{ij}^{(\theta)})^0_\gamma + \sum_k \tau_k (p_{ik}^{(\theta)})^0_{\gamma x_j} \right] \\
&\quad + \frac{1}{2} \sum_j v_j \sum_k v_k \left[2(p_{ik}^{(\theta)})^0_{x_j} + \sum_r \tau_r (p_{ir}^{(\theta)})^0_{x_k x_j} \right] \\
&= \left(\mathcal{J}_0^{(\theta)} u \right)_i + \kappa (\partial_\gamma^0 \mathcal{J}^{(\theta)} v)_i + \sum_j v_j \left(\nabla_x^0 p_{ij}^{(\theta)} \cdot v \right) + \frac{1}{2} \sum_j v_j \sum_k v_k \left[\sum_r \tau_r (p_{ir}^{(\theta)})^0_{x_k x_j} \right].
\end{aligned}$$

We denote this as

$$u = \mathcal{J}_0^{(\theta)} u + \kappa \partial_\gamma^0 \mathcal{J}^{(\theta)} v + D(v)v + H(v)v$$

where $d_{ij}(v) = \nabla_x^0 p_{ij}^{(\theta)} \cdot v$ and $h_{ij}(v) = \frac{1}{2} \sum_k v_k \left[\sum_r \tau_r (p_{ir}^{(\theta)})^0_{x_k x_j} \right]$.

By the Fredholm Alternative,

$$(I - \mathcal{J}_0^{(\theta)})u = \kappa \partial_\gamma^0 \mathcal{J}^{(\theta)} v + D(v)v + H(v)v$$

is solvable for u if and only if

$$\nu(\kappa \partial_\gamma^0 \mathcal{J}^{(\theta)} v + D(v)v + H(v)v) = 0$$

for every ν (row vector) such that $\nu(I - \mathcal{J}_0^{(\theta)}) = 0$, i.e. for every left eigenvector of $\mathcal{J}_0^{(\theta)}$ corresponding to eigenvalue 1, which is all nonzero multiples of w. Let $\nu = c_1 w$. The structure of

$$H(v) = \left(\begin{array}{c} \star_{m\times(m+n)} \\ \hdashline 0_{n\times(m+n)} \end{array} \right) \tag{4.6}$$

along with that of $w = (0_{1\times m}, w_I)$ (see Section 4.1.1) results in $wH(v)v = 0$. Solving for κ, we find

$$\kappa = -\frac{wD(v)v}{w\partial_\gamma^0 \mathcal{J}^{(\theta)} v}.$$

We use (4.4) to simplify the denominator. To simplify the numerator, note that the form of $w = (0_{1\times m}, w_I)$ means that only the bottom-left $n \times m$ and bottom-right $n \times n$ blocks of $D(v)$ affect κ. The bottom-left $n \times m$ block of $D(v)$ is zero because $p_{ij}^{(\theta)} = 0$ implies $d_{ij}(v) = 0$. Let $D_I(v)$ denote the bottom-right $n \times n$ block of $D(v)$. Thus

$$\kappa = -\frac{w_I D_I(v) v_I}{w_I \partial_\gamma^0 P_I^{(\theta)} v_I}. \tag{4.7}$$

Because w_I, v_I are positive, the sign of κ is determined by the signs of the entries in $D_I(v)$ and $\partial_\gamma^0 P_I^{(\theta)}$. If the bifurcation parameter is strictly beneficial to the invader, the entries of $\partial_\gamma^0 P_I^{(\theta)}$ will be positive; on the other hand, if an increase in the bifurcation parameter is detrimental to the invader (e.g. mortality rate), the entries of $\partial_\gamma^0 P_I^{(\theta)}$ may be negative. The bifurcation parameter may have different effects on different classes, but $w_I \partial_\gamma^0 P_I^{(\theta)} v_I$ represents a weighted average of the effect of the bifurcation parameter increasing on the invader. The entries in $D_I(v)$ are directional derivatives representing the sensitivities of the invader to the changes provided by v — where v_R may contain negative entries — with $w_I D_I(v) v_I$ representing a weighted average of the sensitivities. One can write an entry of $D_I(v)$ as

$$d_{ij}(v) = \nabla_{x_R}^0 p_{ij}^{(\theta)} \cdot v_R + \nabla_{x_I}^0 p_{ij}^{(\theta)} \cdot v_I$$

so that (restricting i, j to the integers between and including $m+1$ and $m+n$)

$$w_I D_I(v) v_I = w_I \left(\nabla_{x_R}^0 p_{ij}^{(\theta)} \cdot v_R\right) v_I + w_I \left(\nabla_{x_I}^0 p_{ij}^{(\theta)} \cdot v_I\right) v_I.$$

Here $w_I \left(\nabla_{x_I}^0 p_{ij}^{(\theta)} \cdot v_I\right) v_I$ summarizes how the increase in the invader population provided by v_I affects the invader classes, where negativity implies an overall detrimental effect (which can be caused by high between-class competition) and positivity implies an overall beneficial effect.

The generality of our analysis and model allows for complicated between- and within-species interactions, but a common scenario is a strictly competitive environment. In a competitive environment, where an increase in either population is detrimental to the other, generally the entries of v_R and $\nabla_{x_R}^0 p_{ij}^{(\theta)}$ are negative, so that $w_I \left(\nabla_{x_R}^0 p_{ij}^{(\theta)} \cdot v_R\right) v_I > 0$. In such a case and when the bifurcation parameter is beneficial to the invader ($w_I \partial_\gamma^0 P_I^{(\theta)} v_I > 0$), if the between-class competition is high enough ($w_I \left(\nabla^0_{x_I} p^{(\theta)}_{ij} \cdot v_I\right) v_I$ is negative enough) to outweigh the between-species competition ($w_I \left(\nabla^0_{x_R} p^{(\theta)}_{ij} \cdot v_R\right) v_I$ positivity), then $\kappa > 0$ and the bifurcation is forward. On the other hand, if the between-class competition is low and does not outweigh the between-species competition, the bifurcation is backward.

4.2.2 Stability of the bifurcating cycles

We can determine the stability of the θ-cycles bifurcating from (γ^0, τ) if $\mu_1 \neq 0$: if $\mu_1 < 0$ they are stable, and if $\mu_1 > 0$ they are unstable.

Let

$$\xi(\epsilon) = v + \xi_1 \epsilon + o(\epsilon)$$

denote the eigenvector of $\mathcal{J}^{(\theta)}(\epsilon) = \mathcal{J}^{(\theta)}(\gamma(\epsilon), x(\epsilon))$ corresponding to $\mu(\epsilon)$ whose expansion is justified by Theorem 2. The eigenvalue equation and its differential with respect to ϵ give us

$$\begin{gathered} \mathcal{J}^{(\theta)}(\epsilon)\xi(\epsilon) = \mu(\epsilon)\xi(\epsilon) \\ \mathcal{J}^{(\theta)\prime}(\epsilon)\xi(\epsilon) + \mathcal{J}^{(\theta)}(\epsilon)\xi'(\epsilon) = \mu^{(\theta)\prime}(\epsilon)\xi(\epsilon) + \mu(\epsilon)\xi'(\epsilon). \end{gathered}$$

At $\epsilon = 0$, these reduce to

$$\begin{gathered} \mathcal{J}^{(\theta)}_0 v = v \\ \mathcal{J}^{(\theta)}_1 v + \mathcal{J}^{(\theta)}_0 \xi_1 = \mu_1 v + \xi_1. \end{gathered}$$

The first equation is true because v is a right eigenvector of $\mathcal{J}^{(\theta)}_0$ corresponding to eigenvalue 1. The second equation is equivalent to

$$(\mathcal{J}^{(\theta)}_0 - I)\xi_1 = \mu_1 v - \mathcal{J}^{(\theta)}_1 v$$

which is solvable by the Fredholm Alternative if and only if

$$\nu(\mu_1 v - \mathcal{J}^{(\theta)}_1 v) = 0$$

for every $\nu = c_1 w$ left eigenvector of $\mathcal{J}_0^{(\theta)}$ corresponding to eigenvalue 1. Thus,

$$\mu_1 = \frac{w\mathcal{J}_1^{(\theta)}v}{wv}. \tag{4.8}$$

We then compute $\mathcal{J}_1^{(\theta)}$ using (4.1),

$$\mathcal{J}_1^{(\theta)} = \frac{d}{d\epsilon}\mathcal{J}^{(\theta)}(\epsilon)|_{\epsilon=0},$$

and the ϵ expansions in (4.5):

$$\begin{aligned}
\left(\mathcal{J}_1^{(\theta)}\right)_{ij} &= \frac{d}{d\epsilon}\left(p_{ij}^{(\theta)} + \sum_k x_k \partial_{x_j} p_{ik}^{(\theta)}\right)\Bigg|_{\epsilon=0} \\
&= \kappa\left[(p_{ij}^{(\theta)})_{\gamma}^0 + \sum_k \tau_k (p_{ik}^{(\theta)})_{\gamma x_j}^0\right] + \left(\sum_k v_k (p_{ij}^{(\theta)})_{x_k}^0\right) \\
&\quad + \left(\sum_k v_k (p_{ik}^{(\theta)})_{x_j}^0\right) + \left(\sum_r v_r \sum_k \tau_k (p_{ik}^{(\theta)})_{x_j x_r}^0\right).
\end{aligned}$$

Letting $g_{ij}(v) = \sum_k v_k (p_{ik}^{(\theta)})_{x_j}^0$, we can write this as

$$\mathcal{J}_1^{(\theta)} = \kappa\partial_\gamma^0 \mathcal{J}^{(\theta)} + D(v) + G(v) + 2H(v).$$

Note

$$\begin{aligned}
G(v)v &= \left(\sum_j \sum_k v_k (p_{ik}^{(\theta)})_{x_j}^0 v_j\right) \\
&= \left(\sum_k v_k \sum_j (p_{ik}^{(\theta)})_{x_j}^0 v_j\right) \\
&= \left(\sum_k v_k (\nabla_x^0 p_{ik}^{(\theta)} \cdot v)\right) \\
&= \left(\nabla_x^0 p_{ij}^{(\theta)} \cdot v\right) v \\
&= D(v)v
\end{aligned} \tag{4.9}$$

and recall that $wH(v)v = 0$, so that (4.8) gives

$$\begin{aligned}\mu_1 wv &= w\mathcal{J}_1^{(\theta)} v\\ &= w(\kappa\partial_\gamma^0 \mathcal{J}^{(\theta)} + D(v) + G(v) + 2H(v))v\\ &= w(\kappa\partial_\gamma^0 \mathcal{J}^{(\theta)} + 2D(v))v\\ &= \kappa w\partial_\gamma^0 \mathcal{J}^{(\theta)} v - 2\kappa w\partial_\gamma^0 \mathcal{J}^{(\theta)} v\\ &= -\kappa w\partial_\gamma^0 \mathcal{J}^{(\theta)} v.\end{aligned}$$

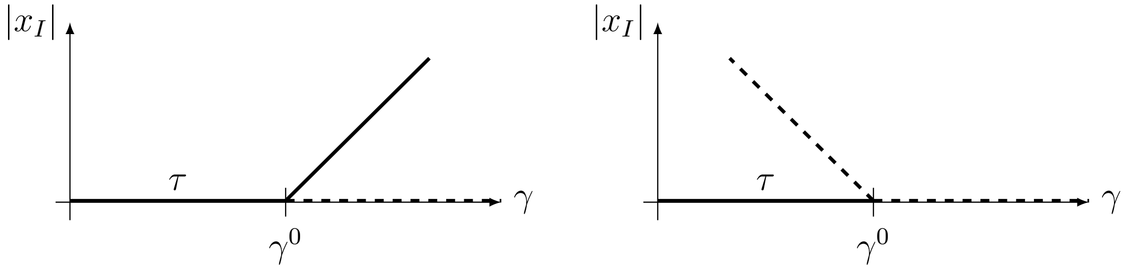
This simplifies to

$$\mu_1 = -\kappa \frac{w_I \partial_\gamma^0 P_I^{(\theta)} v_I}{w_I v_I}. \tag{4.10}$$

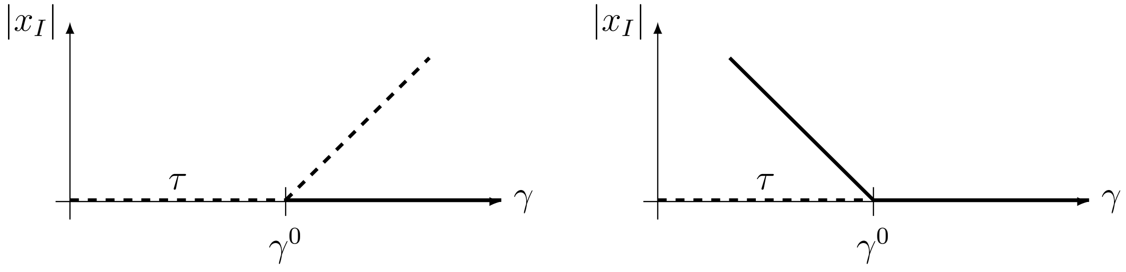
When $\mu_1 < 0$, the bifurcating coexistence θ-cycles are locally stable because all of the eigenvalues of the θ-composite Jacobian are within the unit circle.

Theorem 5. *Under Assumptions A1–A4, the coexistence θ-cycles of system (2.1) on the branch established in Theorem 4 bifurcate forward if $\kappa > 0$ and backward if $\kappa < 0$ (see (4.7)) and, near (γ^0, τ), are asymptotically stable if $\mu_1 < 0$ and unstable if $\mu_1 > 0$ (see (4.10)).*

Note $w_I v_I > 0$, so the sign of μ_1 can be determined by the signs of κ and $w_I \partial_\gamma^0 P_I^{(\theta)} v_I > 0$. As mentioned in Section 4.2.1, the sign of $w_I \partial_\gamma^0 P_I^{(\theta)} v_I$ indicates whether an increase in the bifurcation parameter has an overall beneficial (e.g. a birth rate or survival rate) or detrimental (e.g. a mortality rate or competition rate) effect on the invader. If increasing the bifurcation parameter benefits the invader ($w_I \partial_\gamma^0 P_I^{(\theta)} v_I > 0$), then a forward bifurcation creates coexistence cycles which are stable and thus biologically relevant. On the other hand, the cycles created by a backward bifurcation are unstable and thus not biologically realizable, though the branch may transcritically bifurcate a branch of invader attractors and create a dynamic scenario where the surviving population is initial condition dependent. See Figure 4.1 for sketches of the possible bifurcation diagrams provided by Theorem 5.



(a) $w_I \partial_\gamma^0 P_I^{(\theta)} v_I > 0$ and $\kappa > 0$ (b) $w_I \partial_\gamma^0 P_I^{(\theta)} v_I > 0$ and $\kappa < 0$



(c) $w_I \partial_\gamma^0 P_I^{(\theta)} v_I < 0$ and $\kappa > 0$ (d) $w_I \partial_\gamma^0 P_I^{(\theta)} v_I < 0$ and $\kappa < 0$

Figure 4.1: Sketches of the bifurcation diagrams for the θ-composite system based on Theorem 5. Solid lines indicate stability of the corresponding fixed points, while dashed lines indicate instability. The coexistence θ-cycles appear as fixed points for the θ-composite map and bifurcate in the direction specified by κ.

4.3 Example

To illustrate Theorem 5 we look at a simple example with $m = 1$, $\theta = 1$, $n = 2$. That is, a two-stage invader would like to invade a single-stage resident with a stable equilibrium. We consider the invader to have constant survival rates, s_1 (juvenile survival) and s_2 (adult survival), and a fecundity function dependent on the population densities and a parameter γ. To model this scenario, we use the projection matrix

$$P(\gamma, x) = \begin{pmatrix} \pi(x) & 0 & 0 \\ 0 & 0 & \phi(\gamma, x) \\ 0 & s_1 & s_2 \end{pmatrix}$$

with $\pi(x)$ and $\phi(\gamma, x)$ satisfying the smoothness assumptions set in Assumption A1.

The Jacobian

$$\mathcal{J}(\gamma,\tau) = \begin{pmatrix} \pi(\tau) + \pi_{x_1}(\tau)\tau_1 & \pi_{x_2}(\tau)\tau_1 & \pi_{x_3}(\tau)\tau_1 \\ 0 & 0 & \phi(\gamma,\tau) \\ 0 & s_1 & s_2 \end{pmatrix}$$

has a right eigenvector

$$v = \left(\frac{2s_1\pi^0_{x_3}\tau_1 - 2s_2\pi^0_{x_2}\tau_1 + \pi^0_{x_2}\tau_1\sqrt{4\phi^0 s_1 + (s_2)^2}}{s_1\left(s_2 - 2(\pi^0 + \pi^0_{x_1}\tau_1) + \sqrt{4\phi^0 s_1 + (s_2)^2}\right)}, \frac{-s_2 + \sqrt{4\phi^0 s_1 + (s_2)^2}}{2s_1}, 1 \right)$$

and left eigenvector

$$w = \left(0, \frac{-s_2 + \sqrt{4\phi^0 s_1 + (s_2)^2}}{2\phi^0}, 1 \right)$$

corresponding to eigenvalue 1 at $\gamma = \gamma^0$. To determine the direction of bifurcation and stability of the bifurcating equilibria ($\theta = 1$), note

$$D_I(v) = \begin{pmatrix} 0 & \nabla^0_x \phi(\gamma, x) \cdot v \\ 0 & 0 \end{pmatrix} \quad \text{and} \quad \partial^0_\gamma P^{(\theta)}_I = \begin{pmatrix} 0 & \phi^0_\gamma \\ 0 & 0 \end{pmatrix}.$$

Thus

$$\kappa = -\nabla^0_x \phi(\gamma, x) \cdot v / \phi^0_\gamma, \quad \mu_1 = \frac{w_2 \nabla^0_x \phi(\gamma, x) \cdot v}{w_2 v_2 + 1}.$$

We use Leslie-Gower nonlinearities with nonnegative coefficients for the fecundity functions:

$$\pi(x) = \frac{h_0}{1 + h_1 x_1 + h_2 x_2 + h_3 x_3},$$
$$\phi(f_0, x) = \frac{f_0}{1 + f_1 x_1 + f_2 x_2 + f_3 x_3}.$$

We use the inherent birth rate of the invader, f_0, as the bifurcation parameter in this example. The resident equilibrium solves $x_1 = \pi(x_1, 0, 0)x_1$, i.e. $\tau_R = (h_0 - 1)/h_1$. Thus, for existence of a positive resident equilibrium, $h_0 > 1$ is required. The critical value of the bifurcation parameter is

$$f^0_0 = (1 + f_1\tau_1)(1 - s_2)/s_1, \tag{4.11}$$

which is found by locating when the dominant eigenvalue at the resident equilibrium (as a function of $\gamma = f_0$),

$$\frac{1}{2}\left(s_2 + \sqrt{4s_1\phi(f_0,\tau) + s_2^2}\right),$$

equals 1. Note that

$$w_I \partial_\gamma^0 P_I^{(\theta)} v_I = \frac{h_1 s_1}{h_1 + f_1(h_0 - 1)} > 0,$$

so that a forward bifurcation implies stability and backward bifurcation implies instability of the bifurcating coexistence equilibria. Also, $v_1 < 0$, meaning the value of the resident population is lower than its isolated equilibrium value for coexistence equilibria near (f_0^0, τ). Given the forms of $\pi(x)$ and $\phi(x)$, we find

$$\kappa = \frac{1 - s_2}{s_1^2 h_1}\left[h_1\left(s_1 f_3 + f_2(1 - s_2)\right) - f_1\left(s_1 h_3 + h_2(1 - s_2)\right)\right].$$

Note h_1, f_2, f_3 are within-species competition parameters and h_2, h_3, f_1 are between-species competition parameters, so this expression implies that when within-species competition is greater than between-species competition the bifurcation is forward ($\kappa > 0$), and it is backward if the opposite is true. Intuitively, if within-species competition is greater than between-species competition, it is easier to coexist with the members of the other species than those of one's own species, which promotes coexistence and hence a stable, forward bifurcation.

In Figures 4.2 and 4.3, we choose parameter values to illustrate a forward bifurcation and backward bifurcation. We show the bifurcation diagrams of $x_2 + x_3$ and of x_1 along with time series to illustrate the asymptotic dynamics at points marked in the bifurcation diagrams. In the case of a backward bifurcation (Figure 4.3), the branch of unstable coexistence equilibria transcritically bifurcates a branch of invader equilibria, creating a multi-attractor scenario for $f_0 \lesssim f_0^0$ with a strong Allee effect where the survival of the invader is initial condition dependent. If the invader enters the system with a low population density, then its survival is only dependent on whether f_0 is above or below f_0^0 and not on the direction of bifurcation. When $f_0 < f_0^0$, the orbit will go to the resident equilibrium which is locally attracting. When $f_0 > f_0^0$, the orbit will go to either a coexistence equilibrium or an invader equilibrium.

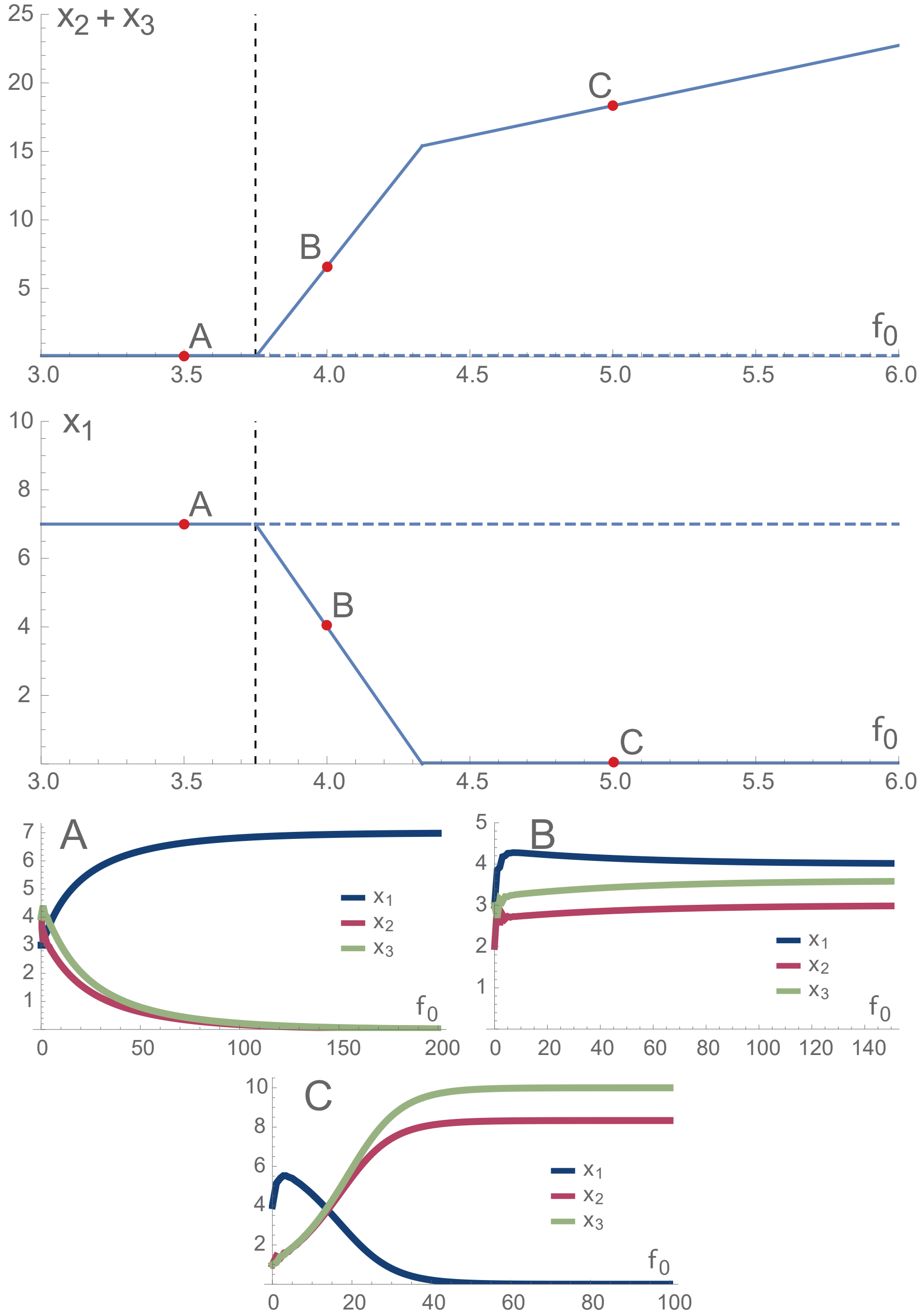


Figure 4.2: An example with $\kappa > 0$ and $\mu_1 < 0$ using parameter values $h_0 = 4.5$, $h_1 = 0.5$, $h_2 = 0.5$, $h_3 = 0$, $f_1 = 0.5$, $f_2 = 0$, $f_3 = 0.5$, $s_1 = .6$, and $s_2 = .5$. These give $\tau_R = 7$, $f_0^0 = 3.75$, $\kappa = 5/72$, and $\mu_1 = -1/162$. The branch of coexistence equilibria bifurcates forward, connecting to the branch of unstable invader equilibria at $f_0 = 13/3$. See plots A, B, and C for example orbits illustrating the asymptotic behavior in the different regions.

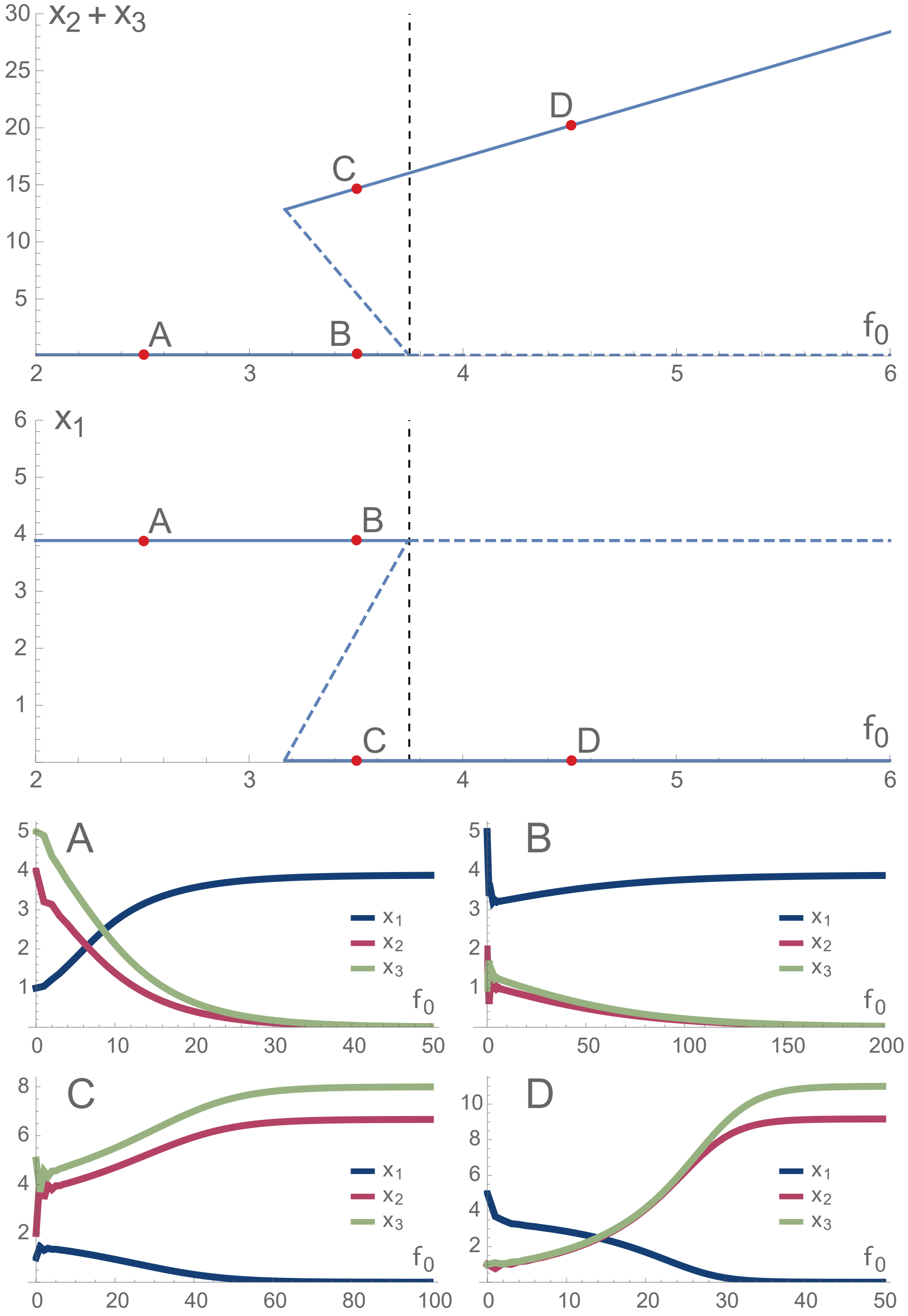


Figure 4.3: An example with $\kappa < 0$ and $\mu_1 > 0$ using parameter values $h_0 = 4.5$, $h_1 = 0.9$, $h_2 = 0.6$, $h_3 = 0$, $f_1 = 0.9$, $f_2 = 0$, $f_3 = 0.4$, $s_1 = .6$, and $s_2 = .5$. These give $\tau_R = 19/6$, $f_0^0 = 3.75$, $\kappa = -1/12$, and $\mu_1 = 1/135$. The branch of coexistence equilibria (dashed) bifurcates backward, connecting to the branch of unstable invader equilibria (solid) at $f_0 = 19/6$. See plots A, B, C, and D for example orbits illustrating the asymptotic behavior in the different regions.

CHAPTER 5

INVADING THE RESIDENT CYCLE: IMPRIMITIVE CASE

In Chapter 4, we assumed that the invader had a primitive composite projection matrix at γ^0, where the resident θ-cycle destabilizes and the dominant eigenvalue of $\mathcal{J}^{(\theta)}(\gamma, \tau)$ leaves the interior of the complex unit circle alone. If, on the other hand, $P_I^{(\theta)}(\gamma^0, x)$ is not primitive, then we are no longer guaranteed a strictly dominant eigenvalue by the Perron-Frobenius Theorem. Instead, multiple eigenvalues (up to n) of $\mathcal{J}^{(\theta)}(\gamma, \tau)$ may leave the unit circle concurrently resulting in more complex bifurcations, such as bifurcations of higher cycle lengths or Neimark-Sacker (discrete-Hopf) bifurcations. In general, $P_I^{(\theta)}(\gamma^0, \tau)$ may not be primitive even if each $P_I(\gamma^0, \tau^{(i)})$ is primitive (see Appendix A for an example of an imprimitive product of primitive matrices).

We consider the simplest invader with an imprimitive projection matrix: a two-stage semelparous species, where each individual only gives birth once during its lifetime. The invader's projection matrix is thus

$$P_I(\gamma, x) = \begin{pmatrix} 0 & \phi(\gamma, x) \\ \sigma(\gamma, x) & 0 \end{pmatrix}. \tag{5.1}$$

We look to find when an invader with this life history can invade the resident θ-cycle.

Assumption A5. *The invader's projection matrix, $P_I(\gamma, x)$, has the form (5.1) where $\phi(\gamma, x)$ and $\sigma(\gamma, x)$ are positive for $\gamma \in \Gamma$ and $x \in \{\tau^{(i)}\}_{i=1}^n$.*

5.1 Destabilization of the resident cycle

Because invasion requires destabilization of the resident θ-cycle, we investigate when an eigenvalue of $\mathcal{J}^{(\theta)}(\gamma, \tau)$ leaves the complex unit circle, how many leave, and in what manner they leave by looking at its eigensystem.

5.1.1 Eigenvectors of the composite Jacobian

Because $\mathcal{J}^{(\theta)}(\gamma,\tau)$ has the form of (4.2) and the eigenvalues of $J_R^{(\theta)}(\gamma,\tau)$ are assumed within the unit circle by Assumption (A2), the stability of the resident θ-cycle can be determined (by linearization) by finding the eigenvalues of $P_I^{(\theta)}(\gamma,\tau)$. We also calculate their corresponding eigenvectors.

First, using $P_I(\gamma,\tau)$ given in (5.1), we determine the form of $P_I^{(\theta)}(\gamma,\tau)$. Define

$$\begin{aligned} a_\theta(\gamma) &= \prod_{\substack{1\le i\le\theta,\\ i \text{ even}}} \phi(\gamma,\tau^{(i)}) \prod_{\substack{1\le i\le\theta,\\ i \text{ odd}}} \sigma(\gamma,\tau^{(i)}),\\ b_\theta(\gamma) &= \prod_{\substack{1\le i\le\theta,\\ i \text{ odd}}} \phi(\gamma,\tau^{(i)}) \prod_{\substack{1\le i\le\theta,\\ i \text{ even}}} \sigma(\gamma,\tau^{(i)}). \end{aligned} \tag{5.2}$$

Note that both quantities, being the product of survival and fecundity terms, are positive. Using (4.3), we prove by induction that

$$P_I^{(\theta)}(\gamma,\tau) = \begin{cases} \begin{pmatrix} 0 & b_\theta(\gamma) \\ a_\theta(\gamma) & 0 \end{pmatrix} & \text{if } \theta \text{ is odd,} \\[2em] \begin{pmatrix} a_\theta(\gamma) & 0 \\ 0 & b_\theta(\gamma) \end{pmatrix} & \text{if } \theta \text{ is even.} \end{cases} \tag{5.3}$$

For the two base cases,

$$\begin{aligned} P_I^{(1)}(\gamma,\tau) &= \begin{pmatrix} 0 & \phi(\gamma,\tau) \\ \sigma(\gamma,\tau) & 0 \end{pmatrix}, \\ P_I^{(2)}(\gamma,\tau) &= \begin{pmatrix} 0 & \phi(\gamma,\tau^{(2)}) \\ \sigma(\gamma,\tau^{(2)}) & 0 \end{pmatrix} \begin{pmatrix} 0 & \phi(\gamma,\tau) \\ \sigma(\gamma,\tau) & 0 \end{pmatrix} \\ &= \begin{pmatrix} \phi(\gamma,\tau^{(2)})\sigma(\gamma,\tau) & 0 \\ 0 & \phi(\gamma,\tau)\sigma(\gamma,\tau^{(2)}) \end{pmatrix}. \end{aligned}$$

We show that if (5.3) holds for $\theta = k$ then it also holds for $\theta = k+1$. If k is odd,

$$\begin{aligned} P_I^{(k+1)}(\gamma, \tau) &= \begin{pmatrix} 0 & \phi(\gamma, \tau^{(k+1)}) \\ \sigma(\gamma, \tau^{(k+1)}) & 0 \end{pmatrix} P_I^{(k)}(\gamma, \tau) \\ &= \begin{pmatrix} \phi(\gamma, \tau^{(k+1)}) a_k(\gamma) & 0 \\ 0 & \sigma(\gamma, \tau^{(k+1)}) b_k(\gamma) \end{pmatrix} \end{aligned}$$

which simplifies to the form given in (5.3). If k is even,

$$\begin{aligned} P_I^{(k+1)}(\gamma, \tau) &= \begin{pmatrix} 0 & \phi(\gamma, \tau^{(k+1)}) \\ \sigma(\gamma, \tau^{(k+1)}) & 0 \end{pmatrix} P_I^{(k)}(\gamma, \tau) \\ &= \begin{pmatrix} 0 & \phi(\gamma, \tau^{(k+1)}) b_k(\gamma) \\ \sigma(\gamma, \tau^{(k+1)}) a_k(\gamma) & 0 \end{pmatrix} \end{aligned}$$

which again simplifies to the form given in (5.3).

If θ is even, the eigenvalues of $P_I^{(\theta)}(\gamma, \tau)$ are the diagonal entries: $a_\theta(\gamma)$ and $b_\theta(\gamma)$. Both are positive, so both may leave the unit circle through 1 and the γ^0 from Assumption A3 is determined by their relative values. Specifically, we require that there exists a γ^0 such that $a_\theta(\gamma^0) = 1$ and $b_\theta(\gamma^0) < 1$ or $b_\theta(\gamma^0) = 1$ and $a_\theta(\gamma^0) < 1$, neglecting the degenerate case[1] where $a_\theta(\gamma^0) = b_\theta(\gamma^0) = 1$ (as formulated in the below assumption). In the former case, where $a_\theta(\gamma^0) = 1$ and $b_\theta(\gamma^0) < 1$, $v_I = (1, 0)^T$ and $w_I = (1, 0)$ are right and left eigenvectors of $P_I^{(\theta)}(\gamma^0, \tau)$ corresponding to eigenvalue 1. In the latter case, where $b_\theta(\gamma^0) = 1$ and $a_\theta(\gamma^0) < 1$, $v_I = (0, 1)^T$ and $w_I = (0, 1)$ are such eigenvectors.

Assumption A6. *If θ is even, the dominant eigenvalue of $P_I^{(\theta)}(\gamma^0, \tau)$ is algebraically simple.*

If θ is odd, the eigenvalues of $P_I^{(\theta)}(\gamma, \tau)$ are $\pm\sqrt{a_\theta(\gamma) b_\theta(\gamma)}$, which leave concurrently through 1 and -1. Eigenvectors corresponding to $\sqrt{a_\theta(\gamma) b_\theta(\gamma)}$ are

$$v_I = \left(\sqrt{b_\theta(\gamma)/a_\theta(\gamma)}, 1\right)^T \quad \text{and} \quad w_I = \left(\sqrt{a_\theta(\gamma)/b_\theta(\gamma)}, 1\right).$$

---

[1] In this case, synchronous θ-cycles will still bifurcate (see Appendix B with $k = 1$) whose analysis would be similar to that presented in Section 5.3.

Eigenvectors corresponding to $-\sqrt{a_\theta(\gamma)b_\theta(\gamma)}$ are

$$\widetilde{v}_I = \left(-\sqrt{b_\theta(\gamma)/a_\theta(\gamma)}, 1\right)^T \quad \text{and} \quad \widetilde{w}_I = \left(-\sqrt{a_\theta(\gamma)/b_\theta(\gamma)}, 1\right).$$

Thus at γ^0, we have $a^0_\theta b^0_\theta = 1$, $v_I = (b^0_\theta, 1)^T$, $w_I = (a^0_\theta, 1)$, $\widetilde{v}_I = (-b^0_\theta, 1)^T$ and $\widetilde{w}_I = (-a^0_\theta, 1)$.

In summary, $P_I^{(\theta)}(\gamma^0\,\tau)$ has eigenvectors

$$v_I = \begin{cases} (1,0)^T & \text{if } \theta \text{ is even and } a^0_\theta = 1 \\ (0,1)^T & \text{if } \theta \text{ is even and } b^0_\theta = 1 \\ (b^0_\theta, 1)^T & \text{if } \theta \text{ is odd} \end{cases}, \quad w_I = \begin{cases} (1,0) & \text{if } \theta \text{ is even and } a^0_\theta = 1 \\ (0,1) & \text{if } \theta \text{ is even and } b^0_\theta = 1 \\ (a^0_\theta, 1) & \text{if } \theta \text{ is odd} \end{cases} \tag{5.4}$$

corresponding to eigenvalue 1, and

$$\widetilde{v}_I = (-b^0_\theta, 1)^T, \quad \widetilde{w}_I = (-a^0_\theta, 1)^T \tag{5.5}$$

corresponding to eigenvalue -1 in the case of odd θ. Based on the block triangular form of the θ-composite Jacobian given in (4.2), we see that eigenvectors of $\mathcal{J}^{(\theta)}(\gamma^0, \tau)$ corresponding to eigenvalue 1 have the forms

$$v = \begin{pmatrix} \star_{m\times 1} \\ \hdashline v_I \end{pmatrix}, \quad w = (0_{1\times m}, w_I), \tag{5.6}$$

and eigenvectors corresponding to eigenvalue -1 have the forms

$$\widetilde{v} = \begin{pmatrix} \star_{m\times 1} \\ \hdashline \widetilde{v}_I \end{pmatrix}, \quad \widetilde{w} = (0_{1\times m}, \widetilde{w}_I). \tag{5.7}$$

2θ-composite Jacobian

Because it will be useful later, we also analyze the eigenvalues and eigenvectors of $\mathcal{J}^{(2\theta)}(\gamma, \tau)$ in the case of odd θ. When θ is odd, the eigenspace of $\mathcal{J}^{(2\theta)}(\gamma^0, \tau)$ corresponding to eigenvalue 1 is two-dimensional. Due to the fact that

$$\mathcal{J}^{(2\theta)}(\gamma, \tau) = \mathcal{J}^{(\theta)}(\gamma, \tau)\mathcal{J}^{(\theta)}(\gamma, \tau),$$

it contains the eigenvectors v and $\widetilde{v}$ of $\mathcal{J}^{(\theta)}(\gamma^0,\tau)$ (corresponding to its eigenvalues of 1 and -1). Any linear combination of these vectors is also contained in the eigenspace of $\mathcal{J}^{(2\theta)}(\gamma^0,\tau)$ corresponding to eigenvalue 1. Two specific linear combinations are

$$v^{(2\theta)} = \frac{v-\widetilde{v}}{2b_\theta^0} = \left(\begin{array}{c} \star_{m\times 1} \\ \hdashline 1 \\ 0 \end{array}\right) \quad \text{and} \quad \widetilde{v}^{(2\theta)} = \frac{v+\widetilde{v}}{2} = \left(\begin{array}{c} \star_{m\times 1} \\ \hdashline 0 \\ 1 \end{array}\right). \tag{5.8}$$

Similarly, w and $\widetilde{w}$ are contained in the left eigenspace of $\mathcal{J}^{(2\theta)}(\gamma^0,\tau)$ corresponding to eigenvalue 1, as well as any linear combination. Two specific linear combinations are

$$w^{(2\theta)} = \frac{w-\widetilde{w}}{2a_\theta^0} = (0_{1\times m},1,0) \quad \text{and} \quad \widetilde{w}^{(2\theta)} = \frac{w+\widetilde{w}}{2} = (0_{1\times m},0,1)\,. \tag{5.9}$$

5.1.2 Existence of bifurcating cycles

Assumption A3 provides the existence of a γ^0 such that the dominant eigenvalue of $P_I^{(\theta)}(\gamma^0,\tau)$ — and hence $\mathcal{J}^{(\theta)}(\gamma^0,\tau)$ — leaves the unit circle. Whether θ is odd or even, the eigenspace corresponding to eigenvalue 1 of $P_I^{(\theta)}(\gamma^0,\tau)$ is one-dimensional (when requiring Assumption A6 to hold). By the structure of w in (5.6), we see that (4.4) holds and we can thus apply Theorem 1 to get the existence of bifurcating fixed points of the map $x' = P^{(\theta)}(\gamma,x)x$, corresponding to the possibility of successful invasion. These fixed points correspond to θ-cycles of the map $x' = P(\gamma,x)x$. Because $v_I \in \overline{\mathbb{R}^n_+}$ with at least one positive entry in both the even and odd cases, the form of $x(\epsilon)$ given in Theorem 1 shows that the fixed points (and hence the θ-cycles) provide coexistence for $\epsilon > 0$. Additionally, if θ is even, the form of (5.3) allows the application of Theorem 12 and Corollary 2 (in Appendix B with $k=1$) which state that the bifurcating θ-cycles are synchronous. These observations lead to the following theorem.

Theorem 6. *Under Assumptions A1, A2, A3, A5, and A6, a branch of coexistence θ-cycles of system (2.1) bifurcates from (γ^0,τ). The corresponding fixed points of system (2.4) have the form*

$$\gamma(\epsilon) = \gamma^0 + \kappa\epsilon + o(\epsilon), \;\; x(\epsilon) = \tau + v\epsilon + u\epsilon^2 + o(\epsilon^2)$$

near $\epsilon = 0$ where v is a right eigenvector of $\mathcal{J}^{(\theta)}(\gamma^0, \tau)$ corresponding to eigenvalue 1 with $v_I \in \overline{\mathbb{R}^n}$ (see (5.4) and (5.6)) and $\epsilon > 0$ corresponds to coexistence. If θ is even, the fixed points are synchronous with $x_{m+2}(\epsilon) = 0$ if $a_\theta^0 = 1$ or $x_{m+1}(\epsilon) = 0$ if $b_\theta^0 = 1$, where $a_\theta(\gamma)$ and $b_\theta(\gamma)$ are given in (5.2).

When θ is odd, an eigenvalue of $P^{(\theta)}(\gamma, \tau)$ — and hence of $\mathcal{J}^{(\theta)}(\gamma, \tau)$ — also leaves through -1 at γ^0. The departure through -1 is suggestive of a branch of 2θ-cycles bifurcating from (γ^0, τ). Indeed, $\mathcal{J}^{(2\theta)}(\gamma, \tau)$ has the form

$$\mathcal{J}^{(2\theta)}(\gamma, \tau) = \left(\begin{array}{c|c} J_R^{(2\theta)}(\tau_R) & \star_{m\times 2} \\ \hline 0_{2\times m} & P_I^{(2\theta)}(\gamma, \tau) \end{array}\right) \tag{5.10}$$

with

$$P_I^{(2\theta)}(\gamma, \tau) = P_I^{(\theta)}(\gamma, \tau) P_I^{(\theta)}(\gamma, \tau) = \begin{pmatrix} a_\theta(\gamma) b_\theta(\gamma) & 0 \\ 0 & a_\theta(\gamma) b_\theta(\gamma) \end{pmatrix}. \tag{5.11}$$

An application of Theorem 12 and Corollary 2 (in Appendix B with $k = 2$) gives the existence of two bifurcating branches of synchronous coexistence 2θ-cycles. The two branches correspond to alternate phases of the same 2θ-cycles and thus bifurcate in the same direction and contain 2θ-cycles of the same stability. We state the expansions of one of the branches in the theorem below.[2]

Theorem 7. *Under Assumptions A1, A2, A3, and A5 with odd θ, a branch of synchronous coexistence 2θ-cycles of system (2.1) bifurcate from (γ^0, τ). The corresponding fixed points of $x' = P^{(2\theta)}(\gamma, x)$ have the form*

$$\gamma(\epsilon) = \gamma^0 + \kappa\epsilon + o(\epsilon), \;\; x(\epsilon) = \tau + v^{(2\theta)}\epsilon + u\epsilon^2 + o(\epsilon^2)$$

near $\epsilon = 0$ where $v^{(2\theta)} = (\star_{1\times m}, 1, 0)^T$ is a right eigenvector of $\mathcal{J}^{(2\theta)}(\gamma^0, \tau)$ corresponding to eigenvalue 1 (see (5.8)) and where $\epsilon > 0$ corresponds to coexistence.

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[2] Note that the other branch will have an expansion of the form $x(\epsilon) = \tau + \widetilde{v}^{(2\theta)}\epsilon + u\epsilon^2 + o(\epsilon^2)$.

We determine the direction of bifurcation and stability of the θ-cycles in Section 5.2 and of the 2θ-cycles in Section 5.3.

5.2 Direction of bifurcation and stability of the coexistence θ-cycles

In this section we find diagnostic quantities which can be used to determine the direction of bifurcation and stability of the bifurcating coexistence θ-cycles established by Theorem 6. We again use (4.5) to parametrize the bifurcating branch of fixed points of the θ-composite system in terms of a parameter $\epsilon > 0$.

5.2.1 Direction of bifurcation

Repeating the steps in Section 4.2.1, we obtain the same expression for κ as in the primitive case:

$$\kappa = -\frac{w_I D_I(v) v_I}{w_I \partial_\gamma^0 P_I^{(\theta)} v_I} \tag{5.12}$$

where v_I and w_I are given by (5.4) and (5.6), and $D_I(v)$ is the bottom-right 2×2 submatrix of $D(v)$ with components $d_{ij}(v) = \nabla_x^0 p_{ij}^{(\theta)} \cdot v$. The sign of κ is again determined by the signs of $w_I \partial_\gamma^0 P_I^{(\theta)} v_I$ (a weighted average of the effect of the bifurcation parameter increasing on the invader) and $w_I D_I(v) v_I$ (a weighted average of the sensitivities of the invader to the changes provided by v).

5.2.2 Stability of the bifurcating cycles

When θ is even, $\mathcal{J}_0^{(\theta)}$ has a simple strictly dominant eigenvalue of 1 under Assumption A6. The result is that the analysis to determine the stability of the bifurcating θ-cycles follows the analysis in Section 4.2.2, where $\mu_1 < 0$ implies stability and $\mu_1 > 0$ implies instability. Here

$$\mu_1 = -\kappa \frac{w_I \partial_\gamma^0 P_I^{(\theta)} v_I}{w_I v_I}. \tag{5.13}$$

Note $w_I v_I > 0$ and so sign of μ_1 is determined by the signs of κ and $w_I \partial_\gamma^0 P_I^{(\theta)} v_I$.

Theorem 8. *Under Assumptions A1, A2, A3, A5, and A6 with even θ, the synchronous coexistence θ-cycles of system (2.1) on the branch established in Theorem 6 bifurcate is forward if $\kappa > 0$ and backward if $\kappa < 0$ (see (5.12)) and, near (γ^0, τ), are asymptotically stable if $\mu_1 < 0$ and unstable if $\mu_1 > 0$ (see (5.13)).*

If increasing the bifurcation parameter benefits the invader ($w_I \partial_\gamma^0 P_I^{(\theta)} v_I > 0$), then a forward bifurcation results in stable coexistence cycles while a backward bifurcation results in unstable coexistence cycles, as in the case where $P_I^{(\theta)}(\gamma^0, \tau)$ is primitive. Similarly, if increasing the bifurcation parameter is detrimental to the invader, then a forward bifurcation results in unstable coexistence cycles while a backward bifurcation results in stable coexistence cycles. Again we expect that a bifurcating branch of unstable cycles may transcritically bifurcate a branch of invader attractors thereby creating a multi-attractor scenario with a strong Allee effect.

When θ is odd, $\mathcal{J}_0^{(\theta)}$ has eigenvalues 1 and -1. In addition to tracking $\mu(\epsilon)$, to determine the stability of the fixed points along the branch we must also track the other relevant eigenvalue of $\mathcal{J}^{(\theta)}(\gamma(\epsilon), x(\epsilon))$, which we parametrize by

$$\eta(\epsilon) = -1 + \eta_1 \epsilon + o(\epsilon).$$

Because $\eta_0 = -1$ is a simple eigenvalue of $\mathcal{J}_0^{(\theta)}$, the expansion is justified by Theorem 2. Note $\eta_0 = -1$, so $\eta(\epsilon)$ is within the unit circle when $\eta_1 > 0$. Thus, for odd θ, stability requires $\mu_1 < 0$ and $\eta_1 > 0$, with instability occurring if either $\mu_1 > 0$, $\eta_1 < 0$, or both. As in the case of even θ, μ_1 is given by (5.13).

To calculate η_1, we follow the same procedure from Section 4.2.2 used to calculate μ_1, except with

$$\xi(\epsilon) = \widetilde{v} + \xi_1 \epsilon + o(\epsilon)$$

denoting the eigenvector corresponding to eigenvalue $\eta(\epsilon)$ (where the expansion is justified by Theorem 2). The right and left eigenvectors of $\mathcal{J}_0^{(\theta)}$ corresponding to eigenvalue -1, $\widetilde{v}$ and $\widetilde{w}$, are given in (5.5) and (5.7). As in Section 4.2.2, we apply the Fredholm Alternative to obtain

$$\eta_1 = \frac{\widetilde{w} \mathcal{J}_1^{(\theta)} \widetilde{v}}{\widetilde{w} \widetilde{v}}. \tag{5.14}$$

As previously, we have

$$\mathcal{J}_1^{(\theta)} = \kappa \partial_\gamma^0 \mathcal{J}^{(\theta)} + D(v) + G(v) + 2H(v),$$

where $d_{ij}(v) = \nabla_x^0 p_{ij}^{(\theta)} \cdot v$, $g_{ij}(v) = \sum_k v_k (p_{ik}^{(\theta)})_{x_j}^0$, and $h_{ij}(v) = \frac{1}{2} \sum_k v_k \left[\sum_r \tau_r (p_{ir}^{(\theta)})_{x_k x_j}^0 \right]$. In this case, however, $G(v)\widetilde{v} \neq D(v)\widetilde{v}$ which prevents the simplification used in Section 4.2.2; nonetheless, we still find $\widetilde{w}H(v)\widetilde{v} = 0$ from the forms of $\widetilde{w}$ (see (5.7)) and $H(v)$ (see (4.6)). Further, given the forms of

$$\partial_\gamma^0 P_I^{(\theta)} = \begin{pmatrix} 0 & \partial_\gamma^0 b_\theta \\ \partial_\gamma^0 a_\theta & 0 \end{pmatrix} \quad \text{and} \quad D_I(v) = \begin{pmatrix} 0 & \nabla_x^0 p_{m+1,m+2}^{(\theta)} \cdot v \\ \nabla_x^0 p_{m+2,m+1}^{(\theta)} \cdot v & 0 \end{pmatrix}$$

with v_I and w_I from (5.4) and $\widetilde{v}_I$ and $\widetilde{w}_I$ from (5.5), we find

$$\widetilde{w}_I \partial_\gamma^0 P_I^{(\theta)} \widetilde{v}_I = -b_\theta^0 \partial_\gamma^0 p_{21}^{(\theta)} - a_\theta^0 \partial_\gamma^0 p_{12}^{(\theta)} = -w_I \partial_\gamma^0 P_I^{(\theta)} v_I$$

and

$$\widetilde{w}_I D_I(v) \widetilde{v}_I = -b_\theta^0 \nabla_x^0 p_{21}^{(\theta)} \cdot v - a_\theta^0 \nabla_x^0 p_{12}^{(\theta)} \cdot v = -w_I D_I(v) v_I.$$

A simplification of (5.14) then gives

$$\begin{aligned} \eta_1 &= \widetilde{w} \left(\kappa \partial_\gamma^0 \mathcal{J}^{(\theta)} + D(v) + G(v) \right) \widetilde{v} / (\widetilde{w}\widetilde{v}) \\ &= \left(-\frac{w_I D_I(v) v_I}{w_I \partial_\gamma^0 P_I^{(\theta)} v_I} \widetilde{w}_I \partial_\gamma^0 P_I^{(\theta)} \widetilde{v}_I + \widetilde{w}_I D(v) \widetilde{v}_I + \widetilde{w} G(v) \widetilde{v} \right) / (\widetilde{w}\widetilde{v}) \\ &= \left(w_I D_I(v) v_I + \widetilde{w}_I D(v) \widetilde{v}_I + \widetilde{w} G(v) \widetilde{v} \right) / (\widetilde{w}\widetilde{v}) \\ &= \widetilde{w} G(v) \widetilde{v} / (\widetilde{w}\widetilde{v}). \end{aligned}$$

Unlike the matrices $D(v)$ and $\partial_\gamma^0 \mathcal{J}^{(\theta)}$, the bottom-left block of $G(v)$ is not zero, so the final expression of η_1 is

$$\eta_1 = \frac{\widetilde{w} G(v) \widetilde{v}}{\widetilde{w}\widetilde{v}}. \tag{5.15}$$

Given our 2 × 2 form of $P_I^{(\theta)}(\gamma, x)$ in (5.3), we can write the following equivalent expression:

$$\eta_1 = \nabla_x^0 \left[-a_\theta^0 p_{m+1,m+2}^{(\theta)} + b_\theta^0 p_{m+2,m+1}^{(\theta)} \right] \cdot \widetilde{v}/2.$$

This could also be rewritten using the fact that $a_\theta^0 b_\theta^0 = 1$. When θ is odd, the coexistence θ-cycles are stable if both $\mu_1 < 0$ and $\eta_1 > 0$.

Theorem 9. *Under Assumptions A1, A2, A3, and A5 with odd θ, the branch of coexistence θ-cycles of system (2.1) established in Theorem 6 bifurcate forward if $\kappa > 0$ and backward if $\kappa < 0$ (see (5.12)) and, near (γ^0, τ), are asymptotically stable if $\mu_1 < 0$ and $\eta_1 > 0$ and unstable if either $\mu_1 > 0$ or $\eta_1 < 0$ (or both) (see (5.13) and (5.15)).*

As in the previous cases, if increasing the bifurcation parameter benefits (is detrimental to) the invader, then a backward (forward) bifurcation results in unstable coexistence cycles. Unlike before, a forward (backward) bifurcation no longer solely determines stability of the coexistence cycles.

5.3 Direction of bifurcation and stability of the coexistence 2θ-cycles

When θ is odd, synchronous coexistence 2θ-cycles also bifurcate from (γ^0, τ) as the resident θ-cycle loses stability, as stated in Theorem 7. In this section we determine their direction of bifurcation and stability. The 2θ-cycles are fixed points of the 2θ-composite system $x' = P^{(2\theta)}(\gamma, x)x$, so we analyze the fixed points of the 2θ-composite map.

We track the branch given by Theorem 7. Along with the state variable $x(\epsilon)$ and bifurcation parameter $\gamma(\epsilon)$ whose expansions are given in Theorem 7, we track both relevant eigenvalues $\mu(\epsilon)$ and $\widetilde{\mu}(\epsilon)$ of $\mathcal{J}^{(2\theta)}(\gamma(\epsilon), x(\epsilon))$ in the ϵ expansions of the 2θ-composite map:

$$\begin{aligned}
\gamma(\epsilon) &= \gamma^0 + \kappa\epsilon + o(\epsilon) \\
x(\epsilon) &= \tau + v^{(2\theta)}\epsilon + u\epsilon^2 + o(\epsilon^2) \\
\mu(\epsilon) &= 1 + \mu_1\epsilon + o(\epsilon) \\
\widetilde{\mu}(\epsilon) &= 1 + \widetilde{\mu}_1\epsilon + o(\epsilon) \\
\mathcal{J}^{(2\theta)}(\gamma(\epsilon), x(\epsilon)) &= \mathcal{J}_0^{(2\theta)} + \mathcal{J}_1^{(2\theta)}\epsilon + o(\epsilon).
\end{aligned} \tag{5.16}$$

Recall from Theorem 7 that $x_{m+2}(\epsilon) = 0$ and $v^{(2\theta)} = (\star_{1\times m}, 1, 0)^T$ is an eigenvector of $\mathcal{J}_0^{(2\theta)}$ corresponding to eigenvalue 1 (see (5.8)). The eigenvalue expansions are justified by Theorem 3 and the Jacobian expansion is justified by the smoothness provided by Assumption A1. Again we consider $\epsilon > 0$. The direction of bifurcation is determined by κ, and the fixed points are stable if both $\mu_1 < 0$ and $\eta_1 < 0$. We follow a similar procedure as that in Section 4.2 with a few added difficulties introduced by the dual eigenvalue multiplicity of $\mathcal{J}_0^{(2\theta)}$.

5.3.1 Direction of bifurcation

To derive a formula for κ, we Taylor expand the 2θ-composite map, substitute the ϵ expansions of $x(\epsilon)$ and $\gamma(\epsilon)$ from (5.16) into the Taylor expansion, and equate orders of ϵ.

Step 1: Taylor expand $P^{(2\theta)}(\gamma, x)x$.

We compute the Taylor expansion of the right-hand side of $x_i = \sum_j x_j p_{ij}^{(2\theta)}(\gamma, x)$ in terms of x and γ near (γ^0, τ).

$$\begin{aligned} x_i = x_i^0 &+ (\gamma - \gamma^0) \sum_j x_j^0 \left(p_{ij}^{(2\theta)}\right)_\gamma^0 + \sum_j (x_j - x_j^0) \left[\left(p_{ij}^{(2\theta)}\right)^0 + \sum_k x_k^0 (p_{ik}^{(2\theta)})_{x_j}^0 \right] \\ &+ \frac{1}{2}(\gamma - \gamma^0)^2 \sum_j x_j^0 \left(p_{ij}^{(2\theta)}\right)_{\gamma\gamma}^0 + (\gamma - \gamma^0) \sum_j (x_j - x_j^0) \left[(p_{ij}^{(2\theta)})_\gamma^0 + \sum_k x_k^0 (p_{ik}^{(2\theta)})_{\gamma x_j}^0 \right] \\ &+ \frac{1}{2} \sum_j (x_j - x_j^0) \sum_k (x_k - x_k^0) \left[2(p_{ik}^{(2\theta)})_{x_j}^0 + \sum_r x_r^0 (p_{ir}^{(2\theta)})_{x_k x_j}^0 \right] \\ &+ o_2 \end{aligned}$$

where o_2 contains all terms of order higher than two in combinations of x and $\gamma - \gamma^0$.

Terms 2 and 4 on the right-hand side evaluate to zero due to the structure of 0's in $\tau = \mathrm{col}(\tau_R, 0, 0)$ and $\partial_\gamma^0 P^{(2\theta)}$ — note $P^{(2\theta)}(\gamma, \tau)$ has the same block structure as $P(\gamma, \tau)$ (see (2.1)) and in its upper-left block γ can only appear in internal arguments attached to x_I terms, making the upper-left block of $\partial_\gamma^0 P^{(\theta)}$ zero.

Step 2: Substitute in ϵ expansions and equate orders of ϵ.

We substitute the expansions of $x(\epsilon)$ and $\gamma(\epsilon)$ from (5.16) into the Taylor expansion and equate orders of ϵ.

At order ϵ^0, we see $\tau_i = \tau_i$.

At order ϵ^1, we see

$$\begin{aligned} v_i^{(2\theta)} &= \sum_j v_j^{(2\theta)} \left[\left(p_{ij}^{(2\theta)} \right)^0 + \sum_k \tau_k (p_{ik}^{(2\theta)})_{x_j}^0 \right] \\ &= (P^{(2\theta)}(\gamma^0, x^0)\tau)_i + \sum_j v_j^{(2\theta)} \sum_k \tau_k (p_{ik}^{(2\theta)})_{x_j}^0, \end{aligned}$$

which is true because $v^{(2\theta)}$ is a right eigenvector of

$$\mathcal{J}_0^{(2\theta)} = P^{(2\theta)}(\gamma^0, \tau) + \left(\sum_k \tau_k (p_{ik}^{(2\theta)})_{x_j}^0 \right)$$

corresponding to eigenvalue 1.

At order ϵ^2, we see

$$\begin{aligned} u_i = &\sum_j u_j \left[\left(p_{ij}^{(2\theta)} \right)^0 + \sum_k \tau_k (p_{ik}^{(2\theta)})_{x_j}^0 \right] + \kappa \sum_j v_j^{(2\theta)} \left[(p_{ij}^{(2\theta)})_\gamma^0 + \sum_k \tau_k (p_{ik}^{(2\theta)})_{\gamma x_j}^0 \right] \\ &+ \frac{1}{2} \sum_j v_j^{(2\theta)} \sum_k v_k^{(2\theta)} \left[2 (p_{ik}^{(2\theta)})_{x_j}^0 + \sum_r \tau_r (p_{ir}^{(2\theta)})_{x_k x_j}^0 \right] \\ = &\left(\mathcal{J}_0^{(2\theta)} u \right)_i + \kappa (\partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)})_i + \sum_j v_j^{(2\theta)} \left(\nabla_x^0 p_{ij}^{(2\theta)} \cdot v^{(2\theta)} \right) \\ &+ \frac{1}{2} \sum_j v_j^{(2\theta)} \sum_k v_k^{(2\theta)} \left[\sum_r \tau_r (p_{ir}^{(2\theta)})_{x_k x_j}^0 \right]. \end{aligned}$$

We denote this as

$$u = \mathcal{J}_0^{(2\theta)} u + \kappa \partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)} + D(v^{(2\theta)}) v^{(2\theta)} + H(v^{(2\theta)}) v^{(2\theta)}$$

where $d_{ij}(v^{(2\theta)}) = \nabla_x^0 p_{ij}^{(2\theta)} \cdot v^{(2\theta)}$ and $h_{ij}(v^{(2\theta)}) = \frac{1}{2} \sum_k v_k^{(2\theta)} \left[\sum_r \tau_r (p_{ir}^{(2\theta)})_{x_k x_j}^0 \right]$.

By the Fredholm Alternative,

$$(I - \mathcal{J}_0^{(2\theta)}) u = \kappa \partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)} + D(v^{(2\theta)}) v^{(2\theta)} + H(v^{(2\theta)}) v^{(2\theta)}$$

is solvable for u if and only if

$$\nu^T \left(\kappa \partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)} + D(v^{(2\theta)}) v^{(2\theta)} + H(v^{(2\theta)}) v^{(2\theta)} \right) = 0 \tag{5.17}$$

for every ν (row vector) such that $\nu(I-\mathcal{J}_0^{(2\theta)})=0$, i.e. for every left eigenvector of $\mathcal{J}_0^{(2\theta)}$ corresponding to eigenvalue 1. This means ν is a linear combination of $w^{(2\theta)}$ and $\widetilde{w}^{(2\theta)}$ (see (5.9)), so we write $\nu=c_1w^{(2\theta)}+c_2\widetilde{w}^{(2\theta)}$. We find $\widetilde{w}^{(2\theta)}\partial_\gamma^0\mathcal{J}^{(2\theta)}v^{(2\theta)}=0$ and $\widetilde{w}^{(2\theta)}D(v^{(2\theta)})v^{(2\theta)}=0$ due to the structure of the zeroes in $\widetilde{w}^{(2\theta)}$ (see (5.9)), $v^{(2\theta)}$ (see (5.8)), $\partial_\gamma^0\mathcal{J}^{(2\theta)}$, and $D(v^{(2\theta)})$, noting that $D(v^{(2\theta)})$ has the same block structure as $\partial_\gamma^0P^{(2\theta)}$ (see (5.11)):

$$\begin{aligned}
\partial_\gamma^0\mathcal{J}^{(2\theta)} &= \left(\begin{array}{c|c} 0_{m\times m} & \star_{m\times 2} \\ \hline 0_{2\times m} & \partial_\gamma^0 P_I^{(2\theta)} \end{array}\right) = \left(\begin{array}{c|cc} 0_{m\times m} & \multicolumn{2}{c}{\star_{m\times 2}} \\ \hline 0_{2\times m} & \begin{array}{cc} \star & 0 \\ 0 & \star \end{array} \end{array}\right), \\
D(v^{(2\theta)}) &= \left(\begin{array}{c|c} \star_{m\times m} & 0_{m\times 2} \\ \hline 0_{2\times m} & \begin{array}{cc} \star & 0 \\ 0 & \star \end{array} \end{array}\right).
\end{aligned} \tag{5.18}$$

The upper-left block of $\partial_\gamma^0\mathcal{J}^{(2\theta)}$ is zero because γ only appears in the upper-left block of $\mathcal{J}^{(2\theta)}$ in internal arguments attached to x_I terms which are zero at τ. See footnote 2 in Section 4.1.2 for reasoning on why the bottom-left block is zero. The structure of

$$H(v^{(2\theta)}) = \left(\begin{array}{c} \star_{m\times(m+2)} \\ \hline 0_{2\times(m+2)} \end{array}\right) \tag{5.19}$$

along with that of $w^{(2\theta)}$ and $\widetilde{w}^{(2\theta)}$ (see (5.9)) results in both $w^{(2\theta)}H(v^{(2\theta)})v^{(2\theta)}=0$ and $\widetilde{w}^{(2\theta)}H(v^{(2\theta)})v^{(2\theta)}=0$.

Solving for κ in (5.17) with $\nu=c_1w^{(2\theta)}+c_2\widetilde{w}^{(2\theta)}$, we find

$$\kappa = -\frac{w^{(2\theta)}D(v^{(2\theta)})v^{(2\theta)}}{w^{(2\theta)}\partial_\gamma^0\mathcal{J}^{(2\theta)}v^{(2\theta)}}, \tag{5.20}$$

which simplifies to

$$\kappa = -\frac{w_I^{(2\theta)}D_I(v^{(2\theta)})v_I^{(2\theta)}}{w_I^{(2\theta)}\partial_\gamma^0P_I^{(2\theta)}v_I^{(2\theta)}} \tag{5.21}$$

where again $D_I(v^{(2\theta)})$ is the bottom-right 2×2 block of $D(v^{(2\theta)})$. Because $v_I^{(2\theta)} = (1,0)^T$ and $w_I^{(2\theta)} = (1,0)$ (see (5.8) and (5.9)), we can further simplify this to

$$\kappa = -\frac{\nabla_x^0 \left(p_{m+1,m+1}^{(2\theta)}\right) \cdot v^{(2\theta)}}{\partial_\gamma^0 (a_\theta b_\theta)} = -\frac{\nabla_x^0 \left(p_{m+1,m+1}^{(2\theta)}\right) \cdot v^{(2\theta)}}{\partial_\gamma^0 (p_{m+1,m+1}^{(2\theta)})}.$$

Thus the direction of bifurcation of the synchronous 2θ-cycles is determined by the sensitivity of $p_{m+1,m+1}^{(2\theta)}$ to the population densities and the bifurcation parameter.

5.3.2 Stability of the bifurcating synchronous cycles

If both $\mu_1 < 0$ and $\widetilde{\mu}_1 < 0$, then the synchronous 2θ-cycles bifurcating from (γ^0, τ) are stable; on the other hand, if either $\mu_1 > 0$ or $\widetilde{\mu}_1 > 0$ (or both) then the bifurcating 2θ-cycles are unstable. In order to apply Theorem 3 to obtain expansions for the eigenvectors — which we will then use to solve for μ_1 and $\widetilde{\mu}_1$ — we must consider the two distinct cases: $\mu_1 \neq \widetilde{\mu}_1$ and $\mu_1 = \widetilde{\mu}_1$. If either term is zero, then the stability remains unknown without analyzing higher order terms.

Case $\mu_1 \neq \widetilde{\mu}_1$

In the case of $\mu_1 \neq \widetilde{\mu}_1$, Theorem 3 provides us with eigenvectors expansions (unique up to scalar multiple) corresponding to each eigenvalue. We write the eigenvectors of $\mathcal{J}^{(2\theta)}(\epsilon)$, corresponding to $\mu(\epsilon)$ and $\widetilde{\mu}(\epsilon)$ respectively, as

$$\xi(\epsilon) = \xi_0 + \xi_1 \epsilon + o(\epsilon)$$
$$\widetilde{\xi}(\epsilon) = \widetilde{\xi}_0 + \widetilde{\xi}_1 \epsilon + o(\epsilon).$$

Let $\eta(\epsilon)$ represent either $\mu(\epsilon)$ or $\widetilde{\mu}(\epsilon)$, and let $\nu(\epsilon)$ represent the corresponding right eigenvector $\xi(\epsilon)$ or $\widetilde{\xi}(\epsilon)$. The eigenvalue equation and its differential with respect to ϵ gives us

$$\mathcal{J}^{(2\theta)}(\epsilon)\nu(\epsilon) = \eta(\epsilon)\nu(\epsilon)$$
$$\mathcal{J}^{(2\theta)'}(\epsilon)\nu(\epsilon) + \mathcal{J}^{(2\theta)}(\epsilon)\nu'(\epsilon) = \eta'(\epsilon)\nu(\epsilon) + \eta(\epsilon)\nu'(\epsilon).$$

At $\epsilon = 0$, these equations reduce to

$$\mathcal{J}_0^{(2\theta)}\nu_0 = \eta_0\nu_0 \tag{5.22}$$

$$\mathcal{J}_1^{(2\theta)}\nu_0 + \mathcal{J}_0^{(2\theta)}\nu_1 = \eta_1\nu_0 + \eta_0\nu_1 \tag{5.23}$$

where $\eta_0 = 1$. Because $v^{(2\theta)}$ and $\widetilde{v}^{(2\theta)}$ (see (5.8)) are a basis for the eigenspace of $\mathcal{J}_0^{(2\theta)}$ corresponding to eigenvalue $\eta_0 = 1$, and because (5.22) implies that ν_0 is in that eigenspace, we write

$$\nu_0 = \alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}.$$

Because ξ_0 and $\widetilde{\xi}_0$ are linearly independent by Theorem 3, we look for two unique values of α. We see (5.23) is equivalent to

$$(\mathcal{J}_0^{(2\theta)} - I)\nu_1 = \eta_1\nu_0 - \mathcal{J}_1^{(2\theta)}\nu_0$$

which is solvable by the Fredholm Alternative if and only if

$$w^{(2\theta)}(\eta_1\nu_0 - \mathcal{J}_1^{(2\theta)}\nu_0) = 0 \quad \text{and} \quad \widetilde{w}^{(2\theta)}(\eta_1\nu_0 - \mathcal{J}_1^{(2\theta)}\nu_0) = 0. \tag{5.24}$$

Before continuing, we compute $\mathcal{J}_1^{(2\theta)}$ using the ϵ expansions in (5.16):

$$\begin{aligned}\left(\mathcal{J}_1^{(2\theta)}\right)_{ij} &= \frac{d}{d\epsilon}\left(p_{ij}^{(2\theta)} + \sum_k x_k \partial_{x_j} p_{ik}^{(2\theta)}\right)\Bigg|_{\epsilon=0} \\ &= \left(\sum_k v_k^{(2\theta)} (p_{ij}^{(2\theta)})^0_{x_k}\right) + \kappa\left[(p_{ij}^{(2\theta)})^0_{\gamma} + \sum_k \tau_k (p_{ik}^{(2\theta)})^0_{\gamma x_j}\right] \\ &\qquad + \left(\sum_k v_k^{(2\theta)} (p_{ik}^{(2\theta)})^0_{x_j}\right) + \left(\sum_r v_r^{(2\theta)} \sum_k \tau_k (p_{ik}^{(2\theta)})^0_{x_j x_r}\right).\end{aligned}$$

With $g_{ij}(v^{(2\theta)}) = \sum_k v_k^{(2\theta)} (p_{ik}^{(2\theta)})^0_{x_j}$, this can be written as

$$\mathcal{J}_1^{(2\theta)} = D(v^{(2\theta)}) + \kappa\partial^0_{\gamma}\mathcal{J}^{(2\theta)} + G(v^{(2\theta)}) + 2H(v^{(2\theta)}). \tag{5.25}$$

Solving for $\eta_1 = \mu_1$.

For $\alpha = 1$, note $\widetilde{w}^{(2\theta)}\nu_0 = 0$ (see Table 5.1). Then the second equation of (5.24) holds

	I	$D(v)$	$\partial_\gamma^0 \mathcal{J}^{(2\theta)}$	$G(v)$	$H(v)$
$w \star v$	$1\ ^{(\mathrm{a})}$	$-\kappa w \partial_\gamma^0 \mathcal{J}^{(2\theta)} v\ ^{(\mathrm{b})}$	$w_I \partial_\gamma^0 P_I^{(2\theta)} v_I\ ^{(\mathrm{d})}$	$wD(v)v\ ^{(\mathrm{e})}$	$0\ ^{(\mathrm{g})}$
$\widetilde{w} \star v$	$0\ ^{(\mathrm{a})}$	$0\ ^{(\mathrm{c})}$	$0\ ^{(\mathrm{c})}$	$\widetilde{w}D(v)v\ ^{(\mathrm{e})}$	$0\ ^{(\mathrm{g})}$
$w \star \widetilde{v}$	$0\ ^{(\mathrm{a})}$	$0\ ^{(\mathrm{c})}$	$0\ ^{(\mathrm{c})}$	–	$0\ ^{(\mathrm{g})}$
$\widetilde{w} \star \widetilde{v}$	$1\ ^{(\mathrm{a})}$	–	$w \partial_\gamma^0 \mathcal{J}^{(2\theta)} v\ ^{(\mathrm{d})}$	$0\ ^{(\mathrm{f})}$	$0\ ^{(\mathrm{g})}$

Table 5.1: A list of equalities for the component matrices of $\mathcal{J}_1^{(2\theta)}$ when multiplied by the eigenvectors of $\mathcal{J}_0^{(2\theta)}$. **For space purposes, we refer to $v^{(2\theta)}$ as v, $\widetilde{v}^{(2\theta)}$ as $\widetilde{v}$, $w^{(2\theta)}$ as w, and $\widetilde{w}^{(2\theta)}$ as $\widetilde{w}$.** See parenthetical letter for reference or explanation. In the leftmost column, a $\star$ indicates a placeholder for the component matrix listed in the top row. Many of the resulting terms are zero. Circular references are not listed; note, for example, that $w^{(2\theta)} G(v^{(2\theta)}) v^{(2\theta)} = -\kappa w^{(2\theta)} \partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)}$ and $\widetilde{w}^{(2\theta)} G(v^{(2\theta)}) v^{(2\theta)} = 0$.

(a) See (5.8) and (5.9).

(b) See (5.20).

(c) Follows from the zero structure in the eigenvectors and block diagonal or block triangular component matrices (see (5.18)).

(d) From (5.10) and (5.11), we see these entries equal $\partial_\gamma^0(a_\theta b_\theta)$ where $a_\theta(\gamma)$ and $b_\theta(\gamma)$ are given by (5.2).

(e) See (4.9).

(f) Note $\widetilde{w}^{(2\theta)} = (0_{1\times m}, 0, 1)$ so that $\widetilde{w}^{(2\theta)} G(v^{(2\theta)}) v^{(2\theta)} = \sum_j g_{m+2,j}(v^{(2\theta)}) v_j^{(2\theta)}$, and $v_{m+2}^{(2\theta)} = 0$ so that

$$g_{m+2,j}(v^{(2\theta)}) = \sum_k v_k^{(2\theta)} (p_{m+2,k}^{(2\theta)})_{x_j}^0 = v_{m+2}^{(2\theta)} (p_{m+2,m+2}^{(2\theta)})_{x_j}^0 = 0.$$

(g) Follows from the zero structure of $H(v^{(2\theta)})$ given in (5.19) and the zeros in the eigenvectors.

for any value of η_1 if $\widetilde{w}^{(2\theta)}\mathcal{J}_1^{(2\theta)}\nu_0 = 0$, which can be seen as true using (5.25) and Table 5.1.

We then solve for η_1 using the first equation of (5.24), labeling the resulting η_1 as μ_1 and the corresponding ν_0 as ξ_0, so that

$$\mu_1 = \frac{w^{(2\theta)}\left(D(v^{(2\theta)}) + \kappa\partial_\gamma^0\mathcal{J}^{(2\theta)} + G(v^{(2\theta)}) + 2H(v^{(2\theta)})\right)v^{(2\theta)}}{w^{(2\theta)}v^{(2\theta)}}.$$

Using Table (5.1) $w^{(2\theta)}v^{(2\theta)} = 1$, we simplify this to

$$\begin{aligned}\mu_1 &= -\kappa w_I^{(2\theta)}\partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)} \\ &= -\kappa\partial_\gamma^0(a_\theta b_\theta) \\ &= \nabla_x^0 p_{m+1,m+1}^{(2\theta)}\cdot v^{(2\theta)}\end{aligned} \tag{5.26}$$

where $a_\theta(\gamma)$ and $b_\theta(\gamma)$ are given by (5.2). Recall that the signs of μ_1 and $\widetilde{\mu}_1$ are both needed to determine the stability of the bifurcating 2θ-cycles; we next derive an expression for $\widetilde{\mu}_1$.

Solving for $\eta_1 = \widetilde{\mu}_1$.

We now solve for the remaining value of $\alpha \neq 1$ to find $\eta_1 = \widetilde{\mu}_1$ and $\nu_0 = \widetilde{\xi}_0$.

The second equation of (5.24) yields an expression for η_1 independent of α:

$$\begin{aligned}\widetilde{\mu}_1 &= \frac{1}{\widetilde{w}^{(2\theta)}\nu_0}\widetilde{w}^{(2\theta)}\mathcal{J}_1^{(2\theta)}\nu_0 \\ &= \frac{1}{1-\alpha}\widetilde{w}^{(2\theta)}\left(D(v^{(2\theta)}) + \kappa\partial_\gamma^0\mathcal{J}^{(2\theta)} + G(v^{(2\theta)})\right)(\alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}) \\ &= \widetilde{w}^{(2\theta)}\left(\kappa\partial_\gamma^0\mathcal{J}^{(2\theta)} + D(v^{(2\theta)})\right)\widetilde{v}^{(2\theta)},\end{aligned}$$

where all simplifications are done using Table 5.1. If $w^{(2\theta)}G(v^{(2\theta)})\widetilde{v}^{(2\theta)} = 0$ and $\alpha = 0$, then the first equation of (5.24) holds for any value of η_1 if $w^{(2\theta)}\mathcal{J}_1^{(2\theta)}\nu_0 = 0$, which can be seen as true using (5.25) and Table 5.1. On the other hand, if $w^{(2\theta)}G(v^{(2\theta)})\widetilde{v}^{(2\theta)} \neq 0$, the first equation of (5.24) is not satisfied by $\alpha = 0$ and yields an expression for η_1

that is dependent on α:

$$\begin{aligned}\widetilde{\mu}_1 &= \frac{1}{w^{(2\theta)}\nu_0} w^{(2\theta)} \mathcal{J}_1^{(2\theta)} \nu_0 \\ &= \frac{1}{\alpha} w^{(2\theta)} \left(D(v^{(2\theta)}) + \kappa \partial_\gamma^0 \mathcal{J}^{(2\theta)} + G(v^{(2\theta)}) \right) (\alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}) \\ &= -\kappa w^{(2\theta)} \partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)} + \left(\frac{1}{\alpha} - 1 \right) w^{(2\theta)} G(v^{(2\theta)}) \widetilde{v}^{(2\theta)}.\end{aligned}$$

Therefore, for $\alpha \neq 0$, α must be chosen so that the two expressions for η_1 are equal. Setting

$$\widetilde{w}^{(2\theta)} \left(\kappa \partial_\gamma^0 \mathcal{J}^{(2\theta)} + D(v^{(2\theta)}) \right) \widetilde{v}^{(2\theta)} = -\kappa w^{(2\theta)} \partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)} + \left(\frac{1}{\alpha} - 1 \right) w^{(2\theta)} G(v^{(2\theta)}) \widetilde{v}^{(2\theta)}$$

and solving for α, we find

$$\alpha = \frac{w^{(2\theta)} G(v^{(2\theta)}) \widetilde{v}^{(2\theta)}}{\kappa w^{(2\theta)} \partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)} + w^{(2\theta)} G(v^{(2\theta)}) \widetilde{v}^{(2\theta)} + \widetilde{w}^{(2\theta)} \left(\kappa \partial_\gamma^0 \mathcal{J}^{(2\theta)} + D(v^{(2\theta)}) \right) \widetilde{v}^{(2\theta)}}.$$

One can check that this does, in fact, satisfy the first equation of (5.24).

We can further simplify the expression for $\widetilde{\mu}_1$ to

$$\begin{aligned}\widetilde{\mu}_1 &= \widetilde{w}_I^{(2\theta)} \left(\kappa \partial_\gamma^0 P_I^{(2\theta)} + D_I(v^{(2\theta)}) \right) \widetilde{v}_I^{(2\theta)} \\ &= \kappa \partial_\gamma^0 (a_\theta b_\theta) + \nabla_x^0 p_{m+2,m+2}^{(2\theta)} \cdot v^{(2\theta)} \\ &= -\nabla_x^0 p_{m+1,m+1}^{(2\theta)} \cdot v^{(2\theta)} + \nabla_x^0 p_{m+2,m+2}^{(2\theta)} \cdot v^{(2\theta)}\end{aligned} \tag{5.27}$$

with $a_\theta(\gamma)$ and $b_\theta(\gamma)$ given by (5.2). Because we are looking for a value of $\alpha \neq 1$ to get two unique values for μ_1 and $\widetilde{\mu}_1$, we require

$$-\kappa w^{(2\theta)} \partial_\gamma^0 \mathcal{J}^{(2\theta)} v^{(2\theta)} \neq \widetilde{w}^{(2\theta)} \left(\kappa \partial_\gamma^0 \mathcal{J}^{(2\theta)} + D(v^{(2\theta)}) \right) \widetilde{v}^{(2\theta)},$$

i.e.

$$2\nabla_x^0 p_{m+1,m+1}^{(2\theta)} \cdot v^{(2\theta)} \neq \nabla_x^0 p_{m+2,m+2}^{(2\theta)} \cdot v^{(2\theta)}. \tag{5.28}$$

In summary, when (5.28) is satisfied, it is true that $\mu_1 \neq \widetilde{\mu}_1$ and we have found expressions for both μ_1 and $\widetilde{\mu}_1$. When both $\mu_1 < 0$ and $\eta_1 < 0$, the bifurcating synchronous coexistence 2θ-cycles are locally stable.

Case $\mu_1 = \widetilde{\mu}_1$

In the case of $\mu_1 = \widetilde{\mu}_1$, Theorem 3 provides us with a two-dimensional eigenprojection of $\mathcal{J}^{(2\theta)}(\epsilon)$ with the expansion

$$S(\epsilon) = S_0 + S_1\epsilon + o(\epsilon)$$

corresponding (up to $o(\epsilon)$) to the eigenprojections of eigenvalues $\mu(\epsilon)$ and $\widetilde{\mu}(\epsilon)$. As noted in Section 3.2, any vector u not orthogonal to the eigenspace projected onto by $S(\epsilon)$ gives a differentiable eigenvector $S(\epsilon)u = S_0u + S_1u\epsilon + o(\epsilon)$. In particular, because $\alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}$ is an eigenvector of $\mathcal{J}_0^{(2\theta)}$ corresponding to eigenvalue 1 for any $\alpha \in \mathbb{R}$, and because S_0 is the eigenprojection of $\mathcal{J}_0^{(2\theta)}$ corresponding to eigenvalue 1, it follows that

$$S(\epsilon)\left[\alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}\right] = \alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)} + S_1\left[\alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}\right]\epsilon + o(\epsilon).$$

Let $\xi(\epsilon,\alpha) = S(\epsilon)\left[\alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}\right]$. Then the eigenvalue equation

$$\mathcal{J}^{(2\theta)}(\epsilon)\xi(\epsilon,\alpha) = \mu(\epsilon)\xi(\epsilon,\alpha) \tag{5.29}$$

holds up to order ϵ for every choice of $\alpha \in \mathbb{R}$. For convenience, we write $\xi(\epsilon,\alpha) = \xi_0(\alpha) + \xi_1(\alpha)\epsilon + o(\epsilon)$.

A calculation of the derivative of (5.29) with respect to ϵ at $\epsilon = 0$ gives

$$\mathcal{J}_1^{(2\theta)}\xi_0(\alpha) + \mathcal{J}_0^{(2\theta)}\xi_1(\alpha) = \mu_1\xi_0(\alpha) + \xi_1(\alpha).$$

Rearranging terms, we have

$$\left(\mathcal{J}_0^{(2\theta)} - I\right)\xi_1(\alpha) = \mu_1\xi_0(\alpha) - \mathcal{J}_1^{(2\theta)}\xi_0(\alpha)$$

which is solvable for $\xi_1(\alpha)$ by the Fredholm Alternative if and only if

$$w^{(2\theta)}\left(\mu_1\xi_0(\alpha) - \mathcal{J}_1^{(2\theta)}\xi_0(\alpha)\right) = 0 \quad \text{and} \quad \widetilde{w}^{(2\theta)}\left(\mu_1\xi_0(\alpha) - \mathcal{J}_1^{(2\theta)}\xi_0(\alpha)\right) = 0. \tag{5.30}$$

Note $\xi_0(\alpha) = \alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}$ so that $w^{(2\theta)}\xi_0(\alpha) = \alpha$ and $\widetilde{w}^{(2\theta)}\xi_0(\alpha) = 1-\alpha$.

Using (5.25) with Table 5.1, we find from the first equation of (5.30) that

$$\begin{aligned}\mu_1 &= \frac{1}{\alpha} w^{(2\theta)} \mathcal{J}_1^{(2\theta)} \left(\alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}\right) \\ &= w^{(2\theta)} \mathcal{J}_1^{(2\theta)} v^{(2\theta)} + \frac{1-\alpha}{a} w^{(2\theta)} \mathcal{J}_1^{(2\theta)} \widetilde{v}^{(2\theta)} \\ &= -\kappa w_I^{(2\theta)} \partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)} + \frac{1-\alpha}{\alpha} w^{(2\theta)} G(v^{(2\theta)}) \widetilde{v}^{(2\theta)}.\end{aligned}$$

Because this equation must hold for every $\alpha \in \mathbb{R}$ and μ_1 is a number independent of α, it must be true that $w^{(2\theta)} G(v^{(2\theta)}) \widetilde{v}^{(2\theta)} = 0$, or equivalently

$$\nabla_x^0 p_{m+1,m+1}^{(2\theta)} \cdot \widetilde{v}^{(2\theta)} = 0. \tag{5.31}$$

Then

$$\mu_1 = -\kappa w_I^{(2\theta)} \partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)}. \tag{5.32}$$

The second equation of (5.30) simplifies, using Table 5.1, to

$$\begin{aligned}\mu_1 &= \frac{1}{1-\alpha} \widetilde{w}^{(2\theta)} \mathcal{J}_1^{(2\theta)} \left(\alpha v^{(2\theta)} + (1-\alpha)\widetilde{v}^{(2\theta)}\right) \\ &= w^{(2\theta)} \mathcal{J}_1^{(2\theta)} \widetilde{v}^{(2\theta)} \\ &= \widetilde{w}^{(2\theta)} \left(D(v^{(2\theta)}) + \kappa \partial_\gamma^0 \mathcal{J}^{(2\theta)}\right) \widetilde{v}^{(2\theta)} \\ &= \widetilde{w}_I^{(2\theta)} \left(D_I(v^{(2\theta)}) + \kappa \partial_\gamma^0 P_I^{(2\theta)}\right) \widetilde{v}_I^{(2\theta)}.\end{aligned} \tag{5.33}$$

Because both (5.32) and (5.33) give expressions for μ_1, it must be true that they are equal, so that[3]

$$-\kappa w_I^{(2\theta)} \partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)} = \widetilde{w}_I^{(2\theta)} \left(D_I(v^{(2\theta)}) + \kappa \partial_\gamma^0 P_I^{(2\theta)}\right) \widetilde{v}_I^{(2\theta)}.$$

Using Table 5.1, this reduces to

$$\widetilde{w}_I^{(2\theta)} \left(D_I(v^{(2\theta)}) + 2\kappa \partial_\gamma^0 P_I^{(2\theta)}\right) \widetilde{v}_I^{(2\theta)} = 0,$$

or

$$\nabla_x^0 \left(p_{m+2,m+2}^{(2\theta)} - 2p_{m+1,m+1}^{(2\theta)}\right) \cdot v^{(2\theta)} = 0.$$

---

[3] Note that the two expressions are those derived for μ_1 and $\widetilde{\mu}_1$ in the case of $\mu_1 \neq \widetilde{\mu}_1$.

Thus, if $\widetilde{w}_I^{(2\theta)}\left(D_I(v^{(2\theta)}) + 2\kappa\partial_\gamma^0 P_I^{(2\theta)}\right)\widetilde{v}_I^{(2\theta)} = 0$ and $w^{(2\theta)}G(v^{(2\theta)})\widetilde{v}^{(2\theta)} = 0$, then $\mu_1 = \widetilde{\mu}_1$ and

$$\mu_1 = -\kappa w_I^{(2\theta)}\partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)}. \tag{5.34}$$

This single quantity then determines the stability of the bifurcating 2θ-cycles.

Theorem 10. *Under Assumptions A1, A2, A3, and A5 with odd θ, the synchronous coexistence 2θ-cycles on the branch established in Theorem 7 bifurcate forward if $\kappa > 0$ and backward if $\kappa < 0$ (see (5.21)).*

Assume (5.28) holds. Then the coexistence 2θ-cycles near (γ^0, τ) are asymptotically stable if $\mu_1 < 0$ and $\widetilde{\mu}_1 < 0$ and unstable if either $\mu_1 > 0$ or $\widetilde{\mu}_1 > 0$ (or both) (see (5.26) and (5.27)).

Assume (5.28) does not hold but (5.31) does hold. Then $\mu_1 = \widetilde{\mu}_1$ in (5.16) and the coexistence 2θ-cycles near (γ^0, τ) are asymptotically stable if $\mu_1 < 0$ and unstable if $\mu_1 > 0$ (see (5.34)).

Theorem 10 together with Theorem 9 give the diagnostic quantities when θ is odd, where both θ-cycles and 2θ-cycles bifurcate from (γ^0, τ). The second alternative in Theorem 10 is non-generic and unlikely to occur in most scenarios. The one case not covered by the above analysis is when (5.28) holds but (5.31) does not; although it may only occur in contrived models, it is unclear how to derive μ_1 or $\widetilde{\mu}_1$ in this context. It may be that (5.28) implies (5.31) or vice versa so that such a scenario is impossible. The sign of μ_1 is determined by the signs of κ and $w_I^{(2\theta)}\partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)}$ (a weighted average of the effect of the bifurcation parameter increasing on the invader). In the case of $\mu_1 \neq \widetilde{\mu}_1$, $\widetilde{\mu}_1$ provides yet another weighted average of the sensitivities of the invader to the changes provided by $v^{(2\theta)}$. If increasing the bifurcation parameter benefits (is detrimental to) the invader, then a backward (forward) bifurcation results in unstable coexistence cycles. If $\mu_1 = \widetilde{\mu}_1$, then a foward (backward) bifurcation results in stable coexistence cycles; otherwise, if $\mu_1 \neq \widetilde{\mu}_1$, a forward (backward) bifurcation does not solely determine stability.

5.4 Dynamic dichotomy

In the case where θ is odd, as proven in Sections 3.2 and 3.3, coexistence θ-cycles and synchronous coexistence 2θ-cycles both bifurcate out of the resident θ-cycle.

When increasing the bifurcation parameter has a positive effect on the invader (i.e. $w_I \partial_\gamma^0 P_I^{(\theta)} v_I > 0$ and $w_I^{(2\theta)} \partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)} > 0$) and both branches bifurcate forward, we expect one of the branches to be stable and the other unstable. If both were stable, we would expect an unstable manifold separating the two basins of attraction to exist; if both were unstable, we would expect some other attractor to exist in that area. Because our analysis does not reveal the bifurcation of any other unstable manifolds or stable attractors, we conjecture that exactly one of the bifurcating branches is stable. Similarly, when increasing the bifurcation parameter has a detrimental effect on the invader (i.e. $w_I \partial_\gamma^0 P_I^{(\theta)} v_I < 0$ and $w_I^{(2\theta)} \partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)} < 0$) and both branches bifurcate backward, we expect exactly one of the branches to be stable. These conjectures, which we refer to as the *dynamic dichotomy*, are motivated by the dynamic dichotomy of the juvenile-adult model presented in Section 1.2.1.

Conjecture. *Under Assumptions A1, A2, A3, and A5 when θ is odd, suppose that $w_I \partial_\gamma^0 P_I^{(\theta)} v_I$, $w_I^{(2\theta)} \partial_\gamma^0 P_I^{(2\theta)} v_I^{(2\theta)}$, κ, and $\kappa^{(2\theta)}$ are all the same sign. Then exactly one of the bifurcating branches established in Theorems 6 and 7 contains stable cycles.*

Specifically, we conjecture that

$$b_\theta^0 \widetilde{\mu}_1^{(2\theta)} = 2\eta_1^{(\theta)}$$

and thus that $\eta_1^{(\theta)}$ and $\widetilde{\mu}_1^{(2\theta)}$ share the same sign, where superscripts ${}^{(\theta)}$ and ${}^{(2\theta)}$ have been added to terms for clarity regarding their branch correspondence. We prove this equality for the case $m = 1$ in Appendix C. The difficulty in proving this conjecture in general arises from the lack of closed-form expressions for the eigenvectors of $\mathcal{J}_0^{(\theta)}$. We do, however, relate the terms used to calculate the diagnostic quantities in the general case in Appendix D, leaving the final step of plugging in the forms of the eigenvectors and proving the equality unfinished. If $\eta_1^{(\theta)}$ and $\widetilde{\mu}_1^{(2\theta)}$ can be proven to share the same sign, then they can be interpreted as the propensity of the invader to exist in a θ-cycle (when positive) versus a 2θ-cycle (when negative).

5.5 Example: single-stage resident

To illustrate Theorems 6, 7, 9, 10, and the dynamic dichotomy proven for $m = 1$ in Appendix C, we start with an example paralleling that in Section 4.3, again using

$m = 1$, $\theta = 1$, $n = 2$. We add the superscript $^{(2)}$ to terms of the branch of bifurcating two-cycles for clarity. This time we consider a semelparous invader with no adult survival, which gives the projection matrix

$$P(\gamma, x) = \begin{pmatrix} \pi(x) & 0 & 0 \\ 0 & 0 & \phi(\gamma, x) \\ 0 & s_1 & 0 \end{pmatrix}.$$

Note that $\pi(\tau) = 1$ because $\pi(\tau)\tau_1 = \tau_1$, and that $a^0_\theta = s_1$, $b^0_\theta = \phi^0$, and $s_1\phi^0 = 1$. The Jacobian

$$\mathcal{J}(\gamma, \tau) = \begin{pmatrix} \pi(\tau) + \pi_{x_1}(\tau)\tau_1 & \pi_{x_2}(\tau)\tau_1 & \pi_{x_3}(\tau)\tau_1 \\ 0 & 0 & \phi(\gamma, \tau) \\ 0 & s_1 & 0 \end{pmatrix}$$

at $\gamma = \gamma^0$ has right and left eigenvectors

$$v = \left(\frac{\tau_1\pi^0_{x_2} + s_1\tau_1\pi^0_{x_3}}{-s_1\tau_1\pi^0_{x_1}}, \frac{1}{s_1}, 1 \right), \quad w = (0, s_1, 1)$$

corresponding to eigenvalue 1, and right and left eigenvectors

$$\widetilde{v} = \left(\frac{\tau_1\pi^0_{x_2} - s_1\tau_1\pi^0_{x_3}}{s_1(2 + \tau_1\pi^0_{x_1})}, -\frac{1}{s_1}, 1 \right), \quad \widetilde{w} = (0, -s_1, 1)$$

corresponding to eigenvalue -1. The remaining quantities used to calculate the direction of bifurcation and stability of the bifurcating equilibria are

$$D_I(v) = \begin{pmatrix} 0 & \nabla^0_x\phi(\gamma, x) \cdot v \\ 0 & 0 \end{pmatrix} \quad \text{and} \quad \partial^0_\gamma P_I = \begin{pmatrix} 0 & \phi^0_\gamma \\ 0 & 0 \end{pmatrix}.$$

These give the diagnostic quantities

$$\kappa = -\nabla^0_x\phi(\gamma, x) \cdot v/\phi^0_\gamma, \quad \mu_1 = \frac{s_1}{2}\nabla^0_x\phi(\gamma, x) \cdot v, \quad \eta_1 = -\frac{s_1}{2}\nabla^0_x\phi(\gamma, x) \cdot \widetilde{v}.$$

The composite Jacobian $\mathcal{J}^{(2)}(\gamma, \tau) = \mathcal{J}(\gamma, \tau)\mathcal{J}(\gamma, \tau)$ at $\gamma = \gamma^0$ has right eigenvectors

$$
\begin{aligned}
v^{(2)} &= \left(-\frac{\tau_1\pi^0_{x_2}(1+\tau_1\pi^0_{x_1})+s_1\tau_1\pi^0_{x_3}}{2\tau_1\pi^0_{x_1}+(\tau_1\pi^0_{x_1})^2},1,0\right),\\
\widetilde{v}^{(2)} &= \left(-\frac{\tau_1\pi^0_{x_3}(1+\tau_1\pi^0_{x_1})+\tau_1\pi^0_{x_2}/s_1}{2\tau_1\pi^0_{x_1}+(\tau_1\pi^0_{x_1})^2},0,1\right)
\end{aligned}
$$

corresponding to eigenvalue 1. From

$$
P_I^{(2)} = \begin{pmatrix} s_1\phi\left(\gamma;\pi(x)x_1,\phi(\gamma,x)x_3,s_1x_2\right) & 0 \\ 0 & s_1\phi(\gamma,x) \end{pmatrix},
$$

we find

$$
\begin{aligned}
D_I^{(2)}(v^{(2)}) &= \begin{pmatrix} s_1\left(\tau_1\phi^0_{x_1}\pi^0_{x_1}+\phi^0_{x_1}\right)v_1^{(2)}+\tau_1\phi^0_{x_1}\pi^0_{x_2}+s_1^2\phi^0_{x_3} & 0 \\ 0 & s_1\left(\phi^0_{x_1}v_1^{(2)}+\phi^0_{x_2}\right) \end{pmatrix},\\
\partial^0_\gamma P_I^{(2)} &= \begin{pmatrix} s_1\phi^0_\gamma & 0 \\ 0 & s_1\phi^0_\gamma \end{pmatrix}.
\end{aligned}
$$

Then the diagnostic quantities for the bifurcating two-cycles are

$$
\begin{aligned}
k^{(2)} &= -\frac{1}{\phi^0_\gamma}\left[\left(\tau_1\phi^0_{x_1}\pi^0_{x_1}+\phi^0_{x_1}\right)v_1^{(2)}+\tau_1\phi^0_{x_1}\pi^0_{x_2}+s_1\phi^0_{x_3}\right],\\
\mu_1^{(2)} &= s_1\left(\tau_1\phi^0_{x_1}\pi^0_{x_1}+\phi^0_{x_1}\right)v_1^{(2)}+\tau_1\phi^0_{x_1}\pi^0_{x_2}+s_1^2\phi^0_{x_3},
\end{aligned}
$$

and from Appendix C we have $\widetilde{\mu}_1^{(2)} = 2s_1\eta_1$.

As before, we use Leslie-Gower nonlinearities with nonnegative coefficients for the fecundity functions:

$$
\begin{aligned}
\pi(x) &= \frac{h_0}{1+h_1x_1+h_2x_2+h_3x_3},\\
\phi(f_0,x) &= \frac{f_0}{1+f_1x_1+f_2x_2+f_3x_3},
\end{aligned}
$$

with f_0, the invader's inherent birth rate, as the bifurcation parameter. With these, the resident equilibrium is located at $\tau_R = (h_0-1)/h_1$ (which requires $h_0 > 1$) and the critical value of the bifurcation parameter is

$$f_0^0 = (1 + f_1\tau_1)/s_1. \tag{5.35}$$

The eigenvector expressions simplify to

$$\begin{aligned}
v &= \left(\frac{h_2 + s_1h_3}{-s_1h_1}, \frac{1}{s_1}, 1\right), & w &= (0, s_1, 1)\\
\widetilde{v} &= \left(\frac{(h_0-1)(s_1h_3 - h_2)}{s_1h_1(1+h_0)}, -\frac{1}{s_1}, 1\right), & \widetilde{w} &= (0, -s_1, 1)\,,\\
v^{(2)} &= \left(-\frac{h_2 + s_1h_0h_3}{h_1(1+h_0)}, 1, 0\right).
\end{aligned}$$

Note v_1 and $v_1^{(2)}$ are always negative, suggesting the resident population decreases upon invasion.

Because $h_0 > 1$,

$$w_I\partial_\gamma^0 P_I v_I = w_I^{(2)}\partial_\gamma^0 P_I^{(2)} v_I^{(2)} = s_1h_1/(h_1 + f_1(h_0-1)) > 0,$$

meaning κ and μ_1 have opposite signs and $\kappa^{(2)}$ and $\mu_1^{(2)}$ have opposite signs. We find

$$\kappa = \frac{h_1(f_2 + s_1f_3) - f_1(h_2 + s_1h_3)}{s_1^2h_1}.$$

Note h_1, f_2, f_3 are within-species competition coefficients, and h_2, h_3, f_1 are between-species competition coefficients, so this can be interpreted as comparing the relative values of within-species and between-species competition. If there is higher between-species competition, i.e. $h_1(f_2 + s_1f_3) < f_1(h_2 + s_1h_3)$, then $\kappa < 0$, the bifurcation is backward, $\mu_1 > 0$, and the coexistence equilibria are unstable. If there is higher within-species competition, i.e. $h_1(f_2 + s_1f_3) > f_1(h_2 + s_1h_3)$, then $\kappa > 0$, the bifurcation is forward, and $\mu_1 < 0$ which promotes the possibility of stable coexistence equilibria dependent on $\eta_1 > 0$ where

$$\eta_1 = \frac{h_1(1+h_0)(s_1f_3 - f_2) - f_1(h_0-1)(h_2 - s_1h_3)}{2s_1(1+h_0)(h_1 + f_1(h_0-1))}.$$

For the direction of bifurcation of the two-cycles, we find

$$\kappa^{(2)} = \frac{s_1 f_3 h_1(1+h_0) - f_1(h_0 h_2 + s_1 h_3)}{s_1 h_1 (1+h_0)}.$$

Similar to κ, this compares within-species competition to between-species competition, though through different expressions. If there is higher between-species competition — i.e. $s_1 f_3 h_1(1+h_0) < f_1(h_0 h_2 + s_1 h_3)$ — then $\kappa^{(2)} < 0$, the bifurcation is backward, and $\mu_1^{(2)} > 0$ making the coexistence two-cycles unstable. If there is higher within-species competition — i.e. $s_1 f_3 h_1(1+h_0) > f_1(h_0 h_2 + s_1 h_3)$ — then $\kappa^{(2)} > 0$, the bifurcation is forward, and $\mu_1^{(2)} < 0$ making the coexistence two-cycles stable if $\widetilde{\mu}_1^{(2)} < 0$ as well.

Because $\widetilde{\mu}_1^{(2)} = 2 s_1 \eta_1$ and stable coexistence equilibria require $\eta_1 > 0$ while stable coexistence two-cycles require $\eta_1 < 0$, η_1 can be viewed as a diagnostic quantity determining the preference of coexistence equilibria versus two-cycles. We see that large values of f_2 and h_2 contribute the stability of coexistence two-cycles, whereas large values of h_3 and f_3 contribute the stability of coexistence equilibria.

Because of the dependencies in the six diagnostic quantities, we can get the full picture of the dynamics near (γ^0, τ) by looking at only three: κ, η_1, and $\kappa^{(2)}$. The signs of μ_1, $\mu_1^{(2)}$, and $\widetilde{\mu}_1^{(1)}$ are determined by the signs of κ, η_1, and $\kappa^{(2)}$. To summarize the effects of the competition coefficients on the three relevant diagnostic quantities, see Table 5.2. In Figures 5.1–5.6 we show example parameter values giving the different combinations of the signs of κ, η_1, and $\kappa^{(2)}$ with the corresponding bifurcation diagrams and time series to show the long-time dynamics at the marked points.

Two combinations that do not seem possible in our example are those where one branch bifurcates backward and the other forward with stable attractors: $\kappa < 0$, $\eta_1 < 0$, $k^{(2)} > 0$ and $\kappa > 0$, $\eta_1 > 0$, $\kappa^{(2)} > 0$. In the observed cases below, we see that if exactly one of the branches bifurcates backward, it connects to a branch of stable invader attractors, creating a strong Allee effect for $f_0 \lesssim f_0^0$. Because the stable branch of invader attractors extends after f_0^0, if the other branch bifurcates forward then there would be two stable attractors for $f_0 \gtrsim f_0^0$, which would require an unstable manifold to separate their basins of attraction. Since we did not find any other bifurcations occurring, it would appear these two scenarios are not possible. Our theory, however, does not address the global properties of the branches — their shape, stability, or even their existence — and thus we cannot rule out these two combinations of diagnostic quantities in general.

As in Section 4.3, if the invader enters the system in low numbers, then its survival is only dependent on whether $f_0 < f_0^0$ or $f_0 > f_0^0$. In the former case orbits go to the resident cycle, while in the latter case orbits go to either a coexistence cycle or an invader attractor. Thus, from the perspective of the invader, it is beneficial to make biological trade-offs that contribute to a lower value of f_0^0. For example, all other things held constant, we can see that increasing adult survival in our example decreases f_0^0; it is therefore advantageous for a species to be iteroparous (see f_0^0 in (4.11)) rather than semelparous (see f_0^0 in (5.35)) if there are no detrimental biological trade-offs.

	κ	η_1	$\kappa^{(2)}$
h_1	$+$		$+$
h_2	$-$	$-$	$-$
h_3	$-$	$+$	$-$
f_1	$-$		$-$
f_2	$+$	$-$	0
f_3	$+$	$+$	$+$

Table 5.2: The signs of κ, η_1, and $\kappa^{(2)}$ to which high levels of each parameter contribute for the example in Section 5.5. An empty cell denotes that it increases the magnitude of a difference whose sign depends on other coefficients, meaning it may contribute to either sign of the diagnostic quantity. Note f_2 is absent from the expression for $\kappa^{(2)}$; we denote this lack of influence in table by 0.

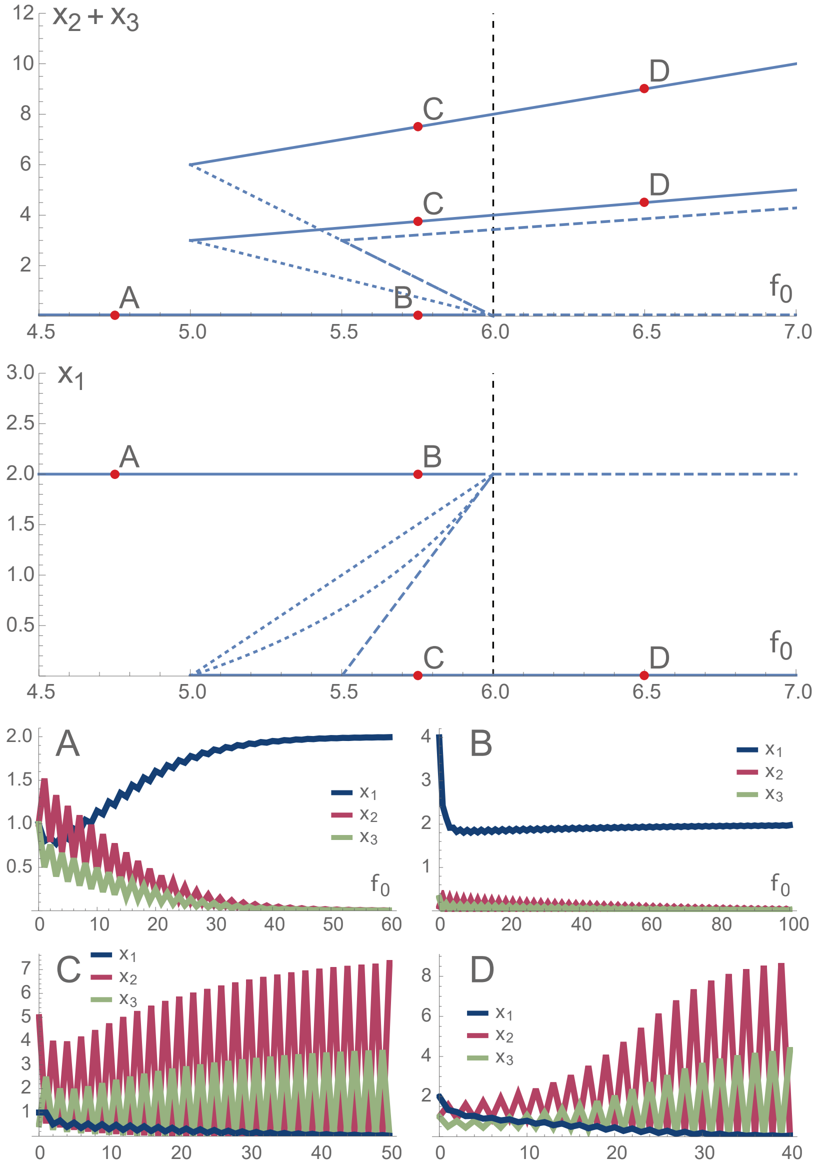

Figure 5.1: An example with $\kappa < 0$, $\eta_1 < 0$, and $\kappa^{(2)} < 0$ using parameter values $h_0 = 2$, $h_1 = 1/2$, $h_2 = 0$, $h_3 = 1$, $f_1 = 1$, $f_2 = 5/8$, $f_3 = 1/2$, and $s_1 = 1/2$. These give $\tau_1 = 2$, $f_0^0 = 6$, $\kappa = -1/2$, $\mu_1 = 1/24$, $\kappa^{(2)} = -1/6$, $\mu_1^{(2)} = 1/36$, and $\eta_1 = \widetilde{\mu}_1 = -1/72$. Both branches bifurcate backward, with the branch of unstable coexistence equilibria (dashed) connecting to the branch of unstable invader equilibria (dashed) and the branch of unstable coexistence two-cycles (dotted) connecting to the branch of stable invader two-cycles (solid). For f_0 between 5 and 6, orbits may go to the resident equilibrium or the invader two-cycle, dependent upon initial conditions. See plots A, B, C, and D for example orbits illustrating the asymptotic behavior in the different regions.

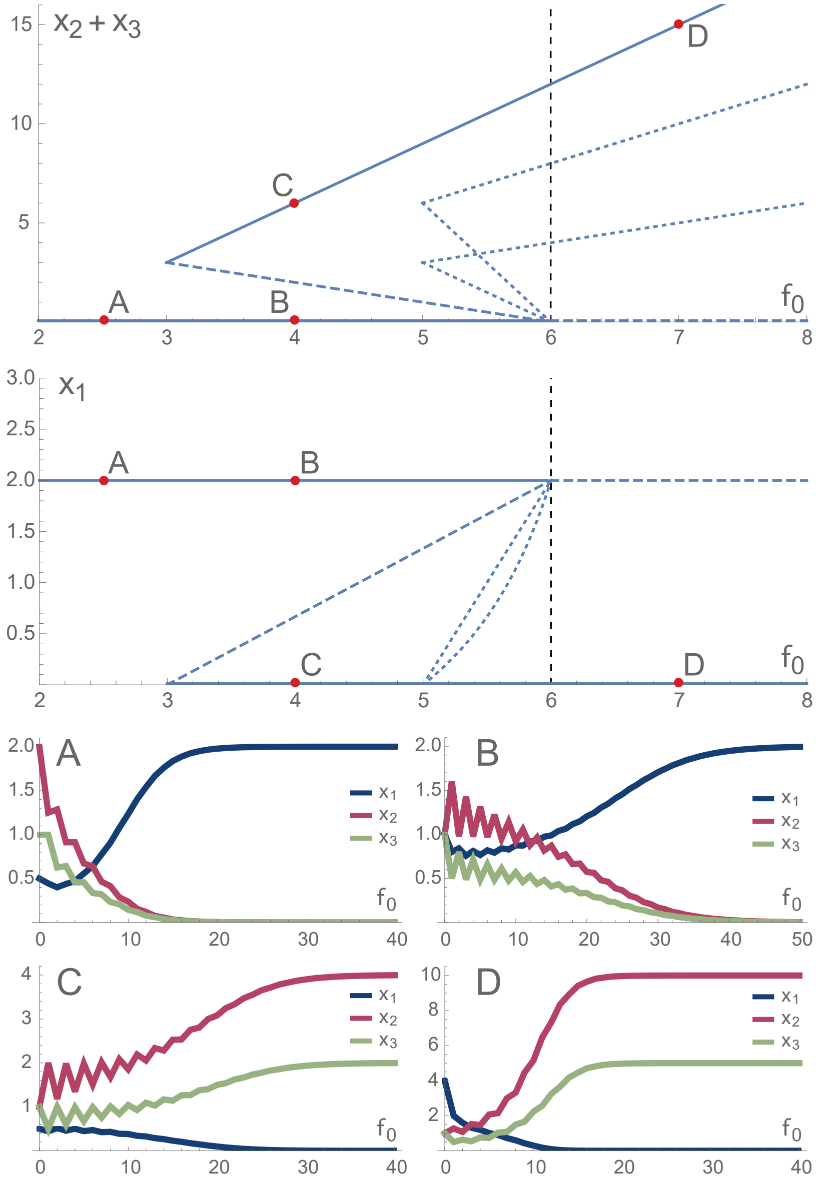

Figure 5.2: An example with $\kappa < 0$, $\eta_1 > 0$, and $\kappa^{(2)} < 0$ using parameter values $h_0 = 2$, $h_1 = 1/2$, $h_2 = 0$, $h_3 = 1$, $f_1 = 1$, $f_2 = 0$, $f_3 = 1/2$, and $s_1 = 1/2$. These give $\tau_1 = 2$, $f_0^0 = 6$, $\kappa = -3$, $\mu_1 = 1/4$, $\kappa^{(2)} = -1/6$, $\mu_1^{(2)} = 1/36$, and $\eta_1 = \widetilde{\mu}_1 = 7/36$. Both branches bifurcate backward, with the branch of unstable coexistence equilibria (dashed) connecting to the branch of stable invader equilibria (solid) and the branch of unstable coexistence two-cycles (dotted) connecting to the branch of stable invader two-cycles (dotted). For f_0 between 3 and 6, orbits may go to the resident equilibrium or the invader equilibrium, dependent upon initial conditions. See plots A, B, C, and D for example orbits illustrating the asymptotic behavior in the different regions.

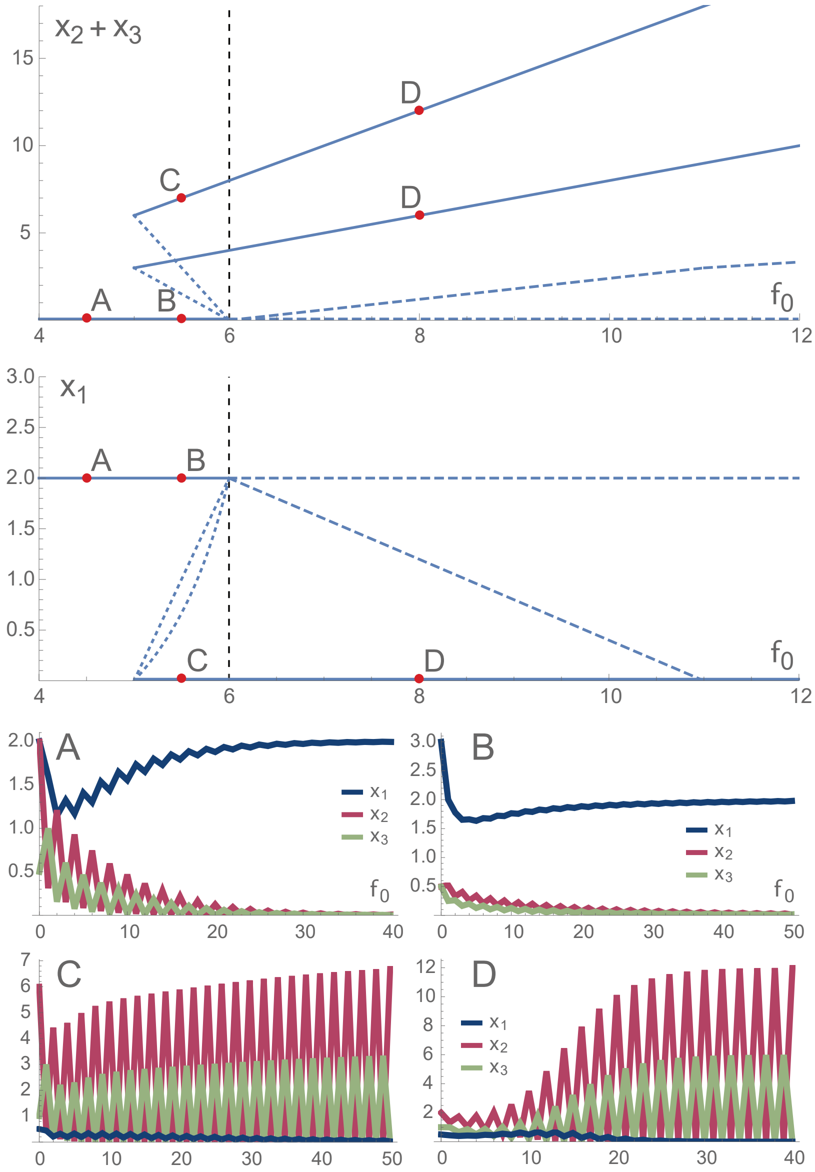

Figure 5.3: An example with $\kappa > 0$, $\eta_1 < 0$, and $\kappa^{(2)} < 0$ using parameter values $h_0 = 2$, $h_1 = 1/2$, $h_2 = 0$, $h_3 = 1$, $f_1 = 1$, $f_2 = 2$, $f_3 = 1/2$, and $s_1 = 1/2$. These give $\tau_1 = 2$, $f_0^0 = 6$, $\kappa = 5$, $\mu_1 = -5/12$, $\kappa^{(2)} = -1/6$, $\mu_1^{(2)} = 1/36$, and $\eta_1 = \widetilde{\mu}_1 = -17/36$. The branch of unstable coexistence equilibria (dashed) bifurcates forward and connects to the branch of unstable invader equilibria (dashed) at $f_0 = 11$. The branch of unstable coexistence two-cycles (dotted) bifurcates backward and connects to the branch of stable invader two-cycles (solid). For f_0 between 5 and 6, orbits may go to the resident equilibrium or the invader two-cycle, dependent upon initial conditions. See plots A, B, C, and D for example orbits illustrating the asymptotic behavior in the different regions.

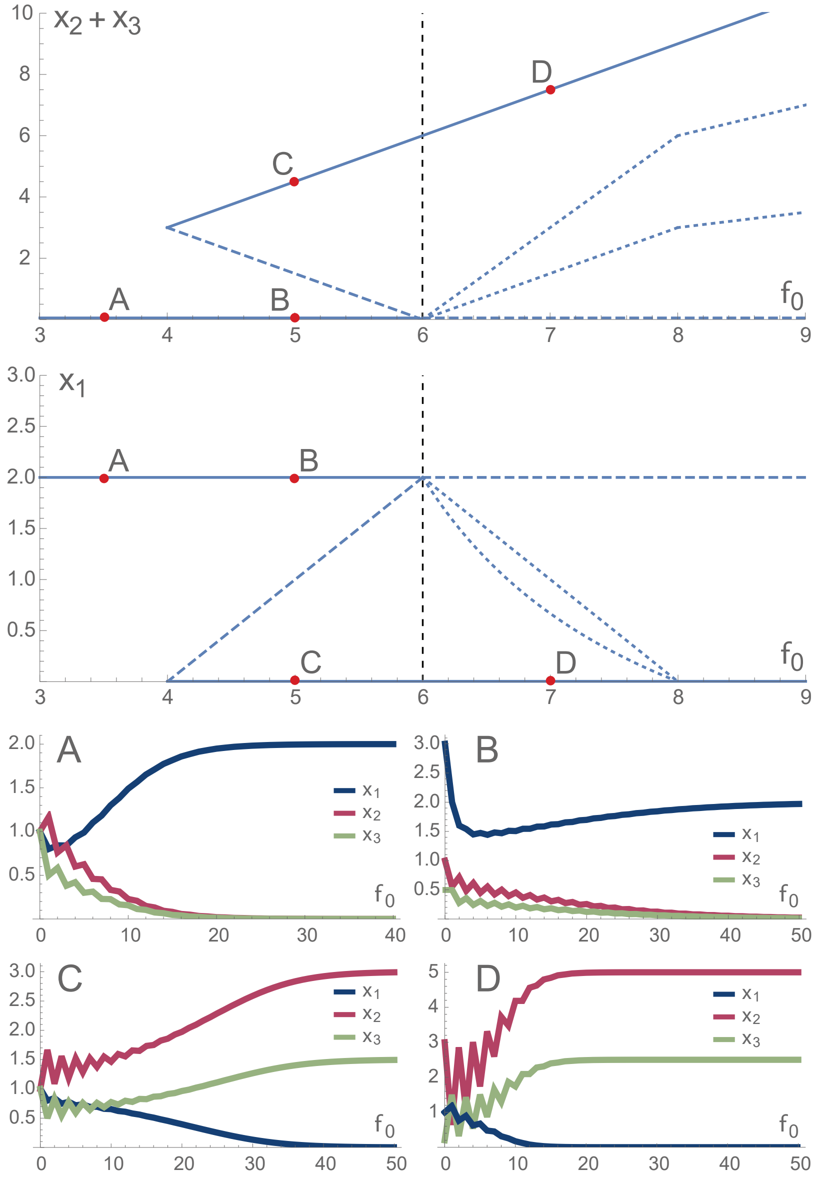

Figure 5.4: An example with $\kappa < 0$, $\eta_1 > 0$, and $\kappa^{(2)} > 0$ using parameter values $h_0 = 2$, $h_1 = 1/2$, $h_2 = 0$, $h_3 = 1$, $f_1 = 1$, $f_2 = 0$, $f_3 = 1$, and $s_1 = 1/2$. These give $\tau_1 = 2$, $f_0^0 = 6$, $\kappa = -2$, $\mu_1 = 1/6$, $\kappa^{(2)} = 1/3$, $\mu_1^{(2)} = -1/18$, and $\eta_1 = \tilde{\mu}_1 = 5/18$. The branch of unstable coexistence equilibria (dashed) bifurcates backward and connects to the branch of unstable invader equilibria (solid). The branch of unstable coexistence two-cycles (dotted) bifurcates forward and connects to the branch of unstable invader two-cycles (dotted) at $f_0 = 8$. For f_0 between 4 and 6, orbits may go to the resident equilibrium or the invader equilibrium, dependent upon initial conditions. See plots A, B, C, and D for example orbits illustrating the asymptotic behavior in the different regions.

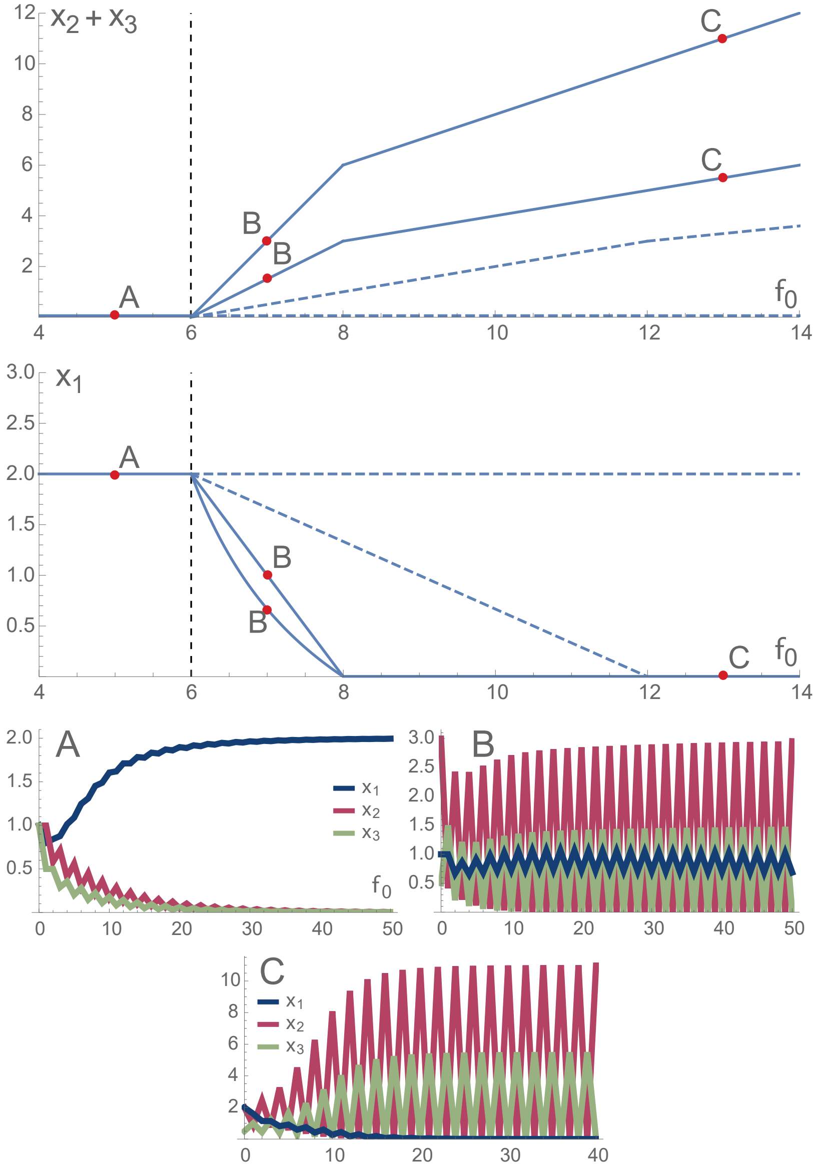

Figure 5.5: An example with $\kappa > 0$, $\eta_1 < 0$, and $\kappa^{(2)} > 0$ using parameter values $h_0 = 2$, $h_1 = 1/2$, $h_2 = 0$, $h_3 = 1$, $f_1 = 1$, $f_2 = 2$, $f_3 = 1$, and $s_1 = 1/2$. These give $\tau_1 = 2$, $f_0^0 = 6$, $\kappa = 6$, $\mu_1 = -1/2$, $\kappa^{(2)} = 1/3$, $\mu_1^{(2)} = -1/18$, and $\eta_1 = \tilde{\mu}_1 = -7/18$. Both branches bifurcate forward, with the branch of unstable coexistence equilibria (dashed) connecting to the branch of unstable invader equilibria (dashed) at $f_0 = 12$ and the branch of stable coexistence two-cycles (solid) connecting to the branch of stable invader two-cycles (solid) at $f_0 = 8$. See plots A, B, and C for example orbits illustrating the asymptotic behavior in the different regions.

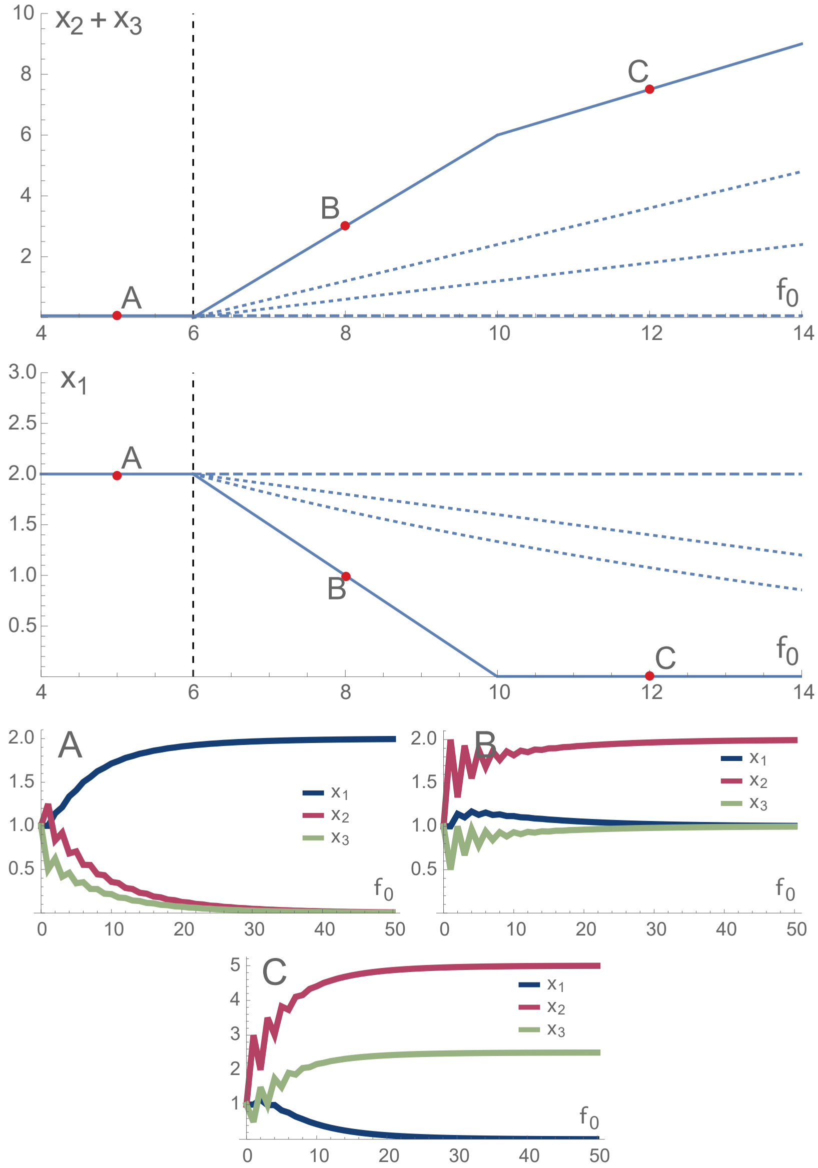

Figure 5.6: An example with $\kappa > 0$, $\eta_1 > 0$, and $\kappa^{(2)} > 0$ using parameter values $h_0 = 2$, $h_1 = 1/2$, $h_2 = 0$, $h_3 = 1/2$, $f_1 = 1$, $f_2 = 0$, $f_3 = 2$, and $s_1 = 1/2$. These give $\tau_1 = 2$, $f_0^0 = 6$, $\kappa = 2$, $\mu_1 = -1/6$, $\kappa^{(2)} = 5/3$, $\mu_1^{(2)} = -5/18$, and $\eta_1 = \tilde{\mu}_1 = 7/18$. Both branches bifurcate forward, with the branch of unstable coexistence equilibria (solid) connecting to the branch of unstable invader equilibria (solid) at $f_0 = 10$ and the branch of stable coexistence two-cycles (dotted) connecting to the branch of stable invader two-cycles (dotted) at $f_0 = 26$. See plots A, B, and C for example orbits illustrating the asymptotic behavior in the different regions.

5.6 Example: two-stage resident

We now show an example with even θ to illustrate Theorem 8 as well as different possible global dynamics than in the previous example. We consider $m = 2$ with a semelparous resident and assume both populations have a constant juvenile survival rate, which gives the projection matrix

$$P(\gamma, x) = \begin{pmatrix} 0 & \pi(x) & 0 & 0 \\ \omega & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi(\gamma, x) \\ 0 & 0 & s_1 & 0 \end{pmatrix}.$$

Because both $\theta = 1$ and $\theta = 2$ are possible (the resident may have a stable equilibrium or a stable two-cycle), we analyze both scenarios.

We again use Leslie-Gower nonlinearities with nonnegative coefficients for the fecundity functions and take the inherent invader birth rate as the bifurcation parameter:

$$\begin{aligned} \pi(x) &= \frac{h_0}{1 + h_1x_1 + h_2x_2 + h_3x_3 + h_4x_4}, \\ \phi(f_0, x) &= \frac{f_0}{1 + f_1x_1 + f_2x_2 + f_3x_3 + f_4x_4}. \end{aligned}$$

When $\theta = 1$, the resident equilibrium is located at

$$\tau = \left(\frac{\omega h_0 - 1}{h_1 + \omega h_2}, \frac{\omega(\omega h_0 - 1)}{h_1 + \omega h_2}, 0, 0 \right). \tag{5.36}$$

When $\theta = 2$, the resident two-cycle is at

$$\tau = \left(\frac{\omega h_0 - 1}{\omega h_2}, 0, 0, 0 \right) \quad \leftrightarrow \quad \tau^{(2)} = \left(0, \frac{\omega h_0 - 1}{h_2}, 0, 0 \right). \tag{5.37}$$

Both scenarios require $h_0\omega > 1$. Positivity of the equilibrium requires $h_1 + \omega h_2 > 0$, while positivity of the two-cycle requires $h_2 > 0$. Based on the eigenvalues of the isolated resident's Jacobian, the equilibrium is stable when $h_1 < \omega h_2$ and the two-cycle is stable when $h_1 > \omega h_2$. From these inequalities, we see $h_2 > 0$ is required in both cases.

5.6.1 Resident with a stable equilibrium

When $h_1 < \omega h_2$, the resident equilibrium (5.36) is stable in isolation and $\theta = 1$. The resident equilibrium loses stability and a bifurcation of both equilibria and two-cycles occur at $f_0^0 = (1 + f_1\tau_1 + f_2\tau_2)/s_1$ by Theorems 9 and 10. We again add the superscript $^{(2)}$ to terms belonging to the branch of bifurcating two-cycles for clarity. The eigenvectors to calculate the diagnostic quantities are

$$\begin{aligned} v &= \left(-\frac{h_3 + s_1h_4}{s_1(h_1 + \omega h_2)}, -\frac{\omega(h_3 + s_1h_4)}{s_1(h_1 + \omega h_2)}, \frac{1}{s_1}, 1\right), & w &= (0, 0, s_1, 1), \\ \widetilde{v} &= \left(\frac{s_1h_4 - h_3}{s_1(\omega h_2 - h_1)}, \frac{\omega(h_3 - s_1h_4)}{s_1(\omega h_2 - h_1)}, -\frac{1}{s_1}, 1\right), & \widetilde{w} &= (0, 0, -s_1, 1), \\ v^{(2)} &= \left(\frac{h_1h_3 - s_1\omega h_2h_4}{\omega^2h_2^2 - h_1^2}, \frac{\omega(s_1h_1h_4 - \omega h_2h_3)}{\omega^2h_2^2 - h_1^2}, 1, 0\right), & w^{(2)} &= (0, 0, 1, 0). \end{aligned}$$

We find that

$$w_I B_I v_I = \frac{s_1(h_1 + \omega h_2)}{h_1 + \omega h_2 + (f_1 + \omega f_2)(\omega h_0 - 1)} > 0,$$

making μ_1 the opposite sign of κ, and

$$w_I^{(2)} B_I^{(2)} v_I^{(2)} = \frac{s_1(h_1 + \omega h_2)}{h_1 + \omega h_2 + \omega(f_1\pi^0 + f_2)(\omega h_0 - 1)} > 0,$$

making $\mu_1^{(2)}$ the opposite sign of $\kappa^{(2)}$.

Calculating κ, we find

$$\kappa = \frac{(h_1 + \omega h_2)(f_3 + s_1f_4) - (h_3 + s_1h_4)(f_1 + \omega f_2)}{s_1^2(h_1 + \omega h_2)}.$$

This can again be seen as a comparison of the strength of within-species competition to between-species competition, where h_1, h_2, f_3, f_4 are within species competition coefficients and h_3, h_4, f_1, f_2 are between-species competition coefficients.

For the remaining two essential diagnostic quantities, the biological interpretation is less clear, where

$$\begin{aligned}
\eta_1 &= \frac{(h_1+\omega h_2)\left[(h_3-s_1h_4)(\omega f_2-f_1)-(f_3-s_1f_4)(\omega h_2-h_1)\right]}{2s_1(\omega h_2-h_1)\left[h_1+\omega h_2+(f_1+\omega f_2)(\omega h_0-1)\right]},\\
\kappa^{(2)} &= \frac{\omega h_3(f_2h_1-f_1h_2)+s_1h_1(f_1h_4-f_4h_1)+s_1\omega^2h_2(f_4h_2-f_2h_4)}{s_1(\omega^2h_2^2-h_1^2)}\\
&= \frac{s_1f_4(\omega^2h_2^2-h_1^2)+\omega f_2(h_1h_3-s_1\omega h_2h_4)+f_1(s_1h_1h_4-\omega h_2h_3)}{s_1(\omega^2h_2^2-h_1^2)}.
\end{aligned}$$

Because $h_1 < \omega h_2$, a high value of f_4 has a positive influence on both quantities. Table 5.3 shows a summary of the effects each coefficient has on the three encompassing diagnostic quantities. The bifurcation dynamics play out the same as in the example in Section 5.5, and again the combinations of $\kappa < 0, \eta_1 < 0, \kappa^{(2)} > 0$ and $\kappa > 0, \eta_1 > 0, \kappa^{(2)} > 0$ are not permissible. Table 5.4 lists a set of parameters giving each of the remaining six sign combinations of the diagnostic quantities.

	κ	η_1	$\kappa^{(2)}$
h_1	$+$		
h_2	$+$		
h_3	$-$		
h_4	$-$		
f_1	$-$		
f_2	$-$		
f_3	$+$	$-$	0
f_4	$+$	$+$	$+$

Table 5.3: The signs of κ, η_1, and $\kappa^{(2)}$ to which high levels of each parameter contribute for the example in Section 5.6.1. An empty cell denotes that it may contribute to either sign of the diagnostic quantity depending on other coefficient values. Note f_3 is absent from the expression for $\kappa^{(2)}$; we denote this lack of influence in table by 0.

5.6.2 Resident with a stable synchronous two-cycle

When $h_1 > \omega h_2$, the resident synchronous[4] two-cycle (5.37) is stable in isolation and $\theta = 2$. By Theorem 8, a bifurcation of coexistence two-cycles occurs. To determine

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[4] In this section we relax the definition of *synchronous* so that, as is clear by context, the resident component of an orbit x_R may be synchronous (i.e. contain a zero at every step). Without the "resident" modifier, *synchronous* still implies synchrony of x_I.

κ	η_1	$\kappa^{(2)}$	h_3	h_4	f_3
-	-	-	3/4	1/8	1/16
-	+	-	3/4	1	1/8
-	+	+	1/2	1	1/8
+	-	-	3/4	1/8	1
+	-	+	1/4	1/8	1
+	+	+	1/4	1/8	1/4

Table 5.4: Coefficient values that give each of the sign combinations possible for $\kappa, \eta_1, \kappa^{(2)}$ using $h_0 = 2$, $h_1 = 1$, $h_2 = 1$, $\omega = 3/4$, $f_1 = 1/2$, $f_2 = 1$, $f_4 = 1$, and $s_1 = 1/2$.

the eigenvectors of $P_I(\gamma^0, \tau)$ given in (5.4), we calculate

$$\begin{aligned} b_\theta(f_0) &= s_1\phi(f_0,\tau) = \frac{s_1 f_0}{1 + f_1(\omega h_0 - 1)/h_2}, \\ a_\theta(f_0) &= s_1\phi(f_0,\tau^{(2)}) = \frac{s_1 f_0}{1 + f_2(\omega h_0 - 1)/(\omega h_2)}. \end{aligned}$$

If $\omega f_2 > f_1$, then the bifurcation occurs when $b_\theta = 1$, corresponding to $f_0^0 = \left(1 + f_2(\omega h_0 - 1)/(\omega h_2)\right)/s_1$. The eigenvectors of $\mathcal{J}_0^{(2)}$ are

$$v = \left(-\frac{h_3}{s_1 \omega h_2}, 0, 0, 1\right), \quad w = (0,0,0,1).$$

As is evident from the eigenvectors, in this case the resident juveniles coexist with the invader adults in the coexistence synchronous two-cycles. Because

$$w_I B_I v_I = \frac{s_1 \omega h_2}{\omega h_2 + f_1(\omega h_0 - 1)} > 0,$$

μ_1 is the opposite sign of κ, where

$$\kappa = \frac{s_1 \omega f_4 h_2 - f_1 h_3}{s_1^2 \omega h_2}.$$

If $\omega f_2 < f_1$, then the bifurcation occurs when $a_\theta = 1$, corresponding to $f_0^0 =$

$(1 + f_1(\omega h_0 - 1)/h_2)/s_1$. The eigenvectors of $\mathcal{J}_0^{(2)}$ are

$$v^{(2)} = \left(-\frac{s_1 h_4}{\omega h_2}, 0, 1, 0\right), \quad w = (0, 0, 1, 0).$$

In this case, the resident juveniles coexist with the invader juveniles in the coexistence synchronous two-cycles. Because

$$w_I B_I v_I = \frac{s_1 h_2}{h_2 + f_2(\omega h_0 - 1)} > 0,$$

again μ_1 is the opposite sign of κ, where

$$\kappa = \frac{f_4 h_2 - f_2 h_4}{h_2}.$$

In both cases, κ can be interpreted as within species competition minus between species competition. When $k > 0$, the coexistence two-cycles exist for $f_0 > f_0^0$ and are stable; and when $\kappa < 0$, the unstable coexistence two-cycles exist for $f_0 < f_0^0$ and orbits go to either the resident or invader exclusion two-cycle dependent upon initial conditions, and for $f_0 > f_0^0$ only the invader two-cycle is stable. Unlike in any of the previous examples, an increase in f_0 does not have to lead to competitive exclusion. As hinted by the eigenvectors above and shown in Figure 5.7, in the case of $\omega f_2 < f_1$, if $h_4 = 0$ then a type of niche sharing occurs where the juveniles of both species are able to coexist even for arbitrarily large values of f_0 by existing in alternate timesteps. A similar phenomenon occurs if $\omega f_2 > f_1$ and $h_3 = 0$.

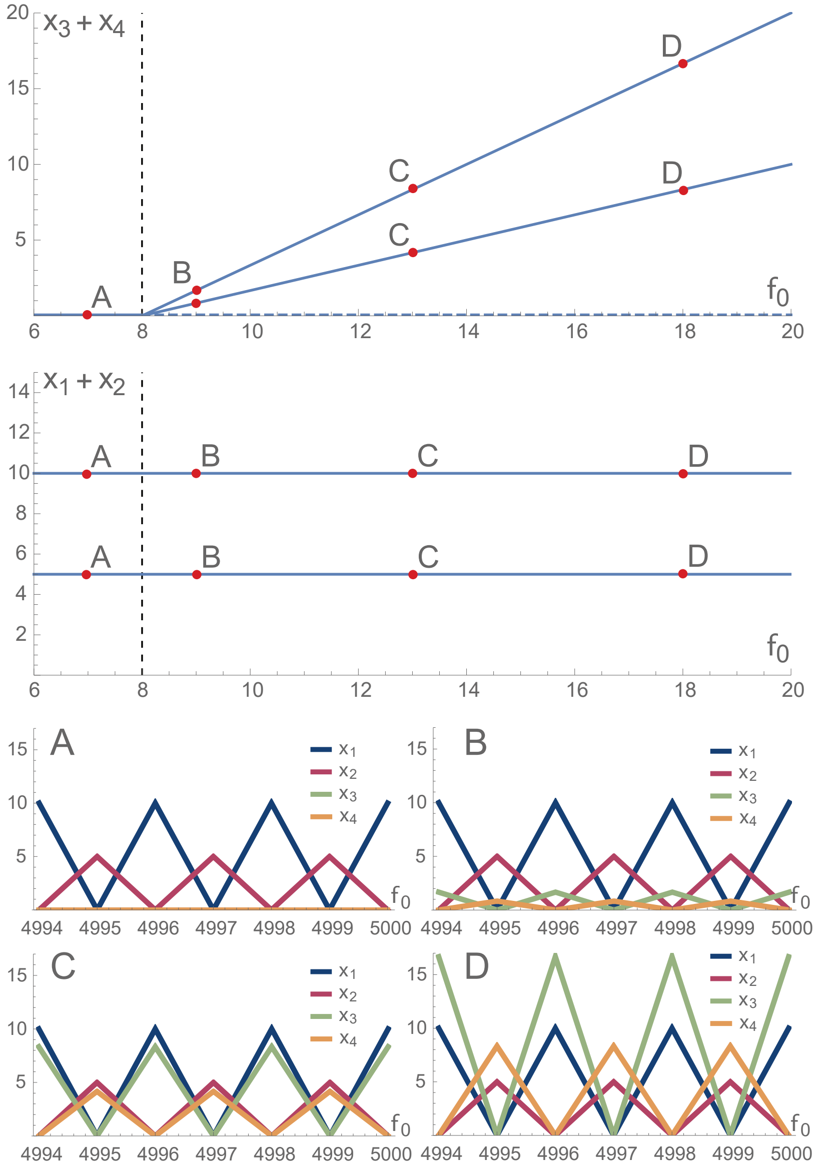

Figure 5.7: An example where increasing f_0 does not lead to competitive exclusion. The parameter values used are $h_0 = 4$, $h_1 = 0.4$, $h_2 = .2$, $h_3 = 0.4$, $h_4 = 0$, $\omega = 0.5$, $f_1 = 0.7$, $f_2 = 0.6$, $f_3 = 0.8$, $f_4 = 0.6$, and $s_1 = 0.5$. These give $h_1 > \omega h_2$ (so that $\theta = 2$, i.e. the resident has a stable two-cycle, as seen in plot A) and $\omega f_2 < f_1$, with $\tau_R = (10, 0)^T$, $\tau_R^{(2)} = (0, 5)^T$, $f_0^0 = 8$, and $\kappa = 0.6$. As seen in plots B, C, and D, $h_4 = 0$ allows the two species to coexist without interacting. Thus, f_0 (and hence the invader's population) can grow without detrimental effect to the resident.

Chapter 6

Concluding Remarks

In this dissertation, we studied a matrix model of two interacting species — a resident and an invader — where the resident has a stable cycle of period θ. The population structure and the density dependence were kept general in the model. In particular, we made no assumptions on the population structure of the resident; as such, the resident can represent a wide variety of populations, from an unstructured population (modeled by a single-stage population) to a community of structured species. We also made no assumptions on the interactions between the populations (or within the populations) other than the existence of a bifurcation parameter which can destabilize the resident cycle in context of the full system. This allows for modeling two populations with mixed-type interactions, such as populations which compete at juvenile stages and realize a predator-prey relationship as adults (see [40] for examples).

We considered two potential structures of the invader's projection matrix: when it is primitive and when it is 2×2 and imprimitive. In both cases, we proved the existence of coexistence cycles bifurcating from the resident cycle and obtained diagnostic quantities to determine the direction of bifurcation and the stability of the coexistence cycles. The direction of bifurcation of the coexistence cycles is always determinable by a single diagnostic quantity. When the invader's projection matrix is primitive, θ-cycles bifurcate whose stability can be determined by a single quantity. When the invader's projection matrix is 2×2 and imprimitive, the properties of the bifurcating cycles depends on whether θ is odd or even. In the case of even θ, synchronous coexistence θ-cycles bifurcate from the resident cycle and their stability can be determined by a single diagnostic quantity. In the case of odd θ, coexistence θ-cycles and synchronous coexistence 2θ-cycles bifurcate from the resident cycle; the stability of the θ-cycles can again be determined by a single diagnostic quantity, while the stability of the 2θ-cycles must be determined by the signs of two diagnostic quantities. See Figure 6.1 for a summary of the types of bifurcating cycles. At the ends of Chapters 4 and 5, we presented examples demonstrating these results and the

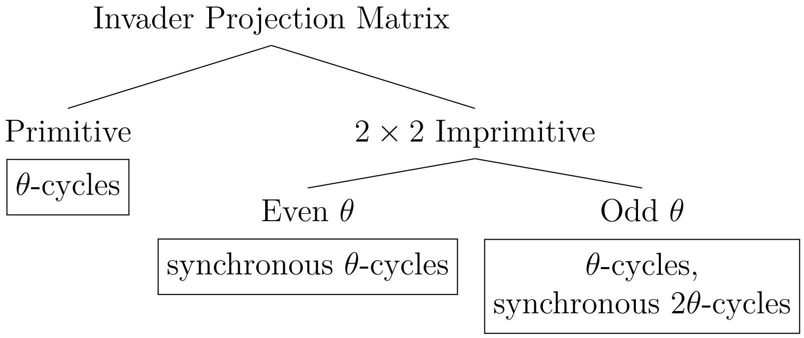

Figure 6.1: A summary of the types of bifurcating coexistence cycles based on the structure of the invader's projection matrix and the parity of period of the resident cycle.

validity of the diagnostic quantities.

If increasing the bifurcation parameter benefits the invader (e.g. the bifurcation parameter is a birth or survival rate), then the backward bifurcating branches contain unstable cycles. In the case of a primitive or 2×2 imprimitive invader projection matrix where the resident cycle has an even period, the forward bifurcating branches contain stable cycles. In the remaining case of a 2×2 imprimitive invader projection matrix where the resident cycle has an odd period, the forward bifurcating branches may contain stable or unstable cycles.

The stable coexistence cycles provide a biologically relevant scenario where the invader and resident can coexist. While the unstable cycles cannot be realized biologically, the examples show that the backward bifurcating branches can transcritically bifurcate a branch of invader cycles, resulting in stable invader attractors and thereby creating a strong Allee effect where the survival of the invader is dependent on the initial conditions. In any of the cases, if the invader is only present initially in small numbers then it is destined to go extinct before the resident cycle destabilizes (due to its local attraction). In this sense, invaders with lower critical values of the bifurcation parameter are more likely to succeed, implying that an iteroparous life history strategy may be more advantageous to an invader than semelparity if there are no other biological costs to maintaining an adult survival.

There are many possible extensions to the work done in this dissertation:

- Our results only prove local existence and stability of coexistence cycles. If the bifurcation parameter changes drastically, we have no global results to say whether the two populations can coexist or to hint at the dynamics.

- Our analysis of an invader with an imprimitive projection matrix was limited to a two-stage population. When considering an invader with $n > 2$ stages, we expect a bifurcation of θ-cycles and of cycles whose period is the least common multiple of n and θ. Kon [28] recently presented a single-species 4-stage model where the dynamic dichotomy does not hold, so is questionable whether the dynamic dichotomy would hold in a higher-dimension two-species model. There may also be other bifurcations that occur, such as discrete-Hopf bifurcations giving rise to invariant loops, since up to n eigenvalues may leave the complex unit circle simultaneously.

- When the invader has an imprimitive 2×2 projection matrix, we neglected the analysis of two specific, non-generic cases. First, when θ is even, we did not study the scenario where both eigenvalues of the composite-Jacobian leave the unit circle simultaneously (see Assumption A6). Second, when θ is odd, we were unable to determine the stability of the bifurcating 2θ-cycles in the specific case mentioned at the end of Section 5.3.2, although it is unclear whether this case can occur or is excluded via our assumptions and the equalities present in the case.

- We were unable to prove the dynamic dichotomy for a general m-stage resident due to lack of a closed-form expression for the eigenvectors of the composite-Jacobian. If one were able to obtain such expressions, checking that the conjectured equality presented at the end Appendix D holds would prove the dynamic dichotomy.

Appendices

Appendix A

Primitivity of a Primitive Matrix Product

A common alternate definition of primitivity to the one presented in Section 2.2 is as follows: a matrix A is primitive if it is nonnegative, irreducible, and there exists an integer $k > 0$ such that A^k is strictly positive, where the minimal such k is called its *index of primitivity.* We give a sufficient condition for the product of primitive matrices to be primitive based on this definition. Specifically, if each factor matrix has at most the zero entries of a known primitive matrix, then the product matrix is primitive. To show that a product of arbitrary primitive matrices is not necessarily primitive, consider

$$A = \begin{pmatrix} 0 & 1 \\ 1 & 1 \end{pmatrix}, \quad B = \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix}, \quad AB = \begin{pmatrix} 1 & 0 \\ 2 & 1 \end{pmatrix}.$$

Both A and B have primitivity indices of 2, whereas AB is imprimitive and one can see that $(AB)^k_{1,2} = 0$ for all positive integers k.

Theorem 11. *Suppose C is a primitive matrix. Then a product of nonnegative matrices $\prod C_k$ is primitive if $(C_k)_{ij} = 0$ implies $(C)_{ij} = 0$ for every k.*

Proof. Let C_B be the Boolean representation of an $m \times m$ primitive matrix C, where the zero entries in C_B correspond to zero entries in C and all nonzero entries in C are 1 in C_B. From Theorem 4.1.2 in [18], if C and D are nonnegative matrices then $(C + D)_B = C_B + D_B$ (using boolean addition) and $(CD)_B = C_B D_B$. Assume the matrices C_i for $i = 1, 2, \ldots, k$ have the same zero-nonzero structure as a known primitive matrix C, so that $(C_i)_B = C_B$. Then

$$\left(\prod_i C_i \right)_B = \prod_i (C_i)_B = (C_B)^k = (C^k)_B. \tag{A.1}$$

If C has primitivity index a, then $C^a \in \mathbb{R}_+^{m\times m}$ and so $(C^a) = 1_{m\times m}$. Also, any power of a primitive matrix is also primitive with maximal primitivity index α: $(C^\beta)^\alpha = (C^\alpha)^\beta \in \mathbb{R}_+^{m\times m}$. Then

$$\left(\left(\prod_i C_i\right)^\alpha\right)_B = \left(\left(\prod_i C_i\right)_B\right)^\alpha = (C_B)^{\alpha k} = \left(C^{\alpha k}\right)_B = 1_{m\times m}.$$

Thus $(\prod_i C_i)^\alpha$ is positive, making $\prod_i C_i$ primitive with maximal primitivity index α.

If $\widehat{C}_i$ is allowed to have less zero entries than C but otherwise the same structure, it can be decomposed as $\widehat{C}_i = C_i + \overline{C}_i$ where $\overline{C}_i$ is also nonnegative. Then, letting $D = \prod_i \widehat{C}_i - \prod_i C_i$ (note D is nonnegative),

$$\begin{aligned}\left(\left(\prod_i \widehat{C}_i\right)^\alpha\right)_B &= \left(\left(\prod_i \widehat{C}_i\right)_B\right)^\alpha \\ &= \left(\left(D + \prod_i C_i\right)_B\right)^\alpha \\ &= \left(D_B + \left(\prod_i C_i\right)_B\right)^\alpha \\ &\geq \left(\left(\prod_i C_i\right)_B\right)^\alpha \\ &= 1_{m\times m}.\end{aligned}$$

Thus $\left(\prod_i \widehat{C}_i\right)^\alpha$ is positive, which implies $\prod_i \widehat{C}_i$ is primitive. ■

Corollary 1. *Assume every factor in a matrix product has the same zero entries as a given imprimitive matrix. If the matrix product is nonnegative and irreducible, then it is imprimitive.*

Proof. Let C be a given imprimitive matrix and $\prod_i C_i$ a matrix product where each C_i has the same zero entries as C. For purposes of contradiction, assume the matrix product is primitive with primitivity index α. Then (A.1) implies that $(C^k)_B$ also has primitivity index α, so that C has primitivity index $k\alpha$. Thus, by contradiction, $\prod_i C_i$ is not primitive and is therefore imprimitive if it is nonnegative and irreducible. ■

APPENDIX B

SYNCHRONOUS CYCLES

If for some integer $k > 1$ the $k\theta$-composite projection matrix has the form

$$P^{(k\theta)}(\gamma, \tau) = \left(\begin{array}{c|cc} \star_{m\times m} & \multicolumn{2}{c}{0_{m\times n}} \\ \hline & f(\gamma) & 0_{1\times(n-1)} \\ 0_{n\times m} & 0_{(n-1)\times 1} & \star_{(n-1)\times(n-1)} \end{array}\right) \tag{B.1}$$

and $f(\gamma)$ passes through 1 at some γ^0, then a bifurcation of $k\theta$-cycles exists for the minimal k in which this holds. We apply Theorem 1 to prove the bifurcation of fixed points of $x' = P^{(k\theta)}(\gamma, x)x$ near τ, which correspond to $k\theta$-cycles of $x' = P(\gamma, x)x$. Note that one is free to renumber classes to achieve this form.

Lemma 1. $\mathbb{R}^j_+ = \{x \in \mathbb{R}^j : x_i > 0 \text{ for } i = 1, 2, ..., j\}$ *is invariant under nonnegative irreducible* $j \times j$ *matrices.*

Proof. First, note $\overline{\mathbb{R}^j_+}$ is invariant under nonnegative matrices [27]. Suppose $x \in \mathbb{R}^j_+$ and $A \in \mathbb{R}^{j\times j}$ is nonnegative and irreducible. If Ax contains a zero, then a row of A must be zero, which would make A reducible and would be a contradiction. ■

Theorem 12. *Suppose there exists a minimal integer* $k \geq 2$ *such that the* $k\theta$*-composite projection matrix* $P^{(k\theta)}(\gamma, \tau)$ *of system (2.1) has the form given in (B.1) where* $n \geq 2$*. Under Assumptions A1 and A2, if there exists a* $\gamma^0 \in \Gamma$ *such that* $f(\gamma^0) = 1$ *and* $f^0_\gamma \neq 0$*, then a branch of coexistence fixed points of* $x' = P^{(k\theta)}(\gamma, x)x$ *bifurcates from* (γ^0, τ) *with the form*

$$\gamma(\epsilon) = \gamma^0 + \kappa\epsilon + o(\epsilon), \quad x(\epsilon) = \tau + v\epsilon + u\epsilon^2 + o(\epsilon^2)$$

where $x_i(\epsilon) = 0$ *for* $i = m+2, \ldots, m+n$ *and* $v^T = (\star_{1\times m}, 1, 0_{1\times(n-1)})$*. Equivalently, a branch of coexistence* $k\theta$*-cycles bifurcates from* (γ^0, τ) *with one of the points in the* *cycle satisfying* $x_{m+2}, \ldots, x_{m+n} = 0$.

Proof. We look for $k\theta$-cycles where one of the points of the cycle is of the form $(\star_{1\times(m+1)}, 0_{1\times(n-1)})$, i.e. where only the first class of the invader is present. To do this, we use the ansatz $x_{m+2}, \ldots, x_{m+n} = 0$. Define $\bar{x} = (x_1, x_2, \ldots, x_{m+1})$, and in general let a bar notation designate the truncated $m+1$ or $(m+1) \times (m+1)$ upper-left portion of a vector or matrix. Finding fixed points of $x' = P^{(k\theta)}(\gamma, x)x$ with the ansatz is equivalent to finding those of $\bar{x}' = \overline{P}^{(k\theta)}\left(\gamma, \operatorname{col}(\bar{x}, 0_{(n+1)\times 1})\right)\bar{x}$ near $\bar{\tau}$.

Near $\bar{\tau}$, $\bar{x} = \overline{P}^{(k\theta)}\left(\gamma, \operatorname{col}(\bar{x}, 0_{(n+1)\times 1})\right)\bar{x}$ takes the form

$$\bar{x} = \bar{\tau} + \overline{\mathcal{J}}^{(k\theta)}(\gamma, \tau)(\bar{x} - \bar{\tau}) + h(\gamma, \bar{x})$$

where

$$\overline{\mathcal{J}}^{(k\theta)}(\gamma, \tau) = \left(\begin{array}{c:c} J_R^{(k\theta)}(\tau_R) & \star_{m\times 1} \\ \hdashline 0_{1\times m} & f(\gamma) \end{array}\right),$$

$h(\gamma, x) = o(|\bar{x} - \bar{\tau}|)$ uniformly on compact intervals of γ, and h is twice continuously differentiable. Note $J_R^{(k\theta)}(\tau_R) = (J_R^{(\theta)}(\tau_R))^k$ and so the eigenvalues of $J_R^{(k\theta)}(\tau_R)$ are those of $J_R^{(\theta)}(\tau_R)$ to the kth power and are thus within the unit circle by Assumption A2. We assume there exists a value $\gamma^0 \in \Gamma$ such that $f(\gamma^0) = 1$, making 1 the dominant eigenvalue of $\overline{\mathcal{J}}^{(k\theta)}(\gamma^0, \tau)$ with a one-dimensional eigenspace right and left eigenvectors $\bar{v} = (\star_{1\times m}, 1)^T$ and $\bar{w} = (0_{1\times m}, 1)$. Note $\bar{w}\overline{\mathcal{J}}^{(k\theta)}(\gamma, \tau)\bar{v} = f_\gamma^0$. Thus if $f_\gamma^0 \neq 0$, then Theorem 1 gives the existence of a branch of bifurcating fixed points of $\bar{x}' = \overline{P}^{(k\theta)}\left(\gamma, \operatorname{col}(\bar{x}, 0_{(n+1)\times 1})\right)\bar{x}$ with the form

$$\gamma(\epsilon) = \gamma^0 + \kappa\epsilon + o(\epsilon), \quad \bar{x}(\epsilon) = \bar{\tau} + \bar{v}\epsilon + \bar{u}\epsilon^2 + o(\epsilon^2).$$

These fixed points correspond to fixed points of the system $x' = P^{(k\theta)}(\gamma, x)x$ of the form

$$\gamma(\epsilon) = \gamma^0 + \kappa\epsilon + o(\epsilon), \quad x(\epsilon) = \tau + v\epsilon + u\epsilon^2 + o(\epsilon^2)$$

where $x_i(\epsilon) = 0$ for $i = m+2, \ldots, m+n$ and $v^T = (\star_{1\times m}, 1, 0_{1\times(n-1)})$. In turn, these fixed points each corresponds to a point in a $k\theta$-cycle of (2.1). Because τ is nonnegative and $v_{m+1} > 0$, the fixed points of the $k\theta$-composite system — and hence the $k\theta$-cycles of (2.1) — correspond to coexistence. ■

Corollary 2. *If $P_I(\gamma, x)$ is irreducible at every γ and x, then the $k\theta$-cycles in Theorem 12 are synchronous (x_I contains a zero at every point in the cycle).*

Proof. Note $x_I' = P_I(\gamma, x)x_I$ and $\mathbb{R}_+^n$ is invariant under mapping by irreducible nonnegative matrices by Lemma 1. Thus, if $P_I(\gamma, x)$ is irreducible at every γ and x, then if the x_I portion of the $k\theta$-cycle ever entered $\mathbb{R}_+^n$ it would remain there. Since it returns to the boundary every $k\theta$ timesteps, the $k\theta$-cycles must be synchronous. ■

APPENDIX C

DYNAMIC DICHOTOMY PROOF: SINGLE-STAGE RESIDENT

Theorem 13. *When $m = 1$, η_1 from Theorem 9 and $\widetilde{\mu}_1$ from Theorem 10 are the same sign.*

Proof. When $m = 1$, the resident is in an equilibrium by Assumption A2 and so $\theta = 1$. The projection matrix in this case is

$$P(\gamma, x) = \begin{pmatrix} \pi(x) & 0 & 0 \\ 0 & 0 & \phi(\gamma, x) \\ 0 & \sigma(\gamma, x) & 0 \end{pmatrix}.$$

We define the following variables for local use:

$$\begin{array}{lll} a = \sigma^0_{x_1}\phi^0 & d = \sigma^0_{x_2}(\phi^0)^2 & \alpha = \pi^0 + \pi_{x_1}x^0_1 \\ b = \phi^0_{x_1}/\phi^0 & e = \sigma^0_{x_3}\phi^0 & \beta = \pi^0_{x_2}x^0_1\phi^0 \\ c = \phi^0_{x_2} & f = \phi^0_{x_3}/\phi^0 & \omega = \pi^0_{x_3}x^0_1. \end{array}$$

The bifurcations of Theorems 6 and 7 occur when $\phi^0\sigma^0 = 1$. At this point, the relevant eigenvectors are

$$v = \left(\frac{-\beta - \omega}{\alpha - 1}, \phi^0, 1\right), \quad \widetilde{v} = \left(\frac{\beta - \omega}{\alpha + 1}, -\phi^0, 1\right), \quad v^{(2)} = \left(\frac{v_1 - \widetilde{v}_1}{2\phi^0}, 1, 0\right),$$

where v and $\widetilde{v}$ are the right eigenvectors of $\mathcal{J}_0$ and $v^{(2)}$ is the right eigenvector of $\mathcal{J}^{(2)}_0$. We add the superscript $^{(2)}$ to terms of the branch of bifurcating two-cycles for clarity.

Calculating η_1 and simplifying with the above defined expressions,

$$\begin{aligned}
2\eta_1 &= \left(\phi\nabla_x^0\sigma - \sigma\nabla_x^0\phi\right)\cdot\widetilde{v} \\
&= \left(\sigma_{x_1}^0\phi^0 - \phi_{x_1}^0\sigma^0\right)\widetilde{v}_1 - \phi^0\left(\sigma_{x_2}^0\phi^0 - \phi_{x_2}^0\sigma^0\right) + \sigma_{x_3}^0\phi^0 - \phi_{x_3}^0\sigma^0 \\
&= (a-b)\widetilde{v}_1 + c - d + e - f.
\end{aligned}$$

We also calculate $\mu_1^{(2)}$ which will be used in the calculation of $\widetilde{\mu}_1^{(2)}$:

$$\begin{aligned}
\phi^0\mu_1^{(2)} &= \phi^0\nabla_x^0\phi\left(\tau(x)x_1, \phi(x)x_3, \sigma(x)x_2\right)\sigma(x)\cdot v^{(2)} \\
&= \left[\phi_{x_1}^0\left(\pi + \pi_{x_1}x_1^0\right)\sigma^0 + \sigma_{x_1}^0\phi^0\right]\phi^0 v_1^{(2)} + \phi_{x_1}\pi_{x_2}x_1^0\sigma^0\phi^0 + \phi_{x_3}^0(\sigma^0)^2\phi^0 + \sigma_{x_2}^0(\phi^0)^2 \\
&= (a+\alpha b)\left(\frac{v_1 - \widetilde{v}_1}{2}\right) + \beta b + d + f.
\end{aligned}$$

Finally, we calculate $\widetilde{\mu}_1^{(2)}$ and relate it to η_1:

$$\begin{aligned}
\phi^0\widetilde{\mu}_1^{(2)} &= \phi^0\nabla_x^0\sigma\left(\tau(x)x_1, \phi(x)x_3, \sigma(x)x_2\right)\phi(x)\cdot v^{(2)} - \phi^0\mu_1^{(2)} \\
&= \left[\sigma_{x_1}^0\left(\pi + \pi_{x_1}x_1^0\right)\phi^0 + \phi_{x_1}^0\sigma^0\right]\phi^0 v_1^{(2)} \\
&\qquad + \sigma_{x_1}\pi_{x_2}x_1^0(\phi^0)^2 + \sigma_{x_3}^0(\phi^0)^2\sigma^0 + \phi_{x_2}^0\sigma^0\phi^0 - \phi^0\mu_1^{(2)} \\
&= (\alpha a + b)\left(\frac{v_1 - \widetilde{v}_1}{2}\right) + \beta a + c + e - \phi^0\mu_1^{(2)} \\
&= (a-b)(\alpha-1)\left(\frac{v_1 - \widetilde{v}_1}{2}\right) + \beta(a-b) + c - d + e - f \\
&= (a-b)(\alpha-1)\left(\frac{v_1 - \widetilde{v}_1}{2}\right) + \beta(a-b) - (a-b)\widetilde{v}_1 + 2\eta_1 \\
&= \frac{v_1}{2}(a-b)(\alpha-1) - \frac{\widetilde{v}_1}{2}(a-b)(\alpha+1) + \beta(a-b) + 2\eta_1 \\
&= \frac{-\beta-\omega}{2}(a-b) - \frac{\beta-\omega}{2}(a-b) + \beta(a-b) + 2\eta_1 \\
&= 2\eta_1.
\end{aligned}$$

Thus η_1 and $\widetilde{\mu}_1^{(2)}$ have the same sign. ■

Recall that the stability of the bifurcating equilibria requires $\mu_1 < 0$ and $\eta_1 > 0$, while the stability of the bifurcating two-cycles requires $\mu_1^{(2)} < 0$ and $\widetilde{\mu}_1^{(2)} < 0$. Thus, at most one of the branches may contain stable attractors near (γ^0, τ). If $w_I\partial_\gamma^0 P_I v_I > 0$ and $w_I^{(2)}\partial_\gamma^0 P_I^{(2)} v_I^{(2)} > 0$, then forward bifurcations also provide $\mu_1 < 0$

and $\mu_1^{(2)} < 0$, meaning that exactly one of the branches contains stable attractors near (γ^0, τ). Similarly, if $w_I \partial_\gamma^0 P_I v_I < 0$ and $w_I^{(2)} \partial_\gamma^0 P_I^{(2)} v_I^{(2)} < 0$ then backward bifurcations provide $\mu_1 < 0$ and $\mu_1^{(2)} < 0$, so that exactly one of the branches contains stable attractors near (γ^0, τ). Thus, we have proven the dynamic dichotomy conjecture in Section 5.4.

Corollary 3. *Under Assumptions A1, A2, A3, and A5 with* $m = 1$*, if* κ*,* $\kappa^{(2)}$*,* $w_I \partial_\gamma^0 P_I v_I$*, and* $w_I^{(2)} \partial_\gamma^0 P_I^{(2)} v_I^{(2)}$ *are all the same sign, then exactly one of the bifurcating branches contains stable attractors.*

The calculations in the above proof required plugging in the values of v_1 and $\widetilde{v}_1$ to obtain the relation $\phi^0 \widetilde{\mu}_1^{(2)} = 2\eta_1$. Without general expressions for $v^{(\theta)}$ and $\widetilde{v}^{(\theta)}$, this is intractable for arbitrary m.

Appendix D

General Dynamic Dichotomy Calculations

In the case of odd θ and imprimitive $P_I(\gamma, x)$ given by (5.1), we proved the bifurcation of θ-cycles and 2θ-cycles at (γ^0, τ) in Chapter 5. To prove the dynamic dichotomy conjectured in Section 5.4 — i.e. that only one of the branches contains stable attractors — we look to prove that $\eta_1^{(\theta)}$ and $\widetilde{\mu}_1^{(2\theta)}$ are of the same sign. Motivated by the $m = 1$ case in Appendix C, we aim to prove that $b_\theta^0 \widetilde{\mu}^{(2\theta)} = 2\eta_1^{(\theta)}$. The simplified expressions for the diagnostic quantities are

$$\begin{aligned} 2\eta_1^{(\theta)} &= -a_\theta^0 \nabla_x^0 p_{m+1,m+2}^{(\theta)} \cdot \widetilde{v}^{(\theta)} + b_\theta^0 \nabla_x^0 p_{m+2,m+1}^{(\theta)} \cdot \widetilde{v}^{(\theta)}, \\ \widetilde{\mu}_1^{(2\theta)} &= -\nabla_x^0 p_{m+1,m+1}^{(2\theta)} \cdot v^{(2\theta)} + \nabla_x^0 p_{m+2,m+2}^{(2\theta)} \cdot v^{(2\theta)}. \end{aligned} \tag{D.1}$$

Because the eigenvectors of $\mathcal{J}_0^{(\theta)}$ corresponding to eigenvalue 1 are eigenvectors of $\mathcal{J}_0^{(2\theta)}$ (as mentioned in Section 5.3), $v^{(2\theta)}$ is a linear combination of the eigenvectors $v^{(\theta)}$ and $\widetilde{v}^{(\theta)}$ found in Section 5.1.1; specifically,

$$v^{(2\theta)} = \frac{v^{(\theta)} - \widetilde{v}^{(\theta)}}{2b_\theta^0} = \frac{v^{(\theta)} - \widetilde{v}^{(\theta)}}{2p_{m+1,m+1}^0}.$$

We relate $\nabla_x^0 p_{m+1,m+1}^{(2\theta)}$ and $\nabla_x^0 p_{m+2,m+2}^{(2\theta)}$ to $\nabla_x^0 p_{m+1,m+2}^{(\theta)}$ and $\nabla_x^0 p_{m+2,m+1}^{(\theta)}$ by relating $p^{(2\theta)}$ terms to $q^{(2\theta)}$ terms, $q^{(2\theta)}$ terms to $q^{(\theta)}$ terms, and $q^{(\theta)}$ terms to $p^{(\theta)}$ terms, i.e.

$$p^{(2\theta)} \leftrightarrow q^{(2\theta)} \leftrightarrow q^{(\theta)} \leftrightarrow p^{(\theta)}.$$

We start by deriving expressions for $\partial_{x_i}^0 p_{m+1,m+1}^{(2\theta)}$ in $p^{(\theta)}$ terms, followed by repeating the approach for $\partial_{x_i}^0 p_{m+2,m+2}^{(2\theta)}$, and conclude by listing the derived requirement for $p_{m+1,m+2}^{(\theta)}(\gamma^0, \tau)\widetilde{\mu}^{(2\theta)} = 2\eta_1^{(\theta)}$.

D.1 Relating $p^{(2\theta)}_{m+1,m+1}$ to $p^{(\theta)}$ terms

Relating $p^{(2\theta)}$ and $q^{(2\theta)}$ terms.

The definition of $q^{(2\theta)}(x) = P^{(2\theta)}(x)x$ from Section 2.1 gives $q_i^{(2\theta)} = \sum_j p_{ij}^{(2\theta)} x_j$. Because we aim to get expressions for $\nabla_x^0 p^{(2\theta)}_{m+1,m+1}$, we look specifically at $\partial_{x_{m+1}} q^{(2\theta)}_{m+1}$ and its derivatives, where

$$\partial_{x_{m+1}} q^{(2\theta)}_{m+1} = p^{(2\theta)}_{m+1,m+1} + x_{m+1}\left(p^{(2\theta)}_{m+1,m+1}\right)_{x_{m+1}}. \tag{D.2}$$

Evaluated at the bifurcation point, this gives $\partial^0_{x_{m+1}} q^{(2\theta)}_{m+1} = \left(p^{(2\theta)}_{m+1,m+1}\right)^0$. A further differentiation of (D.2) gives

$$\partial^0_{x_i}\left(\partial_{x_{m+1}} q^{(2\theta)}_{m+1}\right) = \begin{cases} \partial^0_{x_i} p^{(2\theta)}_{m+1,m+1} & \text{for } i \neq m+1 \\ 2\partial^0_{x_{m+1}} p^{(2\theta)}_{m+1,m+1} & \text{for } i = m+1. \end{cases} \tag{D.3}$$

Relating $q^{(2\theta)}$ and $q^{(\theta)}$ terms.

Here we look to relate $\partial^0_{x_i}\partial_{x_{m+1}} q^{(2\theta)}_{m+1}$ to $q^{(\theta)}$ terms. Note

$$q^{(2\theta)}(x) = q^{(\theta)}(q^{(\theta)}(x)). \tag{D.4}$$

Differentiating (D.4) and applying the chain rule, we get

$$\partial_{x_{m+1}} q^{(2\theta)}_{m+1} = \sum_j \left(q^{(\theta)}_{m+1}\right)_{x_j}\bigg|_{x=q^{(\theta)}(x)} \left(q^{(\theta)}_j\right)_{x_{m+1}}.$$

Further differentiating gives

$$\begin{aligned}\partial_{x_i}\partial_{x_{m+1}} q^{(2\theta)}_{m+1} = &\sum_j \left(q^{(\theta)}_{m+1}\right)_{x_j}\bigg|_{x=q^{(\theta)}(x)} \left(q^{(\theta)}_j\right)_{x_{m+1},x_i} \\ &+ \sum_j \left[\sum_k \left(q^{(\theta)}_{m+1}\right)_{x_j,x_k}\bigg|_{x=q^{(\theta)}(x)} \left(q^{(\theta)}_k\right)_{x_i}\right] \left(q^{(\theta)}_j\right)_{x_{m+1}}\end{aligned}$$

which, when evaluated at the bifurcation point, gives

$$\partial^0_{x_i}\partial_{x_{m+1}} q^{(2\theta)}_{m+1} = \sum_j \left(q^{(\theta)}_{m+1}\right)^0_{x_j} \left(q^{(\theta)}_j\right)^0_{x_{m+1},x_i} + \sum_j \left[\sum_k \left(q^{(\theta)}_{m+1}\right)^0_{x_j,x_k} \left(q^{(\theta)}_k\right)^0_{x_i}\right] \left(q^{(\theta)}_j\right)^0_{x_{m+1}}. \tag{D.5}$$

Relating $q^{(\theta)}$ and $p^{(\theta)}$ terms.

To relate $q^{(\theta)}$ and $p^{(\theta)}$ terms, we simply recall the definition $q^{(\theta)}(x) = P^{(\theta)}(x)x$ which gives $q_i^{(\theta)} = \sum_j p_{ij}^{(\theta)} x_j$, and specifically $q_{m+1}^{(\theta)} = p_{m+1,m+2}^{(\theta)} x_{m+2}$ when simplified.

Relating $p_{m+1,m+1}^{(2\theta)}$ and $p^{(\theta)}$ terms.

Finally, we plug in the $p^{(\theta)}$ expansions of the $q^{(\theta)}$ terms into (D.5):

$$\begin{aligned}\partial_{x_i}^0 \partial_{x_{m+1}} q_{m+1}^{(2\theta)} = &\sum_j \left(p_{m+1,m+2}^{(\theta)} x_{m+2}\right)_{x_j}^0 \left(\sum_k p_{j,k}^{(\theta)} x_k\right)_{x_{m+1},x_i}^0 \\ &+ \sum_j \left[\sum_k \left(p_{m+1,m+2}^{(\theta)} x_{m+2}\right)_{x_j,x_k}^0 \left(\sum_a p_{k,a}^{(\theta)} x_a\right)_{x_i}^0\right] \left(\sum_k p_{j,k}^{(\theta)} x_k\right)_{x_{m+1}}^0 .\end{aligned} \tag{D.6}$$

In the first summation, the only nonzero term comes from $j = m+2$ and is equal to

$$\begin{aligned}&\left(p_{m+1,m+2}^{(\theta)}\right)^0 \left(p_{m+2,m+1}^{(\theta)} + p_{m+2,m+1}^{(\theta)} x_{m+1}\right)_{x_i}^0 \\ &\qquad = \begin{cases} \left(p_{m+1,m+2}^{(\theta)}\right)^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_i}^0 & \text{for } i \neq m+1 \\ 2\left(p_{m+1,m+2}^{(\theta)}\right)^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_{m+1}}^0 & \text{for } i = m+1. \end{cases}\end{aligned}$$

In the second j summation, the $j = m+1$ term is zero because in the final k summation $(p_{m+1,m+2}^{(\theta)} x_{m+2})_{x_{m+1}}^0 = 0$. The $j = 1, \ldots, m$ terms only allow $k = m+2$ in the first k summation which then only allows $a = m+1$, so that

$$\begin{aligned}&\left[\sum_k \left(p_{m+1,m+2}^{(\theta)} x_{m+2}\right)_{x_j,x_k}^0 \left(\sum_a p_{k,a}^{(\theta)} x_a\right)_{x_i}^0\right] \left(\sum_k p_{j,k}^{(\theta)} x_k\right)_{x_{m+1}}^0 \\ &\quad = \left(p_{m+1,m+2}^{(\theta)}\right)_{x_j}^0 \left(p_{m+2,m+1}^{(\theta)} x_{m+1}\right)_{x_i}^0 \left(\sum_k p_{j,k}^{(\theta)} x_k\right)_{x_{m+1}}^0 \\ &\quad = \begin{cases} 0 & \text{for } i \neq m+1 \\ \left(p_{m+1,m+2}^{(\theta)}\right)_{x_j}^0 \left(p_{m+2,m+1}^{(\theta)}\right)^0 \sum_{k=1}^{m} \left(p_{j,k}^{(\theta)}\right)_{x_{m+1}}^0 \tau_k & \text{for } i = m+1 \end{cases}\end{aligned}$$

for $j = 1, \dots, m$. For $j = m+2$,

$$\begin{aligned}
&\left[\sum_k \left(p^{(\theta)}_{m+1,m+2} + x_{m+2}\partial_{x_{m+2}} p^{(\theta)}_{m+1,m+2}\right)^0_{x_k} \left(\sum_a p^{(\theta)}_{k,a} x_a\right)^0_{x_i}\right] \left(p^{(\theta)}_{m+2,m+1}\right)^0 \\
&\quad = \left(p^{(\theta)}_{m+2,m+1}\right)^0 \sum_{k=1}^m \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_k} \left(p^{(\theta)}_{k,i} + \sum_{a=1}^m \left(p^{(\theta)}_{k,a}\right)_{x_i} x_a\right)^0 \\
&\qquad + \left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_{m+1}} \left(p^{(\theta)}_{m+1,i}\right)^0 + 2\left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_{m+2}} \left(p^{(\theta)}_{m+2,i}\right)^0.
\end{aligned}$$

Thus, combining (D.6) and (D.3), we find

$$\begin{aligned}
\partial^0_{x_i} p^{(2\theta)}_{m+1,m+1} = {} & \left(p^{(\theta)}_{m+1,m+2}\right)^0 \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_i} \\
& + \left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_{m+1}} \left(p^{(\theta)}_{m+1,i}\right)^0 \\
& + \left(p^{(\theta)}_{m+2,m+1}\right)^0 \sum_{j=1}^m \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_j} \left(\left(p^{(\theta)}_{j,i}\right)^0 + \sum_{k=1}^m \left(p^{(\theta)}_{j,k}\right)^0_{x_i} \tau_k\right)
\end{aligned} \tag{D.7}$$

for $i \neq m+1$ and

$$\begin{aligned}
\partial^0_{x_{m+1}} p^{(2\theta)}_{m+1,m+1} = {} & \left(p^{(\theta)}_{m+1,m+2}\right)^0 \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_{m+1}} \\
& + \left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_{m+2}} \left(p^{(\theta)}_{m+2,m+1}\right)^0 \\
& + \left(p^{(\theta)}_{m+2,m+1}\right)^0 \sum_{j=1}^m \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_j} \left(\sum_{k=1}^m \left(p^{(\theta)}_{j,k}\right)^0_{x_{m+1}} \tau_k\right)
\end{aligned} \tag{D.8}$$

for $i = m+1$.

D.1.1 Relating $p^{(2\theta)}_{m+2,m+2}$ to $p^{(\theta)}$ terms

Repeating the calculations above, to parallel (D.3) we find

$$\partial^0_{x_i}\left(\partial_{x_{m+2}} q^{(2\theta)}_{m+2}\right) = \begin{cases} \partial^0_{x_i} p^{(2\theta)}_{m+2,m+2} & \text{for } i \neq m+2 \\ 2\partial^0_{x_{m+2}} p^{(2\theta)}_{m+2,m+2} & \text{for } i = m+2. \end{cases} \tag{D.9}$$

To parallel (D.6) we find

$$\begin{aligned} \partial^0_{x_i}\partial_{x_{m+2}} q^{(2\theta)}_{m+2} = {} & \sum_j \left(p^{(\theta)}_{m+2,m+1} x_{m+1}\right)^0_{x_j} \left(\sum_k p^{(\theta)}_{j,k} x_k\right)^0_{x_{m+2},x_i} \\ & + \sum_j \left[\sum_k \left(p^{(\theta)}_{m+2,m+1} x_{m+1}\right)^0_{x_j,x_k} \left(\sum_a p^{(\theta)}_{k,a} x_a\right)^0_{x_i}\right] \left(\sum_k p^{(\theta)}_{j,k} x_k\right)^0_{x_{m+2}}. \end{aligned} \tag{D.10}$$

In the first summation, the only nonzero term comes from $j = m+1$ and is equal to

$$\begin{aligned} & \left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2} + p_{m+1,m+2} x_{m+2}\right)^0_{x_i} \\ & \qquad = \begin{cases} \left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_i} & \text{for } i \neq m+2 \\ 2\left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_{m+2}} & \text{for } i = m+2. \end{cases} \end{aligned}$$

In the second j summation of (D.10), the $j = m+2$ term is zero because in the final k summation $\left(p^{(\theta)}_{m+2,m+1} x_{m+1}\right)^0_{x_{m+2}} = 0$. The $j = 1, \ldots, m$ terms only allow $k = m+1$ in the first k summation which then only allows $a = m+2$, making

$$\begin{aligned} & \left[\sum_k \left(p^{(\theta)}_{m+2,m+1} x_{m+1}\right)^0_{x_j,x_k} \left(\sum_a p^{(\theta)}_{k,a} x_a\right)^0_{x_i}\right] \left(\sum_k p^{(\theta)}_{j,k} x_k\right)^0_{x_{m+2}} \\ & \quad = \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_j} \left(p^{(\theta)}_{m+1,m+2} x_{m+2}\right)^0_{x_i} \left(\sum_k p^{(\theta)}_{j,k} x_k\right)^0_{x_{m+2}} \\ & \quad = \begin{cases} 0 & \text{for } i \neq m+2 \\ \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_j} \left(p^{(\theta)}_{m+1,m+2} x_{m+2}\right)^0_{x_i} \displaystyle\sum_{k=1}^{m} \left(p^{(\theta)}_{j,k}\right)^0_{x_{m+2}} x^0_k & \text{for } i = m+2 \end{cases} \end{aligned}$$

for $j = 1, \ldots, m$. For $j = m+1$,

$$\begin{aligned}
&\left[\sum_k \left(p^{(\theta)}_{m+2,m+1} + x_{m+1}\partial_{x_{m+1}} p^{(\theta)}_{m+2,m+1}\right)^0_{x_k} \left(\sum_a p^{(\theta)}_{k,a} x_a\right)^0_{x_i}\right] \left(p^{(\theta)}_{m+1,m+2}\right)^0 \\
&\quad = \left(p^{(\theta)}_{m+1,m+2}\right)^0 \sum_{k=1}^{m} \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_k} \left(p^{(\theta)}_{k,i} + \sum_{a=1}^{m} \left(p^{(\theta)}_{k,a}\right)_{x_i} x_a\right)^0 \\
&\qquad + \left(p^{(\theta)}_{m+1,m+2}\right)^0 \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_{m+2}} \left(p^{(\theta)}_{m+2,i}\right)^0 + 2\left(p^{(\theta)}_{m+1,m+2}\right)^0 \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_{m+1}} \left(p^{(\theta)}_{m+1,i}\right)^0 .
\end{aligned}$$

Thus, combining (D.10) and (D.9) gives

$$\begin{aligned}
\partial^0_{x_i} p^{(2\theta)}_{m+2,m+2} = {} & \left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_i} \\
& + \left(p^{(\theta)}_{m+1,m+2}\right)^0 \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_{m+2}} \left(p^{(\theta)}_{m+2,i}\right)^0 \\
& + \left(p^{(\theta)}_{m+1,m+2}\right)^0 \sum_{j=1}^{m} \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_j} \left(\left(p^{(\theta)}_{j,i}\right)^0 + \sum_{k=1}^{m} \left(p^{(\theta)}_{j,k}\right)^0_{x_i} \tau_k\right)
\end{aligned} \tag{D.11}$$

for $i \neq m+2$ and

$$\begin{aligned}
\partial^0_{x_{m+2}} p^{(2\theta)}_{m+2,m+2} = {} & \left(p^{(\theta)}_{m+2,m+1}\right)^0 \left(p^{(\theta)}_{m+1,m+2}\right)^0_{x_{m+2}} \\
& + \left(p^{(\theta)}_{m+1,m+2}\right)^0 \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_{m+1}} \left(p^{(\theta)}_{m+1,m+2}\right)^0 \\
& + \left(p^{(\theta)}_{m+1,m+2}\right)^0 \sum_{j=1}^{m} \left(p^{(\theta)}_{m+2,m+1}\right)^0_{x_j} \left(\sum_{k=1}^{m} \left(p^{(\theta)}_{j,k}\right)^0_{x_{m+2}} \tau_k\right)
\end{aligned} \tag{D.12}$$

for $i = m+2$.

D.2 General Case

Now that we have related the entries of $\nabla^0_x p^{(2\theta)}_{m+1,m+1}$ and $\nabla^0_x p^{(2\theta)}_{m+2,m+2}$ to $p^{(\theta)}$ terms (see (D.7), (D.8), (D.11), and (D.12)), we return to (D.1) to look at what is required to prove $b^0_\theta \widetilde{\mu}^{(2\theta)} = 2\eta^{(\theta)}_1$. Recall that $a^0_\theta = \left(p^{(\theta)}_{m+2,m+1}\right)^0$, $b^0_\theta = \left(p^{(\theta)}_{m+1,m+2}\right)^0$, and $a^0_\theta b^0_\theta = 1$.

We write $2\eta_1^{(\theta)}$ as

$$\begin{aligned} 2\eta_1^{(\theta)} &= \left(b_\theta^0 \nabla_x^0 p_{m+2,m+1}^{(\theta)} - a_\theta^0 \nabla_x^0 p_{m+1,m+2}^{(\theta)}\right) \cdot \widetilde{v}^{(\theta)} \\ &= \sum_{i=1}^{m+2} \left[b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_i}^0 - a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_i}^0 \right] \widetilde{v}_i^{(\theta)} \end{aligned}$$

and define

$$\alpha_{i,j,k} = \left(p_{j,i}^{(\theta)}\right)^0 + \sum_{k=1}^{m} \left(p_{j,k}^{(\theta)}\right)_{x_i}^0 \tau_k. \tag{D.13}$$

We then expand $b_\theta^0 \widetilde{\mu}_1^{(2\theta)}$ and relate it to $2\eta_1^{(\theta)}$:

$$\begin{aligned} b_\theta^0 \widetilde{\mu}_1^{(2\theta)} &= \left(\nabla_x^0 p_{m+2,m+2}^{(2\theta)} - \nabla_x^0 p_{m+1,m+1}^{(2\theta)}\right) \cdot \frac{v^{(\theta)} - \widetilde{v}^{(\theta)}}{2} \\ &= b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_{m+2}}^0 - a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_{m+2}}^0 \\ &\quad + \sum_{i=1}^{m+1} \left[a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_i}^0 - b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_i}^0 \right] \frac{v_i^{(\theta)} - \widetilde{v}_i^{(\theta)}}{2} \\ &\quad + \sum_{i=1}^{m+1} \frac{v_i^{(\theta)} - \widetilde{v}_i^{(\theta)}}{2} \sum_{j=1}^{m} \alpha_{i,j,k} \left(b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_j}^0 - a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_j}^0 \right) \\ &= 2\eta_1^{(\theta)} - \sum_{i=1}^{m+1} \left[b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_i}^0 - a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_i}^0 \right] \widetilde{v}_i^{(\theta)} \\ &\quad + \sum_{i=1}^{m+1} \left[a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_i}^0 - b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_i}^0 \right] \frac{v_i^{(\theta)} - \widetilde{v}_i^{(\theta)}}{2} \\ &\quad + \sum_{i=1}^{m+1} \frac{v_i^{(\theta)} - \widetilde{v}_i^{(\theta)}}{2} \sum_{j=1}^{m} \alpha_{i,j,k} \left(b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_j}^0 - a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_j}^0 \right) \\ &= 2\eta_1^{(\theta)} + \sum_{i=1}^{m+1} \left[a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_i}^0 - b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_i}^0 \right] \frac{v_i^{(\theta)} + \widetilde{v}_i^{(\theta)}}{2} \\ &\quad + \sum_{i=1}^{m+1} \frac{v_i^{(\theta)} - \widetilde{v}_i^{(\theta)}}{2} \sum_{j=1}^{m} \alpha_{i,j,k} \left(b_\theta^0 \left(p_{m+2,m+1}^{(\theta)}\right)_{x_j}^0 - a_\theta^0 \left(p_{m+1,m+2}^{(\theta)}\right)_{x_j}^0 \right). \end{aligned}$$

Thus, if one can prove that

$$\sum_{i=1}^{m+1} \left[a_\theta^0 \left(p_{m+1,m+2}^{(\theta)} \right)_{x_i}^0 - b_\theta^0 \left(p_{m+2,m+1}^{(\theta)} \right)_{x_i}^0 \right] \frac{v_i^{(\theta)} + \widetilde{v}_i^{(\theta)}}{2} + \sum_{i=1}^{m+1} \frac{v_i^{(\theta)} - \widetilde{v}_i^{(\theta)}}{2} \sum_{j=1}^{m} \alpha_{i,j,k} \left(b_\theta^0 \left(p_{m+2,m+1}^{(\theta)} \right)_{x_j}^0 - a_\theta^0 \left(p_{m+1,m+2}^{(\theta)} \right)_{x_j}^0 \right) = 0$$

(where $\alpha_{i,j,k}$ is defined in (D.13)) by finding and substituting in the forms of $v_i^{(\theta)}$ and $\widetilde{v}_i^{(\theta)}$, then $b_\theta^0 \widetilde{\mu}_1^{(2\theta)} = 2\eta_1^{(\theta)}$ and the dynamic dichotomy conjecture in Section 5.4 holds.

References

[1] Ackleh, Azmy S., Jim M. Cushing, and Paul L. Salceanu. On the dynamics of evolutionary competition models. *Natural Resource Modeling*, 28(4):380–397, 2015.

[2] Assas, Laila, Saber Elaydi, Eddy Kwessi, George Livadiotis, and David Ribble. Hierarchical competition models with Allee effects. *Journal of Biological Dynamics*, 9(sup1):32–44, 2015.

[3] Berman, Abraham and Robert J Plemmons. *Nonnegative matrices in the mathematical sciences.* SIAM, 1994.

[4] Caswell, Hal. *Matrix Population Models: Construction, Analysis, and Interpretation.* Sinauer Associates, 2nd edition, 2001.

[5] Chow, Yunshyong and Sophia Jang. Multiple attractors in a Leslie-Gower competition system with Allee effects. *Journal of Difference Equations and Applications*, 20(2):169–187, 2014.

[6] Cushing, Jim M. Two species competition in a periodic environment. *Journal of Mathematical Biology*, 10(4):385–400, 1980.

[7] Cushing, Jim M. *An Introduction to Structured Population Dynamics.* CBMS-NSF Regional Conference Series in Applied Mathematics. Society for Industrial and Applied Mathematics, Philadelphia, 1998.

[8] Cushing, Jim M. Three stage semelparous Leslie models. *Journal of Mathematical Biology*, 29(1):75–104, 2009.

[9] Cushing, Jim M. A bifurcation theorem for Darwinian matrix models. *Nonlinear Studies*, 17(1):1–13, 2010.

[10] Cushing, Jim M, Shandelle M Henson, and Lih-ing Roeger. Coexistence of competing juvenile-adult structured populations. *Journal of Biological Dynamics*, 1(2):201–231, 2007.

[11] Cushing, Jim M., Sheree Levarge, Nakul Chitnis, and Shandelle M. Henson. Some discrete competition models and the competitive exclusion principle. *Journal of Difference Equations and Applications*, 10(13–15):1139–1151, 2004.

[12] Cushing, Jim M. and Simon Maccracken Stump. Darwinian dynamics of a juvenile-adult model. *Mathematical Biosciences and Engineering*, 10(4):1017–1044, 2013.

[13] Ebenman, Bo. Niche differences between age classes and intraspecific competition in age-structured populations. *Journal of Theoretical Biology*, 124(1):25–33, 1987.

[14] Edmunds, Jeffrey. *A study of a stage-structured model of two competing species.* PhD thesis, The University of Arizona, 2001.

[15] Edmunds, Jeffrey, J.M. Cushing, R.F. Costantino, Shandelle M. Henson, Brian Dennis, and R.A. Desharnais. Park's tribolium competition experiments: a non-equilibrium species coexistence hypothesis. *Journal of Animal Ecology*, 72(5):703–712, 2003.

[16] Elaydi, Saber. *An Introduction to Difference Equations.* Undergraduate Texts in Mathematics. Springer-Verlag New York, 2005.

[17] Feigenbaum, Mitchell J. Quantitative universality for a class of nonlinear transformations. *Journal of Statistical Physics*, 19(1):25–52, 1978.

[18] Fiedler, Miroslav. *Special Matrices and Their Applications in Numerical Mathematics.* Dover Publications, Inc., Mineola, NY, 2nd edition, 2008.

[19] Guckenheimer, John and Philip Holmes. *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields.* Applied Mathematical Sciences. Springer New York, 2002.

[20] Horn, Roger A. and Charles R. Johnson. *Matrix Analysis.* Cambridge University Press, 2nd edition, 2012.

[21] Kang, Yun. Scramble competitions can rescue endangered species subject to strong Allee effects. *Mathematical Biosciences*, 241(1):75–87, 2013.

[22] Kang, Yun. Dynamics of a generalized Ricker-Beverton-Holt competition model subject to Allee effects. *Journal of Difference Equations and Applications*, 22(5):687–723, 2016.

[23] Kapçak, S., S. Elaydi, and Ü. Ufuktepe. Stability of a predator-prey model with refuge effect. *Journal of Difference Equations and Applications*, 22(7):989–1004, 2016.

[24] Kato, Tosio. *Perturbation Theory for Linear Operators*. Springer-Verlag, Berlin, 1966.

[25] Kato, Tosio. *A Short Introduction to Perturbation Theory for Linear Operators*. Springer-Verlag, New York, 1982.

[26] Kielhöfer, Hansjörg. *Bifurcation Theory: An Introduction with Applications to Partial Differential Equations*. Springer Science+Business Media, LLC, 2nd edition, 2012.

[27] Kon, Ryusuke. Nonexistence of synchronous orbits and class coexistence in matrix population models. *SIAM Journal on Applied Mathematics*, 66(2):616–626, 2005.

[28] Kon, Ryusuke. Non-synchronous oscillations in four-dimensional nonlinear semelparous Leslie matrix models. *Journal of Difference Equations and Applications*, preprint.

[29] Liu, Pingzhou and Saber N. Elaydi. Discrete competitive and cooperative models of Lotka-Volterra type. *Journal of Computational Analysis and Applications*, 3(1):53–73, 2001.

[30] Livadiotis, G., L. Assas, B. Dennis, S. Elaydi, and E. Kwessi. A discrete-time host-parasitoid model with an Allee effect. *Journal of Biological Dynamics*, 9(1):34–51, 2015.

[31] Livadiotis, G., L. Assas, S. Elaydi, E. Kwessi, and D. Ribble. Competition models with Allee effects. *Journal of Difference Equations and Applications*, 20(8):1127–1151, 2014.

[32] Livadiotis, G. and Saber Elaydi. General Allee effect in two-species population biology. *Journal of Biological Dynamics*, 6(2):959–973, 2012.

[33] Lotka, Alfred J. *Elements of Physical Biology.* Williams & Wilkins Company, Baltimore, 1925.

[34] Marden, Morris. *The Geometry of the Zeros of a Polynomial in a Complex Variable*, volume 3 of *Mathematical Surveys.* American Mathematical Society, New York, 1949.

[35] Munkres, James R. *Analysis on Manifolds.* Addison-Wesley, Reading, MA, 1991.

[36] Rael, R.C., T.L. Vincent, and Jim M. Cushing. Competitive outcomes changed by evolution. *Journal of Biological Dynamics*, 5(3):227–252, 2011.

[37] Serre, Denis. *Matrices: Theory and Applications.* Springer-Verlag, New York, 2nd edition, 2010.

[38] Takeuchi, Yasuhiro and Zhengyi Lu. Permanence and global stability for competitive Lotka-Volterra diffusion systems. *Nonlinear Analysis: Theory, Methods & Applications*, 24(1):91–104, 1995.

[39] Volterra, Vito. *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi.* C. Ferrari, 1927.

[40] Werner, Earl E. and James F. Gilliam. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, 15(1):393–425, 1984.