Using Transfer Function Analysis in Modelling Biological Invasions

Submitted by

Hanan Ali Dreiwi

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..............................

Hanan Ali Dreiwi
To My Mother Fatma, My Father Ali, and My Husband Aiman
Abstract

This thesis is made up of seven chapters and two appendices. Chapter 1 provides an introduction whilst Chapter 7 offers a conclusion. In Chapter 2 we provide preliminaries on population projection models and robustness analysis. In Chapter 3 we introduce a stage-structured model in a context of biological invasions. Using a Transfer Function Approach, we provide a detailed analysis of the invasion model where the existence and local stability of all possible equilibria are characterised in terms of the underlying parameters of the model. In Chapter 4 a Lyapunov function approach is used to estimate the basin of attraction for each equilibrium. In Chapter 5 harvesting is incorporated into the model and we specifically examine the effect of harvesting on whether one or both of the species are eliminated. In Chapter 6 we introduce a novel technique to measure the possibility of invasion in non-normal systems where the traditional invasion exponent technique is unreliable.
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CONTENTS

3.2 The Extended Model ........................................................................... 35
  3.2.1 Conditions for Existence of Equilibria ........................................... 38
  3.2.2 Conditions for the Local Stability of Equilibria .............................. 39
3.3 A $2 \times 2$ Example ............................................................................ 53
3.4 Examples .................................................................................................. 57
  3.4.1 $2 \times 2$ Numerical Examples .......................................................... 57
  3.4.2 A $5 \times 5$ Numerical Examples ....................................................... 68
3.5 Conclusion ............................................................................................... 77

4 Basins of Attraction of Non-zero Equilibria ........................................... 79
  4.1 Introduction ........................................................................................... 79
  4.2 Global Asymptotic Stability, Basin of Attraction and Lyapunov Analysis .................................................. 80
    4.2.1 A Lyapunov Function Approach ..................................................... 80
  4.3 The Basins of Attraction of inclusive and Coexistence Equilibria .......... 84
    4.3.1 Preliminaries ................................................................................... 84
    4.3.2 Main Theorem ............................................................................... 92
    4.3.3 Examples ........................................................................................ 95
  4.4 Conclusion .............................................................................................. 99

5 Harvesting Efforts ..................................................................................... 100
  5.1 Introduction ........................................................................................... 100
  5.2 Harvesting a Single Population ............................................................. 101
    5.2.1 Examples ....................................................................................... 108
  5.3 Harvesting Effort in a Resident-Invader System ..................................... 113
    5.3.1 Harvesting State ............................................................................. 114
    5.3.2 Examples ....................................................................................... 118
List of Figures

3.1 The orange area represents the region for the coexistence equilibrium $\alpha c < 0.07778 < c$ and $c < 0.7778 < \alpha c$, while the bottom orange region $c < 0.7778 < \alpha c$ represents the stable region of the coexistence equilibrium. The left green region together with the top orange region $0 < c < 0.7778$ is the stable region for the resident-only equilibrium where the resident wins. The right green region $\alpha c > 0.7778$ represents the stability region of the invader-only type equilibrium where the invader wins.

3.2 This figure shows, in the case when $c = c'$, the effect of $c$ becoming negligible so that only $\alpha$ has an effect on the coexistence equilibrium, $c$ does not have any effect on the dynamics. The value of $\alpha$ itself makes a difference where $\alpha = 0.7778$ is a threshold: there is coexistence when $\alpha < 0.7778$ and the invader wins otherwise.
3.3 In this example $c' = 1$, $\beta = 1$. The coexistence equilibrium exists in the region $\alpha c < 0.3174 < c$ and $c < 0.3174 < \alpha c$. However the region $c < 0.3174 < \alpha c$ is dynamically unstable which means one of the phenotype will win while when $\alpha c < 0.3174 < c$ the coexistence solution is stable. Similarly the stability region of the $x$-axis equilibrium, which means the resident type wins, is the region when $c < 0.3174$ while the stability region of the $z$-axis equilibrium, which means the invader type will win, is when $\alpha c > 0.3174$. 

3.4 The graph shows the region of existence for the coexistence equilibrium is $\alpha c < 0.6668 < c$ or $c < 0.6668 < \alpha c$. The the stability of the coexistence equilibrium is $\alpha c < 0.6668 < c$. Similarly the stability region of the $x$-axis equilibrium, which means the resident type wins, is the region when $c < 0.6668$, while the stability region of the $z$-axis equilibrium, which means the invader type will win, is when $\alpha + c > 0.6668$.

3.5 Figures (1), (2) shows the root locus of $(x^*, 0)$ equilibrium inside the unit circle, as (1) gives the root locus graph before adding the range of $k$ and (2) gives the graph with the range of $k$.

3.6 (1), (2) shows the root locus of $(x^*, 0)$ equilibrium inside the unit circle, as (1) gives the root locus graph before adding the range of $k$ and (b) gives the graph with the range of $k$.

3.7 (1), (2) shows the root locus of $(x^*, 0)$ equilibrium inside the unit circle, as (1) gives the root locus graph before adding the range of $k$ and (b) gives the graph with the range of $(k)$. 

5.1 The blue line shows the non-linear function \( yf(y) = \frac{(8+y)y}{1+y} \), the line with slope \( f_0 = 8 \) is in green and the line with slope \( f_\infty = 1 \) is in red. ............................................................ 103

5.2 This graph depicts the region in the harvesting parameter space for which we have extinction \( x(t) \to 0 \), explosion \( x(t) \to \infty \) or convergence to a positive steady state. ............................ 106

5.3 This curve partitions the harvesting values so that either \( x = 0 \) is globally asymptotically stable or there is a positive, globally asymptotically stable equilibrium. In these calculations \( V = 8 \) and \( K = 4 \). ............................................................ 111

5.4 Above the curve the higher harvesting values force the equilibrium \((0,0)\) to be globally asymptotically stable obtained by varying the values of \( h_1 \) and \( h_2 \) between zero and one. Here \( V = 8, K = 14 \). ............................................................ 112

5.5 Above the curve gives the harvesting values which force the resident population \( x(t) \) to tend to zero. ............................................................ 120

5.6 Above the curve gives the harvesting values which force the resident population \( z(t) \) to tend to zero. ............................................................ 121

5.7 Above the curve gives the harvesting values which force the resident population \( x(t) \) to tend to zero. ............................................................ 123

5.8 Above the curve gives the harvesting values which force the resident population \( z(t) \) to tend to zero. ............................................................ 124
6.1 Allee effects. The Allee effect function is $a(N) = \frac{N^{\gamma}_a - 1}{1 + bN^{\delta}_a}$ as a function of invader density with $b = 0.3$ and $\delta = 2.5$. The left graph shows a weak Allee effect with $0.5a(N)$. The right graph represents a strong Allee effect with $1.5a(N)$. . . . . . . . . . . . . . 134

6.2 Invasion exponent predicts successful invasion. The left-hand graph shows the invader growing in density from small density of 0.005, while the one on the right shows the decline of the resident from high density of 1 down to 0. . . . . . . . . . . . . . 137

6.3 Invasion exponent predicts failed invasion. The left-hand graph shows the invader failing to establish from low density, while the right-hand graph shows the resident still at its carrying capacity. 138

6.4 Population densities of resident and invader during a sequence of invasion attempts at times $t = 0, 100, 200, 300, ...$. As time progresses, the Allee effect strength increases. In the left-hand graph, this increasing Allee effect has minimal impact on the invasion and invasion fails. In the graph on the right, as the Allee effect increases, so the invasion becomes more persistent, finally achieving successful invasion. The resident is represented by red solid lines, the invader by black dashed lines. . . . . . . . 141

6.5 The values of $||A^t||_1$ over time for the hypothetical PPM (Left), and the tropical fruit tree PPM (Right). . . . . . . . . . . . . . 145

6.6 We depict the pseudo-spectra of two different PPMs. The left-hard graph shows the pseudo-spectrum of a normal matrix. The right-hard graph shows the pseudo-spectrum of a non-normal matrix . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 149
6.7 Plots of “transient strength” of the invasion demography (x-axis) and minimum strength of Allee effect required for successful invasion (y-axis) for four different measure of non-normality:

Top Left: Non-normality of $A_{inv}$; Top Right: Reactivity of $A_{inv}$; Bottom Left: Population Momentum of $A_{inv}$; Bottom Right: Steady State Gain of $A_{inv}$. Each sub-plot has four different magnitudes of initial density of invader: 5%, 1%, 0.5% and 0.1% of the density of the resident at carrying capacity in the absence of an invader. .......................... 154

6.8 These three plots show the invasion stage specific momentum according to initial invader density. The top plot shows the invasion stage class momentum with initial invader density $\delta(1 0 0)^T$. The middle and the bottom plots show the invasion stage specific momentum with initial invader density at stage two and three, respectively. .......................... 155
List of Tables

A.1 Existence Conditions for the Coexistence Equilibria . . . . . . 174
Glossary

**Vector Multiplication:** If $E$ is $1 \times n$ ($n$ is an integer) row vector and $D$ is an $n \times 1$ column vector, then $ED$ is a scaler and $DE$ is a matrix of order $n \times n$.

**Total population density:** The total population density is the sum of the densities of each stage (exactly the sum of the population individuals). For instance, if a $k$-stage structure vector at time $t$ is given as

\[
 n(t) = \begin{pmatrix}
 n_1(t) \\
 n_2(t) \\
 n_3(t) \\
 \vdots \\
 n_k(t)
\end{pmatrix}
\]

and if $e = (1 \ 1 \ 1 \ \cdots \ 1)$, then the total population density say $N$ can be written as

\[
 N = en = (1 \ 1 \ 1 \ \cdots \ 1) \begin{pmatrix}
 n_1 \\
 n_2 \\
 n_3 \\
 \vdots \\
 n_k
\end{pmatrix}
\]
hence

\[ N = e^T n = n_1 + n_2 + n_3 + \cdots + n_k \]

**Weighted sum density:** The weighted sum density can be defined the same way as in the total sum apart from substituting the vector by any arbitrary one. Generally, the entries of this vector reflect the importance of the corresponding stages. Suppose \( \alpha \) is a row vector such that:

\[ \alpha = (\alpha_1 \alpha_2 \alpha_3 \cdots \alpha_k) \]

where \( \alpha_1 \cdots \alpha_2 > 0 \). Hence, the weighted sum density, say \( N_w \) of the above \( k \)-stage vector \( n(t) \) is

\[ N_w = \alpha^T n = \alpha_1 n_1 + \alpha_2 n_2 + \cdots + \alpha_k n_k \]
Chapter 1

Introduction

1.1 Overview

Invasion processes are widely evident in nature. Native species are continuously threatened by the invasion of exotics and this can adversely affect their persistence and the biodiversity of the habitat they occupy[1]. Invader species can be from within the habitat (e.g. mutants) or can be aliens that by some means reached the ecosystem. In some cases invasion leads to the extinction of the indigenous resident(s) and hence for economically important residents this can have a hugely negative economic impact[2], [3]. On the other hand, it is worth adding that invasion is not always “bad”; in some settings (e.g. some conservation policies) pesticides are introduced in order to eradicate undesirable resident(s)[4].

Extensive research efforts have studied biological invasion[5], [6], [7]. Mathematical models provide an easy, testable framework for understanding invasion processes[5]. As resident and invader species are mostly structured in
stages, sizes, or ages, population projection matrices (PPMs) have became an efficient methodological tool for understanding stage-based invasion models [8], [9]. Caswell [5] is an excellent source of material for understanding how modelling with PPMs can be performed. It provides a comprehensive package on the utility of PPMs in modelling various structured population interactions.

Several methods have been developed to model invasion in stage-structured populations, and to understand how carrying capacity controls the dynamics of the invader [6], [10], [11]. Takada and Nakajima (1992, 1998) used a sensitivity analysis approach to this problem. They proved several theorems that connect the population size at equilibrium with the evolution of the invader phenotype. In this work the effect of density is taken as a weighted sum of the stages.

Encouraged by the work of [6], we use PPMs to study stage-structured resident-invader models. The basic limitations of the results in Takada and Nakajima [6] are that they rely on sensitivity analysis and are concerned with the local information. Here we aim to link Robust Control (a.k.a “Transfer Function Approach”) and the dynamic theory of invasion in ecosystems by introducing and analysing an invasion model. This robust control approach allows us to move away from local results based on sensitivity analysis.

1.2 Literature Review

Recently, population projection matrices have been extensively used as the principle tools for analysing a wide variety of interactions among species. “Ma-
Matrix Population Models” [5] by Hal Caswell is an excellent source that provides a broad framework on utilising matrices in ecological modelling. However, PPM entries are likely mismatched to the real underlying vital rates of species under consideration. Therefore it is important to look at all PPMs with entries near a nominal one, as this will be more informative. Mathematically speaking, we start with a nominal (or estimate) of a PPM, say $A$ and consider a perturbation $A + \Delta$, where $\Delta$ is a matrix of uncertainty levels [12]. Moreover, the matrix $\Delta$ can be purposefully added for particular reasons (conservation, genetic modifications or climate changes). The basic aim of setting a problem in a perturbed form is to understand and quantify the effect of $\Delta$ on the eigendata [5], [12], [13].

Invasion is one biological setting where PPMs can be exploited. Invasion plays a crucial role in structuring ecological systems. Invasive species threaten native biodiversity worldwide - indeed, considerable changes can be caused by the appearance of an exotic species in an otherwise stable ecosystem. The dynamics of biological invasions are influenced by environmental stresses, exploitation, habitat fragmentation and pollution [14]. Testing for patterns from real case studies has led to a potentially fruitful increase in mathematical models of invasion, [15], and modelling of biological invasions has received considerable attention in recent years (see for example [16], [17], [5], [18]).

The key question in invasion modelling is: Can an invasive phenotype be established, or can we characterise when invasion is possible? In addressing this question we must acknowledge that ecological models are simplifications of reality. There are severe problems with data quality and poor parameterisation, resulting in models of invasion processes that are inevitably highly
uncertain. A classical approach to handling model uncertainty in ecological models is to use sensitivity analysis ([5], p.560). In an invasion context, Takada and Nakajima (1992, 1998) use sensitivity analysis applied to stage-structured, density dependent, population projection models to understand the influence of model parameters on coexistence and stability. They connect population size at equilibrium with the possibility of successful invasion by the mutant phenotype. This sensitivity analysis is extended in other work, specifically in [19]. More recently, an alternative to this infinitesimal sensitivity analysis of stage-structured ecological models has emerged. Using ideas from control engineering, Hodgson, Townley et al., (see [20], [13]) have developed “a Transfer Function Approach” which aims to quantify the impact of non-infinitesimal perturbations on the dynamics of ecological models. A key aspect used in this approach is to exploit the high degree of structure in the equations which describe ecological dynamics. This degree of structure is highly prevalent in the analysis of invasion dynamics (see equations (3.2), (3.7), and (3.8)). In this thesis we use a Transfer Function Approach (TFA) [21], [22] to explore the ranges of parameters for which we have exclusive or coexisting equilibria. We also use TFA to determine the stability type of these equilibria by obtaining the non-linear relationship between the magnitude of a perturbation parameter and the eigenvalues of corresponding linearised PPMs. In particular, using this general approach based around transfer functions and uncertain, structurally perturbed models, we are able to understand how the carrying capacity of the resident can control the invasion of the mutant phenotype. We compare our results with those of Takada and Nakajima (1992, 1988), to demonstrate the utility of the transfer.
1.2.1 Mutation and Biological invasion

In biology, the invasion phenomena is very vast and often challenging. Broadly speaking biological invasion is the appearance of new (referred as alien/exotic) species in the ecosystem. This new species will generally affect (positively or negatively) the existence and the persistence of the resident species [23]. In the existence literatures, mutation-a developing of a new species from the resident as a result of certain genetic alterations, is often considered as a form of biological invasion. However, the biological invasion and mutation are a completely different biological phenomena and this assumption is conceptionally wrong. Mutants usually carry almost the same vital rates as the resident phenotype whereas in the case of biological invasion the invaders and the resident are almost have completely different vital rates. It is worth to mention here that, in the context of mathematical modelling, they are treated as they are the same, simply because in both cases a new dynamics is introduced to the system and this, often, is misleading.

Throughout this thesis we considered a model of biological invasion. Mutation, will be a particular case when we restrict the parameter values of the model as we shall see later.

1.3 Key Contributions of the Thesis

In Chapter 3 we introduce a structured model of invasion. Transfer functions are utilised to fully analyse the local stability properties of all possible equilibria. We show the advantages of this approach in analysing invasion in comparison to other approaches found in the literature, namely sensitivity analysis. Chapter 4 is essentially a complementary analysis of Chapter 3 where
the basin of attraction of each equilibrium has been estimated using the Lyapunov function technique. The findings are summarised in Subsection 4.3.2.

In Chapter 5 a harvesting effect has been incorporated in both the resident and invader dynamics. The key result can be found in Section 5.3. It has been shown that stability properties can be controlled by tuning the harvesting effort. Our main result in Chapter 6 is to introduce a new indicator for predicting invasion, namely the invader momentum that can be found in (6.4) and summarised in Figure 6.7 [24].
Chapter 2

Preliminaries

In this chapter we will present background materials which are used throughout the thesis. Other preliminary material specific to particular chapters is dealt with as and when relevant.

2.1 Population projection matrices (PPMs)

Population projection matrices are essentially an elegant way to summarise species life cycles. PPM entries capture the transition rates per unit time. They are non-negative. The eigendata (eigenvalues and eigenvectors) of such matrices provide important information about the behaviour of modelled populations [5]. Here we will give some insight on how models which are based on PPMs are constructed. For simplicity we will consider the case of age-structured models. Following [5], the species of interest is divided into $n$ age...
classes. Following [5] the density of each age class is augmented in a vector as

\[
x(t) = \begin{pmatrix}
x_1(t) \\
x_2(t) \\
x_3(t) \\
\vdots \\
x_n(t)
\end{pmatrix}
\]

where \( x_i, i \in 1, \ldots, n \), is the density of age class \( i \). The density of the first age class after one time step can be written as

\[
x_1(t + 1) = f_0 x_0(t) + f_1 x_1(t) + \ldots + f_n x_n(t)
\]

and for an age class \( i \geq 2 \) we can have

\[
x_i(t + 1) = s_{i-1} x_{i-1}(t + 1)
\]

Here \( f_i, \ i \in 1, \ldots, n \) are the fecundities of the each stage and \( s_i, \ i \in 1, \ldots, n - 1 \) are the survival rate of each age. For all age classes the above descriptions can be summarised as

\[
\begin{pmatrix}
x_1 \\
x_2 \\
x_3 \\
\vdots \\
x_n
\end{pmatrix}
(t + 1) =
\begin{pmatrix}
f_1 & f_2 & f_3 & \cdots & f_n \\
s_1 & 0 & 0 & \cdots & 0 \\
0 & \ddots & 0 & \cdots & 0 \\
\vdots & \vdots & \ddots & \ddots & \vdots \\
0 & \cdots & 0 & s_{n-1} & 0
\end{pmatrix}
\begin{pmatrix}
x_1 \\
x_2 \\
x_3 \\
\vdots \\
x_n
\end{pmatrix}
(t)
\]

where the matrix on the right hand side is known as the PPM of the species.
Definition 2.1.1 (Positive matrices). A matrix is positive (non-negative) if all its entries are positive (non-negative).

Definition 2.1.2 (Irreducible matrix).\footnote{25} A square $n \times n$ matrix $A$ is reducible if either:

1. $n = 1$ and $A = 0$ or;

2. $n \geq 2$ and there is an $n \times n$ permutation matrix $P$ and an integer $r$, with $1 \leq r \leq n - 1$ such that:

$$P^T AP = \begin{bmatrix} B & C \\ 0 & D \end{bmatrix}$$

where $B$ is $r \times r$ matrix, $D$ is $(n-r) \times (n-r)$ matrix, $C$ is $r \times (n-r)$ matrix, and $0$ is a zero matrix with order $(n-r) \times r$.

If $A$ is not reducible then it is called irreducible. In the context of life cycle graphs, irreducibility refers to the situation where every pair of nodes can be connected by a path.\footnote{25} A life cycle graph is a graph consisting of node(s) and path(s) connecting them. Each node represents a stage or age class of the population and the paths refer to the transition between stages or ages.

Definition 2.1.3 (Primitive matrices).\footnote{25} An irreducible non-negative matrix $A$ is primitive if there exists a positive number $k$ such that

$$A^k > 0.$$ 

Definition 2.1.4 (Positive definite matrices).\footnote{25} A symmetric matrix $P$ is positive definite (positive semi definite) if all its eigenvalue are positive.
Chapter 2. Preliminaries

A matrix $P$ is called

Theorem 2.1.1 (Perron-Frobenius Theorem). Let $A$ be a non-negative and irreducible matrix. If $\lambda_{\text{max}}$ is the dominant eigenvalue of $A$ (i.e. the eigenvalue of largest modulus), then

1. $\lambda_{\text{max}}(A) > 0$

2. The right and left eigenvectors are positive.

3. $\lambda_{\text{max}}$ is simple and unique.


2.1.1 Perturbations

In our context, PPMs are good predictors if their entries are finely estimated in a very controlled circumstances. Unfortunately this is not always the case as there are usually errors associated with estimating the vital rates. Henceforth, using matrix perturbation theory will be so natural. Perturbing a PPM is simply the changing one or more of its entries. In general, there are several reasons that may cause these changes such as conservation efforts, genetic modification or climate changes [12] [13].

We will write

$$A \rightarrow A + P,$$

where $P$ is the perturbation matrix [12]. The structure of the perturbation matrix $P$ is crucial and determines which element(s) are uncertain or to be perturbed. For instance $P = \delta DE$, where $\delta$ is scalar (the magnitude of
the perturbation) and \( D, E \) are column and row vectors, represents a single parameter perturbation, rank one perturbation. Here, the matrix \( DE \) (see the Glossary) can be used to target a specific entry of \( A \) that are desired for perturbation. If we want to change different elements of \( A \) with different amounts \( P \) can be written as:

\[
P = \sum_{j=1}^{l} \delta_j \left( \sum_{i=1}^{k_j} D^i_j E^j_i \right),
\]

where \( \delta_j, j \in \{1, \ldots, l\} \) are perturbation magnitudes and each of \( \delta_j D^i_j E^j_i \) is a rank one perturbation.

**Example 2.1.1.** Consider the structure

\[
A + 3.4 D_1 E_1 + 0.05 D_2 E_2,
\]

where

\[
A = \begin{bmatrix}
0 & 0 & 15 & 16 & 17 \\
0.0131 & 0 & 0 & 0 & 0 \\
0 & 0.8 & 0 & 0.2 & 0 \\
0 & 0 & 0.7896 & 0 & 0 \\
0 & 0 & 0 & 0.6728 & 0
\end{bmatrix},
\]

with structured matrices

\[
E_1 = \begin{bmatrix}
0 & 0 & 1 & 0 & 0
\end{bmatrix}, \quad E_2 = \begin{bmatrix}
0 & 1 & 0 & -1 & 0
\end{bmatrix};
\]
\[ D_1 = \begin{bmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \quad D_2 = \begin{bmatrix} 1 \\ -1 \\ 0 \\ 1 \\ 0 \end{bmatrix} \]

We can write

\[ \delta_1 D_1 E_1 + \delta_2 D_2 E_2 = 3.4 \begin{bmatrix} 1 \\ 0 \\ 0 \\ 0 \end{bmatrix} + 0.05 \begin{bmatrix} 0 \\ 1 \\ 0 \\ -1 \\ 0 \end{bmatrix} \]

\[ \begin{bmatrix} 0 & 0.05 & 3.4 & -0.05 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & -0.05 & 0 & -0.05 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0.05 & 0 & -0.05 & 0 \end{bmatrix} \]

Hence this perturbation hits the elements: (1, 2), (1, 3), (1, 4), (3, 2), (3, 4), (5, 2) and (5, 4). Now we have

\[ A + 3.4 D_1 E_1 + 0.05 D_2 E_2 = \begin{bmatrix} 0 & 0.05 & 18.4 & 15.95 & 17 \\ 0.0131 & 0 & 0 & 0 & 0 \\ 0 & 0.75 & 0 & 0.15 & 0 \\ 0 & 0 & 0.7896 & 0 & 0 \\ 0 & 0.05 & 0 & 0.6228 & 0 \end{bmatrix} \]
2.2 A Robustness Tool: Transfer Function (TF)

A system, or more precisely a property of it, is said to be robust if it has the capability to ignore any perturbations it might be affected by, that is the property holds in spite of the perturbations. A focus for robustness analysis is the robustness of stability of a system. The literature is rich with various types of tools for analysing robustness of systems stability see [12], and the numerous references therein. Amongst numerous tool, sensitivity, spectral values sets and stability radii are very common and useful indicators of systems stability robustness. They are essentially different approaches for testing the locations of system eigendata. Throughout this work we will use transfer function as the main device to study robustness. One of the characteristics of transfer functions is that they precisely capture the actual relationship between perturbation magnitude and eigendata.

For the sake of illustration lets consider the simple case of a system

\[ x(t + 1) = (A + \delta DE)x(t) \] (2.1)

perturbed by a rank one perturbation \( P = \delta DE \) where \( E \) is a row and \( D \) is a column. If \( \lambda \) is an eigenvalue of \( A + \delta DE \) with corresponding eigenvector \( v \), then we will have

\[ \lambda v = (A + \delta DE)v \]

Rearranging terms we get

\[ (\lambda I - A)v = \delta DEv \]
Assuming that $\lambda$ is not an eigenvalue of $A$ then

$$v = \delta(\lambda I - A)^{-1}DEv$$

Multiplying both sides by $E$ and dividing by $Ev$ ($Ev$ cannot be zero since $v$ would be too) we will have

$$1 = \delta E(\lambda I - A)^{-1}D$$

(2.2)

Hence

$$\delta = \frac{1}{E(\lambda I - A)^{-1}D} := \frac{1}{G_{ED}(\lambda)}.$$ 

$G_{ED}(\lambda)$ is the transfer function which captures the relationship between the perturbation $\delta$ and the eigenvalue of the perturbed system $\lambda$. In other words, a desired $\lambda^*$ can be achieved by perturbing the system with $\delta^*$ obtained by solving (2.2) so that

$$\delta^* = \frac{1}{G_{ED}(\lambda^*)}.$$ 

**Example 2.2.2.** Assume the system (2.1) with $A, D_1$ and $E_1$ stated in the example (2.1.1). In this example $\lambda_{\text{max}}(A) = 0.8355$. Here we can calculate the perturbation $\delta$ needed to achieve $\lambda_{\text{max}}(A) = 1$ using the transfer function $G_{D_1E_1}(1)$ as follows:

$$G_{D_1E_1}(1) = E_1(I - A)^{-1}D_1 = 0.0229$$

and the value of $\delta$ needed to have $\lambda_{\text{max}} = 1$ is:

$$\delta = \frac{1}{E(I - A)^{-1}D} = \frac{1}{0.0229} = 43.6864$$
CHAPTER 2. PRELIMINARIES

The next formula is usually utilised to expand the expression \((\lambda I - A - P)^{-1}\) for complicated perturbation structures.

### 2.3 The Sherman-Morrison-Woodbury Formula

The Sherman-Morrison-Woodbury Formula \([26]\) is primarily introduced as a way of getting around the possible cumbersome computation efforts which may be faced as one determines the value of the resolvent \((\lambda I - A - P)^{-1}\) when \(P\) is a perturbation. Once the inverse of the matrix is computed then all the rest will be a usual matrix multiplication which is much easier to conduct.

For an invertible matrix \(A\) and any dimensionally compatible matrices \(U\) and \(V\) the formula reads

\[
(M + UV)^{-1} = M^{-1} - (M^{-1}U(I + VM^{-1}U)^{-1}VM^{-1})
\]  
(2.3)

For more illustration we choose the values \(M, U\) and \(V\) such that:

\(M = I - A\), \(U = -D\) and \(V = \delta E\) then we have:

\[
(I - A - \delta DE)^{-1} = (I - A)^{-1} + \delta(I - A)^{-1}D \left(1 - \delta E(I - A)^{-1}D\right)^{-1} E(I - A)^{-1}
\]
Chapter 3

Invasion Models

3.1 Introduction

Several methods have been developed to model invasion in stage structured populations, and to understand how density dependence controls the dynamics of the invading population [6], [27]. The aim of this chapter is to apply robustness tools on a particular invasion model. We illustrate and compare the obtained results with a classical research approach of sensitivity analysis (see [28]). Takada and Nakajima (1992, 1998) [10], [6] have applied the sensitivity analysis approach to analyse an invasion model. They have proved several theorems that connect the population size at equilibrium with the evolution of the invading population.

In this chapter we re-examine the general case of Takada’s model by using a Transfer function approach and show how we have obtained the same results but in a more flexible way by utilising a more extended model. Before we introduce the more extended model, we give a brief description of
the approach adopted, and results obtained, by Takada-Nakajima (1992, 1998; related earlier applications can be found Hastings 1978 and Charlesworth 1980) [29], [30]. Suppose that the population dynamics of the resident and wild-mutant are given by:

\[
\begin{align*}
  n_{t+1} &= L(N_t)n_t \\
  n'_{t+1} &= L'(N_t)n'_t
\end{align*}
\]

(3.1)

under the following assumptions:

1. \(n'_t\) and \(n_t\) are the stage class vectors of the mutant and the resident respectively at time \(t\).

2. \(L(N_t)\) and \(L'(N_t^1)\) are the density dependent PPMs of the resident and the mutant individuals respectively.

3. The difference between \(L(N_t)\) and \(L'(N_t^1)\) is assumed to be sufficiently small. So this paper is concerned more with mutation than biological invasion.

4. The resident is supposed to be at (or near to) carrying capacity so the the total population \(N_t\) of the resident described as \(N_t = N^*\). This means that the dominant eigenvalue of the matrix \(L(N^*)\) is equal to one.

5. \(N_t^1\) is the total population density of the mutant-type.

6. The density \(N_t\) is the weighted sum of the population densities at each stage. That is

\[
N_t = \sum_{i=1}^{s} w_i n_{it}
\]
where \(s\) is the number of stage classes, \(n_i\) is the population density of stage class \(i\), and \(w_i\) determine the contribution of \(n_i\) (For more details see the Glossary).

We can summarise the results obtained in the Takada et. al. as follows:

1. Sensitivity of the dominant eigenvalue at equilibrium has to be positive in order to have an invasion (\(\delta \lambda > 0\)).

2. Invadability and the increase of the weighted sum at equilibrium are equivalent under certain conditions.

3. Sensitivity of the dominant eigenvalue is linearly dependent on the sensitivity for the weighted sum at equilibrium.

4. Coexistence occurs only when both the mutant and the resident have different weighted sums, i.e. if \(N_i\) is the resident type density, and \(N_i^1\) is the mutant type density. Then

\[
N_t = wn_t + w'n_t',
\]

\[
N_t^1 = vn_t + v'n_t'
\]

where \(w, w', v, \) and \(v'\) are row vectors and represent the weight of each class of \(n_t\) and \(n_t'\) and \(w\) and \(v\) and \(w'\) and \(v'\) cannot both be equal.

The approach adopted in these papers is reliant on sensitivity analysis. Hence all the above results hold when the difference between \(L(N_t)\) and \(L'(N_t^1)\) is sufficiently small. However this is not always the case in nature. More recently, an alternative to this infinitesimal sensitivity analysis of stage-structured ecological models has emerged. Using ideas from control engineering, Hodgson,
Townley have developed a “transfer function approach” (TFA) which aims to quantify the impact of non-infinitesimal perturbations on the dynamics of ecological models. A key aspect used in this approach is to exploit the high degree of structure in the equations which describe ecological dynamics.

As we will see in the ensuing analysis, this degree of structure is highly prevalent in the analysis of invasion dynamics (see, for example, equations and ). We will use TFA to explore the ranges of parameters for which we have exclusive or coexisting equilibria. We also use TFA to determine the stability type of these equilibria by obtaining the non-linear relationship between the magnitude of a perturbation parameter and the eigenvalues of corresponding linearised PPMs. In particular, using this general approach based around transfer functions and uncertain, structurally perturbed models, we are able to understand how carrying capacity of the resident can control the invasion of the mutant population. We compare our results with those of Takada et. al., to demonstrate the utility of the transfer function approach.

3.2 The Extended Model

To overcome the limitations discussed above we first introduce a more general, extended model. Consider a discrete-time, non-linear system of coupled resident-invader:

\[
x(t + 1) = (A + f(M(t))DE)x(t)
\]

\[
z(t + 1) = (A + pBC + g(N(t))DE)z(t)
\]
We make the following assumptions:

1. The dynamics of both resident and invader are stage-structured and density dependent. The population structures at time $t$ of the resident and the invader are described by $x(t)$ and $z(t)$ respectively.

2. The dominant eigenvalue of the matrix $A$ is less than 1 i.e. $\lambda_{\text{max}}(A) < 1$.

3. $M(t)$ represents the contribution made by population density to the resident dynamics and $N(t)$ is the contribution of population density to invader dynamics. Following Takada and co-workers, we assume weighted sum contributions

$$M(t) = |x|_1 + \alpha |z|_1, \quad \alpha > 0$$

$$N(t) = |x|_1 + \beta |z|_1, \quad \beta > 0$$

4. $D$ and $B$ are column vectors, and $E$ and $C$ are row vectors and determine how density dependence and parameters arise as structured uncertainty in the model.

5. The functions $f$ and $g$ are non-negative density dependent, decreasing functions affecting (for simplicity) the same entry in the resident and invader PPMs, as captured by the matrix $DE$.

6. The perturbation parameter $p$ affects entries of the invader PPM, as captured by $BC$, and describes the difference in demography between the resident and the invader. In contrast to the sensitivity approach, $p$ need not be small.
We are seeking conditions so that the coupled system has a co-existing equilibrium \((x', z')\). At equilibrium:

\[
x' = (A + f(M^*)DE)x'
\]

and

\[
z' = (A + pBC + g(N^*)DE)z'
\]

where

\[
M^* = |x'|_1 + \alpha|z'|_1, \quad N^* = |x'|_1 + \beta|z'|_1
\]

Analysing these equations at equilibrium, by exploiting the algebraic structure, we find that:

\[
f(M^*) = f^* = \frac{1}{G_{ED}} \quad (3.3)
\]

where \(G_{ED} = E(I - A)^{-1}D\), and

\[
g(N^*) = g^* = \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} \quad (3.4)
\]

The population densities at equilibrium can be calculated from the previous formula as follows:

\[
M^* = f^{-1}(f^*), \quad N^* = g^{-1}(g^*)
\]

The equilibrium stage structure of the resident is then given by:

\[
x' = \frac{1}{\beta - \alpha} \left( \beta f^{-1}(f^*) - \alpha g^{-1}(g^*) \right) U(I - A)^{-1}D \quad (3.5)
\]
where
\[ U(I-A)^{-1}D = \frac{(I - A)^{-1}D}{||(I - A)^{-1}D||} \]

For the invader we have
\[ z' = \frac{1}{\alpha - \beta} \left( f^{-1}(f^*) - g^{-1}(g^*) \right) U(I-A-pBC)^{-1}D \quad (3.6) \]

where
\[ U(I-A-pBC)^{-1}D = \frac{(I - A - pBC)^{-1}D}{||(I - A - pBC)^{-1}D||} \]

There are four types of equilibria:

- The extinction state equilibrium \((0, 0)\);
- \(x\) - axis or marginal equilibrium \((x^*, 0)\) - where the wild type displaces the mutant type;
- \(z\) - axis or marginal equilibrium \((0, z^*)\) - where the invader type becomes established and the wild type extinct;
- Coexistence equilibrium \((x', z')\) with \(x', z' > 0\) - we are especially interested in this equilibrium, which is achieved when the formulas for \(x'\) and \(z'\) yield positive vectors and the resident and invader can coexist.

### 3.2.1 Conditions for Existence of Equilibria

**Theorem 3.2.2.** Consider the coupled resident-invader system \([3,2]\). Then the existence region of equilibria are:

1. \((0, 0)\) : always exists.
2. \((x^*, 0)\): the existence condition of this equilibrium is

\[ f^{-1}(f^*) > 0 \]

3. \((0, z^*)\): the existence condition of this equilibrium is

\[ g^{-1}(g^*) > 0 \]

4. \((x', z')\): we obtain two conditions which ensure we have a coexistence equilibrium:

\[
\frac{\alpha}{\beta} < \frac{f^{-1}(f^*)}{g^{-1}(g^*)} < 1 \quad \text{or} \quad 1 < \frac{f^{-1}(f^*)}{g^{-1}(g^*)} < \frac{\alpha}{\beta}
\]

**Proof.** These follow immediately from the definition and construction of each equilibrium. Full details of the proof are given in Appendix A.

### 3.2.2 Conditions for the Local Stability of Equilibria

The stability of an equilibrium can be determined via standard linearisation of (3.2) near to each equilibrium. This yields a Jacobian matrix \( J \) which represents the linear part of the system near an equilibrium. In our case, \( J \) is given by:

\[
\begin{pmatrix}
A + fDE + Ex'f'Da^T & Ex'f'Db^T \\
Ez'g'Da^T & A + pBC + gDE + Ez'g'Dc^T
\end{pmatrix}
\]
In the Jacobian matrix, we think of $f, Ex', f', Ez'$ and $g, g', p$ as parameters and write $J$ as the sum of two matrices:

$$J = AA + P$$  \hspace{1cm} (3.7)$$

where:

$$AA = \begin{pmatrix} A & 0 \\ 0 & A \end{pmatrix}$$

and $P$ is a dimensionally compatible perturbation matrix structured so that:

$$P = D_1E_1 + D_2E_2 + D_3E_3$$  \hspace{1cm} (3.8)$$

Here each $D_iE_i$ is a sparse matrix with a special structure, $I$ is $n \times n$ identity matrix, and 0 is zero matrix of compatible dimension. The structuring of $P$ is determined by matrices

$$D_1 = \begin{bmatrix} 0 & \end{bmatrix}, D_2 = \begin{bmatrix} D & \\ 0 & \end{bmatrix}, D_3 = \begin{bmatrix} 0 & \end{bmatrix};$$

$$E_1 = \begin{bmatrix} 0 & pC \end{bmatrix}, E_2 = \begin{bmatrix} fE + yf'a^T & \alpha yf'a^T \end{bmatrix}, E_3 = \begin{bmatrix} y'g'a^T & gE + \beta y'g'a^T \end{bmatrix}.$$

The key point is that we break the linearisation matrix $J$ into a known part $AA$ and a structured perturbation $P$ where $P$ itself is further broken down into components made from fixed matrices $a^T, B, C, D$ and $E$ and parameters $\alpha, \beta, p, f, g, f', g', Ex'$ and $Ez'$. For a detailed explanation see (Appendix A).

**Remark 3.2.1.** Takada-Nakajema restricted their detailed analysis to a simple $2 \times 2$ case to illustrate their ideas. However, their approach may not be
easily applied to more general cases. To overcome this limitation we use the structured perturbation technique to change the form of the model (3.2) to a more amenable structured form (3.7) and (3.8) which is then much clearer and easier to analyse using TFA-type analysis.

The key to analysing the stability of structured perturbation matrix \( J = AA + P \) is the following proposition.

**Proposition 3.2.1.** (Townley et. al., 2006. [20]) Suppose that \( \lambda \) is not an eigenvalue of \( A \). Then \( \lambda \) is an eigenvalue of \( A + \sum_{i=1}^{q} p_i D_i E_i \), if, and only if, \( 1 \) is an eigenvalue of the \( q \times q \) matrix:

\[
JJ = \begin{bmatrix}
G_{11}(\lambda) & \cdots & G_{1q}(\lambda) \\
\vdots & \ddots & \vdots \\
G_{q1}(\lambda) & \cdots & G_{qq}(\lambda)
\end{bmatrix}
\]

Here \( G_{ij}(\lambda) = E_i(\lambda I - A)^{-1} D_j \) is the transfer function of the triple \((A, D, E)\).

In our case we have \( q = 3 \). So according to Proposition 3.2.1 we see importantly that: \( \lambda \) is an eigenvalue of the complicated, \( 2n \times 2n \) multi-parametrized linearisation matrix \( J \) if, and only if, \( 1 \) is an eigenvalue of the \( 3 \times 3 \) matrix

\[
JJ = \begin{bmatrix}
pG_{CB}(\lambda) & 0 & pG_{CD}(\lambda) \\
\alpha yf'G_{aT_B}(\lambda) & fG_{ED}(\lambda) + yf'G_{aT_D}(\lambda) & \alpha yf'G_{aT_D}(\lambda) \\
gG_{EB}(\lambda) + \beta y'g'G_{aT_B}(\lambda) & y'g'G_{aT_D}(\lambda) & gG_{ED}(\lambda) + \beta y'g'G_{aT_D}(\lambda)
\end{bmatrix}
\]
CHAPTER 3. INVASION MODELS

To elaborate further: $\lambda$ is an eigenvalue of $J$ if, and only if, 1 is a zero of the characteristic polynomial $\text{char}_{JJ(\lambda)}(s)$ of $JJ(\lambda)$ so that

$$\text{char}_{JJ(\lambda)}(1) = 0. \quad (3.9)$$

Then

$J$ is stable $\iff \lambda \notin \Lambda(J)$ for $|\lambda| \geq 1 \iff \text{char}_{JJ(\lambda)}(1) \neq 0$ for all $|\lambda| \geq 1$

Here, depending on which equilibrium we are studying, equation (3.9) can be simplified to yield checkable linearised stability criteria. To emphasize, using Transfer functions we reduce the problem of analysing the eigenvalues of a multi-parameter $2n \times 2n$ matrix $J$ to analysing a simpler $3 \times 3$ matrix $JJ$, albeit parametrized by $\lambda$.

Here we should note that each transfer function has the form

$$G_{ED} = E(\lambda I - A)^{-1} D = \frac{N_{ED}(\lambda)}{\det(\lambda I - A)}$$

where $N_{ED}$ is a polynomial of degree less than $n$ (the dimension of $A$) and $\det(\lambda I - A)$ is the characteristic polynomial of $A$.

**Theorem 3.2.3.** For the system (3.2) with the Assumptions 1-5, the following rules determine the local stability type of each equilibrium based on a synthesis of our findings on the conditions for existence of equilibria with the corresponding stability conditions above:

1. $(0, 0)$: is always an unstable equilibrium.

2. $(x^*, 0)$: the general stability condition is:
\[(1 - f(G_{ED} - f'Ex^*G_{aT_D}) (1 - p(G_{CB} - gG_{ED} + pgG_{CB}G_{ED} - pgG_{EB}G_{CD}) \neq 0
\]

for all \(|\lambda| \geq 1\).

From this point on and throughout the remainder of the thesis, each transfer function term \(G\) means \(G(\lambda)\).

3. \((0, z^*)\): the general stability condition is:

\[(1 - fG_{ED}) [(1 - pG_{CB})(1 - gG_{ED} - \beta g' Ez^*G_{aT_D} - pG_{CD}(gG_{EB} + \beta g' Ez^*G_{aT_B})] \neq 0
\]

for all \(|\lambda| \geq 1\).

4. \((x', z')\): The stability condition for this equilibrium is

\[(1 - pG_{CB})(1 - fG_{ED} - f'Ex'G_{aT_D}) \left[ \left( 1 - gG_{ED} - \beta Ez^*g'G_{aT_D} - \frac{(gG_{EB} + \beta Ez'g'G_{aT_D})pG_{CD}}{1 - pG_{CB}} \right) - Ez'g'G_{aT_D}(\alpha Ex'f'G_{aT_D} + \frac{\alpha pEx'f'G_{aT_B}G_{CD}}{1 - pG_{CB}}) \right] \neq 0
\]

for all \(|\lambda| \geq 1\).

**Corollary 3.2.1.** Consider the special case of the Model [3.3], when the density dependent functions \(f\) and \(g\) and the perturbation parameter \(p\) hit the same entry of the invader PPM. That is, \(D = B\) and \(E = C\). In this case the stability rules given in Theorem 3.2.3 provide the following conditions:

1. For the stability of the equilibrium \((x^*, 0)\) the condition is:

\[\text{det}(I - JJ) = (1 - fG_{CB} - p_1G_{aT_D}) (1 - pG_{CB} - gG_{ED}) \neq 0\]
for all $|\lambda| \geq 1$.

Moreover, examining the block matrix $JJ$ for this equilibrium shows that:

$$f'(M^*)Ex^*D < 0 \quad \text{and} \quad p + g > f^*$$

is also a necessary condition. Here

$$f^* = \frac{1}{G_{ED}(1)}$$

2. For the stability of the equilibrium $(0, z^*)$ the stability condition is:

$$\text{det}(I - JJ) = (1 - fG_{ED})[(1 - pG_{ED})(1 - gG_{ED} - \beta p_2 G_{a\tau D}) - pG_{ED}(gG_{ED} + \beta p_2 G_{a\tau D})] \neq 0$$

for all $|\lambda| \geq 1$.

Also, a necessary condition for this equilibrium is:

$$g'(N^*)Ez^*D < 0 \quad \text{and} \quad f < f^*$$

3. For the equilibrium $(x', z')$ the stability condition is:

$$(S - Ex^*f'G_{a\tau D})(S - \beta Ez^*g'G_{a\tau D}) - \alpha Ez' Ex' f'g'G_{a\tau D}^2 \neq 0$$

for all $|\lambda| \geq 1$, where $S = 1 - f^*G_{ED}$.

**Proof of Theorem 3.2.3** We appeal to the idea summarised in Proposition 3.2.1 on characterising the eigenvalues of multi-structured perturbation matrices. We apply this result to the linearisation matrices for each equilibrium as
follows:

- $(0, 0)$: In this case the linearised matrix is given by

\[
\begin{pmatrix}
A + fDE & 0 \\
0 & A + pBC + gDE
\end{pmatrix}
\]

Because both density dependent functions are decreasing (Assumption 3B), then

\[
A + f(0)DE > A + f(M^*)DE
\]

But at equilibrium the resident will be at carrying capacity so that

\[
\lambda_{max}(A + f(M^*)DE) = 1
\]

Hence

\[
\lambda_{max}(A + f(0)DE) > 1
\]

So $\lambda_{max}(JJ)$ in this case will always be greater than one, which means that $(0, 0)$ is always an unstable equilibrium.

- $(x^*, 0)$: The linearised matrix is

\[
J = \begin{pmatrix}
A + fDE + Ex^*f'Da^T & Ex^*f'Db^T \\
0 & A + pBC + gDE
\end{pmatrix}
\]
In this case, the $JJ$ matrix calculated using Proposition 3.2.1 becomes:

$$JJ = \begin{pmatrix}
pG_{CB} & 0 & pG_{CD} \\
\alpha Ex^* f'G_{a^TB} & fG_{ED} + Ex^* f'G_{a^TD} & \alpha Ex^* f'G_{a^TD}
gG_{EB} & 0 & gG_{ED}
\end{pmatrix}$$

Computing the matrix $I - JJ$ we have:

$$I - JJ = \begin{pmatrix}
1 - pG_{CB} & 0 & -pG_{CD} \\
-\alpha Ex^* f'G_{a^TB} & 1 - fG_{ED} - Ex^* f'G_{a^TD} & -\alpha Ex^* f'G_{a^TD}
-gG_{EB} & 0 & 1 - gG_{ED}
\end{pmatrix}$$

so,

$$\det(I - JJ) = (1 - fG_{ED} - f'Ex^*G_{a^TD}) (1 - pG_{CB} - gG_{ED} + pgG_{CB}G_{ED} - pgG_{ED}G_{CD}) = 0$$

Then the general stability condition for $(x^*, 0)$ equilibrium is:

$$(1 - fG_{ED} - f'Ex^*G_{a^TD}) (1 - pG_{CB} - gG_{ED} + pgG_{CB}G_{ED} - pgG_{ED}G_{CD}) \neq 0,$$

for all $|\lambda| \geq 1$
• \((0, z^*)\): The linearised matrix in this case is
\[
\begin{pmatrix}
A + fDE & 0 \\
Ez^*g'Da^T & A + pBC + gDE + Ez^*g'Dc^T
\end{pmatrix}
\]
and the Jacobian matrix \(JJ\) becomes:
\[
JJ = \begin{pmatrix}
pG_{CB}(\lambda) & 0 & pG_{CD}(\lambda) \\
0 & fG_{ED}(\lambda) & 0 \\
gG_{EB}(\lambda) + \beta y'g'G_{a\tau B}(\lambda) & y'g'G_{a\tau D}(\lambda) & gG_{ED}(\lambda) + \beta y'g'G_{a\tau D}(\lambda)
\end{pmatrix}
\]
Then \(I - JJ\) is:
\[
JJ = \begin{pmatrix}
1 - pG_{CB}(\lambda) & 0 & -pG_{CD}(\lambda) \\
0 & 1 - fG_{ED}(\lambda) & 0 \\
-gG_{EB}(\lambda) + \beta y'g'G_{a\tau B}(\lambda) & -y'g'G_{a\tau D}(\lambda) & 1 - gG_{ED}(\lambda) - \beta y'g'G_{a\tau D}(\lambda)
\end{pmatrix}
\]
\[
det(I - JJ) = (1 - fG_{ED}) \\
[(1 - pG_{CB})(1 - gG_{ED} - \beta y'Ez^*G_{a\tau D}) - pG_{CD}(gG_{EB} + \beta y'Ez^*G_{a\tau B})] = 0
\]
Hence $J$ is stable under the following condition:

$$(1 - fG_{ED}) \left[ (1 - pG_{CB})(1 - gG_{ED} - \beta g'Ez^*G_{aT_D}) - pG_{CD}(gG_{EB} + \beta g'Ez^*G_{aT_B}) \right] \neq 0$$

for all $|\lambda| \geq 1$.

- $(x', z')$: The linearised matrix $J$ in this case

$$J = \begin{pmatrix}
A + fDE + Ex'f'Da^T & Ex'f'Db^T \\
Ez'g'Da^T & A + pBC + gDE + Ez'g'Dc^T
\end{pmatrix}$$

Then the Jacobian matrix calculated using Proposition(3.2.1) is:

$$JJ = \begin{pmatrix}
pG_{CB}(\lambda) & 0 & pG_{CD}(\lambda) \\
\alpha yf'G_{aT_B}(\lambda) & fG_{ED}(\lambda) + yf'G_{aT_D}(\lambda) & \alpha yf'G_{aT_D}(\lambda) \\
gG_{EB}(\lambda) + \beta y'g'G_{aT_B}(\lambda) & y'g'G_{aT_D}(\lambda) & gG_{ED}(\lambda) + \beta y'g'G_{aT_D}(\lambda)
\end{pmatrix}$$

So $I - JJ$ matrix becomes:

$$I - JJ = \begin{pmatrix}
1 - pG_{CB} & 0 & -pG_{CD} \\
-\alpha yf'G_{aT_B} & 1 - fG_{ED} + yf'G_{aT_D} & -\alpha yf'G_{aT_D} \\
-gG_{EB} + \beta y'g'G_{aT_B} & -y'g'G_{aT_D} & 1 - gG_{ED} + \beta y'g'G_{aT_D}
\end{pmatrix}$$
The stability condition for this equilibrium comes immediately from the following statement:

\[
\text{det}(I - JJ) = (1 - pG_{CB})[(1 - fG_{ED} - f'Ex'a^TD) \\
\left(1 - gG_{ED} - \beta Ez'a'G_{a^TD} - \frac{(gG_{EB} + Ez'a'G_{a^TD}pG_{CD})}{1 - pG_{CB}}\right) - Ez'a'G_{a^TD}(\alpha Ex'a'G_{a^TD} \\
+ \frac{\alpha pEx'a'G_{a^TD}G_{CD}}{1 - pG_{CB}})] - \frac{\alpha pEx'a'G_{a^TD}G_{CD}}{1 - pG_{CB}} \neq 0,
\]

for all \(|\lambda| \geq 1\).

**Proof of Corollary 3.2.1**

1. \((x^*, 0)\): The linearised matrix of this equilibrium becomes:

\[
J_{(x^*, 0)} = \begin{pmatrix} A + f^*DE + Ex^*f'Da^T & \alpha Ex^*f'Da^T \\
0 & A + pDE + gDE \end{pmatrix}
\]

The stability condition when \(D = B\) and \(C = E\) comes immediately from the general condition.

The necessary condition for stability of this equilibrium depends on the stability of the \((1, 1)\) and \((2, 2)\) blocks in \(J_{(x^*, 0)}\) i.e. we need both:

\[A + f^*DE + Ex^*f'Da^T \quad \text{and} \quad A + pDE + gDE\]

to be stable. Both are single structured perturbations

\[A + D(f^*E + Ex^*f'a^T) \quad \text{and} \quad A + (p + g(N^*))DE\]
Now the dominant eigenvalue of $A + f^*DE$ is equal to 1. Therefore we want the term $DEx^*f'a^T$ to be stabilizing, since if this term is positive then it destabilizes. So we must have:

$$f'(M^*)Ex^*D < 0$$

But this term cannot be too negative since otherwise we will force other eigenvalues to have modules greater than 1. This is where later we use the root locus type argument \cite{31}.

As for the other matrix. We have

$$A + (p + g(N^*))DE$$

Since $A + f^*DE$ has eigenvalue 1, then $p + g(N^*)$ can not be bigger than $f^*$ since then it would destabilize. So we must have

$$p + g(N^*) < f^*$$

But assuming we are allowing negative $p$ - although $p$ cannot be so negative as to make $A + pDE$ have negative entries - then this term (as above) cannot be too negative.

2. $(0, z^*)$: The stability condition in the case of $D = B$ and $E = C$ comes as an immediate consequence from applying these values in the general
condition. The linearised matrix becomes:

\[ J_{(0,z^*)} = \begin{pmatrix}
A + f(M^*)DE & 0 \\
Ez^*g'Da^T & A + pDE + gDE + \beta Ez^*g'Da^T
\end{pmatrix} \]

Again, the stability of \( J_{(0,z^*)} \) depends on the stability of the \((1,1)\) and \((2,2)\) block matrices. That is:

\[ A + f(M^*)DE \quad \text{and} \quad A + pDE + g^*DE + \beta Ez^*g'Da^T \]

have to be stable. As before, both are single structured perturbations

\[ A + f(M^*)DE \quad \text{and} \quad A + D(p + g^*)E + \beta Ez^*g'a^T \]

In this case, the dominant eigenvalue of \( A + (p + g^*)DE \) is equal to 1. Therefore we want the term \( \beta Ez^*g'Da^T \) to be stabilizing. If this term is positive then it destabilizes. So it must be negative and hence

\[ g'(N^*)Ez^*D < 0 \]

is necessary. But this term cannot be too negative since otherwise it will force other eigenvalues to have modulus greater than 1. Again, this is where later we use the root locus type argument [31].

As for the other matrix. We have

\[ A + f(M^*)DE \]
At this equilibrium \( g^* = f^* - p \), so \( A + f^*DE \) has eigenvalue 1, then we can say:

\[
0 < f(M^*) < f^*
\]

since \( f \) is a non-negative function (Assumption). Here we should note that in this case \( f^* \) is different from \( f(M^*) \) as the first is \( 1/G_{ED}(1) \) while the second is just the value of the function \( f \) evaluated at \( M^* \).

3. \((x', z')\): The general stability rule in this case becomes:

\[
(1-f^*G_{ED}-Ex'f'G_{aD})(1-(p+g^*)G_{ED}+\beta Ez'f'G_{aD})-\alpha Ex'Ex'f'G_{aD}^2 \neq 0,
\]

for all \(|\lambda| \geq 1\), where

\[
f^* = \frac{1}{G_{ED}(1)}, \quad g^* = f^* - p
\]

So

\[
(1-f^*G_{ED}-Ex'f'G_{aD})(1-f^*G_{ED}+\beta Ez'f'G_{aD})-\alpha Ex'Ex'f'G_{aD}^2 \neq 0,
\]

for all \(|\lambda| \geq 1\)

This completes the proof.

**Remark 3.2.2.** The key point to Theorem 3.2.3 is that we obtain conditions for stability in terms of well defined transfer functions. As we will see in applications, the stability conditions in terms of transfer functions furnish readily checkable stability criteria. Even in tricky high dimensional models, we can resort to classical root locus results to obtain graphically checkable criteria. In many cases, we would obtain stability conditions directly without recourse to
root locus arguments.

### 3.3 A 2 × 2 Example

In this section we explore the conditions determining stability of the equilibria \((x^*, 0)\) and \((0, z^*)\) in the two dimensional case. In the case of the equilibrium \((x^*, 0)\) the crucial matrix is the \((1, 1)\) block of \(J\), that is the matrix

\[
A + f^*DE + Ex^*f'Da^T
\]

We know from Corollary 3.2.1 that \(f'\) must be negative. The key issue is how negative. Now \(A + f^*DE\) is a non-negative matrix with dominant eigenvalue equal to 1. Let

\[
A + f^*DE = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}
\]  \(\tag{3.10}\)

If \(\mu\) is the other eigenvalue of \(A + f^*DE\) then

\[
\mu = a_{11} + a_{22} - 1
\]

We assume that \(D = [1 \ 0]^T\) and set \(k = -Ex^*f'\). So we want to know how large \(k\) can be so that

\[
\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} - k \begin{pmatrix} 1 \\ 0 \end{pmatrix}[1 \ 1]
\]

is stable. We start with \(k = 0\) where this matrix has eigenvalues \(1\) and \(\mu = a_{11} + a_{22} - 1 \in (-1, 1)\). As we increase \(k\), then these eigenvalues move inside the unit circle. So when do these eigenvalues first depart the unit circle. Ideally
the departure point is at $-1$ and then the critical $k = -Ex^*f'$ is

$$k = -\frac{1}{a^T(-I - A - f^*DE)^{-1}D}$$

However, it is possible that the departure point occurs with non-zero imaginary part. Let this eigenvalue be $e^{i\theta}$.

If $v$ is the corresponding eigenvector, then

$$(A + f^*DE - kDa^T)v = \exp(i\theta)v \quad \text{or} \quad \left(\begin{array}{cc} a_{11} & a_{12} \\ a_{21} & a_{22} \end{array}\right) - k \left(\begin{array}{c} 1 \\ 0 \end{array}\right) \left[\begin{array}{c} 1 \\ 1 \end{array}\right] v = \exp(i\theta)v \cdot$$

Then

$$-1 = ka^T(\exp(i\theta)I - A - f^*DE)^{-1}D = k[1 \ 1] \left(\begin{array}{cc} e^{i\theta} - a_{11} & -a_{12} \\ -a_{21} & e^{i\theta} - a_{22} \end{array}\right)^{-1} \left(\begin{array}{c} 1 \\ 0 \end{array}\right).$$

So

$$-k = \frac{1}{(\exp(i\theta) - 1)(\exp(i\theta) - a_{11} - a_{22} + 1)} \left[\begin{array}{c} 1 \\ 1 \end{array}\right] \left(\begin{array}{cc} e^{i\theta} - a_{22} & a_{12} \\ a_{21} & e^{i\theta} - a_{11} \end{array}\right) \left(\begin{array}{c} 1 \\ 0 \end{array}\right).$$

Then

$$-k = \frac{\exp(i\theta) - a_{22} + a_{21}}{(\exp(i\theta) - 1)(\exp(i\theta) - a_{11} - a_{22} + 1)}.$$  

Equating real and imaginary parts we obtain that either $\sin \theta = 0$, corresponding to a departure at $-1$, or $\sin \theta \neq 0$ and then

$$k = \frac{-a_{11} + a_{22} - 2}{a_{21} - a_{22}} \quad \text{and} \quad \cos \theta = \frac{-k + a_{11} + a_{22}}{2}. $$
CHAPTER 3. INVASION MODELS

Since the trace of $A + f^*DE = a_{11} + a_{22} < 2$, because $\lambda_{\text{max}}(A + f^*DE) < 0$, then

$$k > 0 \quad \text{only if} \quad a_{21} > a_{22} \quad \text{and then} \quad \cos \theta \in \left(-\frac{k + a_{11} + a_{22}}{2}, \frac{k + a_{11} + a_{22}}{2}\right) \subset (-1, 1).$$

When either of these two conditions fail, then the critical $k$ is given by

$$k = -\frac{1}{a^T(-I - A - f^*DE)^{-1}D}$$

and then $(x^*, 0)$ is stable when

$$0 < k < -\frac{1}{a^T(-I - A - f^*DE)^{-1}D} \quad \text{and} \quad p + g(N^*) < f^*.$$

Otherwise, the critical $k$ is given by

$$-\frac{a_{11} + a_{22} - 2}{a_{21} - a_{22}}$$

and then $(x^*, 0)$ is stable when

$$0 < k < -\frac{a_{11} + a_{22} - 2}{a_{21} - a_{22}} \quad \text{and} \quad p + g(N^*) < f^*.$$

For the equilibrium $(0, z^*)$ the linearised matrix is

$$J_{(0, z^*)} = \begin{pmatrix} A + f(M^*)DE & 0 \\ Ez^*g' \text{Da}^T & A + pDE + g^*DE + Ez^*g' \text{Da}^T \end{pmatrix}.$$
As in the case of the equilibrium at \((x^*, 0)\), we must have \(k' = -Ez^*g' > 0\). But how large can \(k'\) be? We focus on the matrix \(A + pDE + g^*DE\). This matrix is non-negative with dominant eigenvalue equal to one. Again, we must determine the critical value of \(k'\) so that the eigenvalues of the \((2, 2)\) block \(A + pDE + g^*DE - k'Da^T\) depart the unit circle. Let 

\[
A + pDE + g^*DE = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}
\]

(note \(p + g^* = f^*\) as above).

Using similar arguments as above we have that when 

\[
a_{21} > a_{22} \quad \text{and} \quad \cos \theta \in \left[\frac{-k' + a_{11} + a_{22}}{2}\right] \in (-1, 1),
\]

then the critical \(k'\) is 

\[
-\frac{a_{11} + a_{22} - 2}{a_{21} - a_{22}}
\]

and then \((0, z^*)\) is stable when 

\[
0 < k' < -\frac{a_{11} + a_{22} - 2}{a_{21} - a_{22}} \quad \text{and} \quad f(M^*) < f^*.
\]

When either of these two conditions fail, then the critical \(k' = -Ez^*g'\) is given by 

\[
k' = -\frac{1}{a^T(-I - A - (p + g^*)DE)^{-1}D}
\]

and then \((0, z^*)\) is stable when 

\[
0 < k' < -\frac{1}{a^T(-I - A - (p + g^*)DE)^{-1}D} \quad \text{and} \quad f(M^*) < f^*.
\]
CHAPTER 3. INVASION MODELS

3.4 Examples

We illustrate our findings through two examples. The first example is a hypothetical $2 \times 2$ invasion model. The second is a modified $5 \times 5$ invasion model based on a simple population projection matrix model for Chinook Salmon found in [32]. In each case we consider three different types of density dependent functions.

3.4.1 $2 \times 2$ Numerical Examples

Suppose the model given in [6] as follows:

$$
A = \begin{bmatrix}
0 & 0 \\
0.5 & 0.7
\end{bmatrix},
E = C = \begin{bmatrix}
0 & 1
\end{bmatrix},
D = B = \begin{bmatrix}
1 \\
0
\end{bmatrix},
$$

and,

$$
c' = 1, p = 0.4, a = \begin{bmatrix}
1 & 1
\end{bmatrix}, M^* = |x'| + \alpha |z'|, N^* = |x'| + |z'|
$$

In this case using the transfer functions for these specific populations we obtain:

$$
f^* = 0.6 \quad \text{and} \quad g^* = 0.2
$$

1. Firstly, we choose the density dependent function given in [6]:

$$
f = 2 - cM, g = 2 - c'N.
$$
To apply our analysis we calculate:

\[ f' = -c, \quad g' = -1, \quad f^{-1} = \frac{2-f^*}{c}, \quad g^{-1} = 2 - g^*. \]

So the conditions for each equilibrium become:

i) \((x^*, 0)\): Since the existence condition is

\[ f^{-1}(f^*) > 0, \]

then \((x^*, 0)\) always exists because \(\frac{14}{c} > 0\) always holds.

ii) \((0, z^*)\): The existence condition for this equilibrium is

\[ g^{-1}(g^*) > 0. \]

So \((0, z^*)\) always exists because \(g^{-1}(g^*) = 1.8\).

iii) \((x', z')\): The existence condition is:

\[ \frac{\alpha}{\beta} < \frac{f^{-1}(f^*)}{g^{-1}(g^*)} < 1 \quad \text{or} \quad 1 < \frac{f^{-1}(f^*)}{g^{-1}(g^*)} < \frac{\alpha}{\beta}. \]

Then \((x', z')\) exists in this region

\[ \alpha c < \frac{7}{9} < c \quad \text{or} \quad c < \frac{7}{9} < \alpha c. \]

The stability conditions for these equilibria are given as follows:

a) \((x^*, 0)\). Here \(a_{21} = 0.5 < a_{22} = 0.7\). So we know the critical \(k\) is
determined when eigenvalues depart the unit circle at $-1$. In this case

$$\frac{1}{a^T(-I - A - f^*DE)^{-1}D} = \frac{-7}{6}$$

and so in general $(x^*, 0)$ is stable under the following condition:

$$0 < k < \frac{7}{6} \quad \text{and} \quad p + g(N^*) < \frac{1}{G_{ED}}$$

For this specific choice of $f$ we have that $f' = -c$ so that

$$k = cEx^* = c||x^*||EU_x$$

where $U_x$ is the unit vector of $x$ and

$$||x^*|| = \frac{1}{1 - \alpha} (M^* - \alpha N^*) = \frac{1}{1 - \alpha} \left( \frac{1.4}{c} - \alpha \frac{1.4}{c} \right).$$

This gives a fixed (independent of parameters in $f$) value of

$$k = (cEU_x) \left( \frac{1.4}{c} \right) = 1.4EU_x = 0.875$$

and

$$0 < k < \frac{7}{6}$$

holds.

So for stability we only require

$$p + g(N^*) < f^* = \frac{1}{G_{ED}}$$
But
\[ p + g(N^*) = 2.4 - \frac{1.4}{c} \quad \text{and} \quad \frac{1}{G_{ED}} = 0.6 \]

So the stability condition becomes:
\[ c < 0.7778. \]

b) \((0, z^*)\). Again we have that \(a_{21} = 0.5 < a_{22} = 0.7\). So in general we have stability when
\[ 0 < k' < \frac{7}{6} \quad \text{and} \quad f(M^*) < f^* \]
The latter requires
\[ \alpha c > \frac{7}{9} \]
whilst for this specific choice of density dependence we have
\[ k' = 1 \]
So the condition of stability of the \(z\)-axis equilibrium is simply
\[ \alpha c > \frac{7}{9} \]

c) \((x', z')\): the linearised matrix is:
\[
J_{JJ} = \begin{pmatrix}
-k & 0.6 - k & -\alpha k & -\alpha k \\
0.5 & 0.7 & 0 & 0 \\
-k' & -k' & -k' & 0.6 - k' \\
0 & 0 & 0.5 & 0.7
\end{pmatrix}
\]
with
\[ k = \frac{1.125\alpha c}{\alpha - 1} - \frac{0.875}{\alpha - 1} \]

and
\[ k' = \frac{0.875}{(\alpha - 1)c} - \frac{1.125}{\alpha - 1} \]

Analysing the characteristic polynomial of \( J \) in this case and combining this with the existence condition we have:

\[ \frac{\alpha}{\beta} < \frac{f^{-1}(f^*)}{g^{-1}(g^*)} < 1 \]

That is:
\[ \alpha < \frac{7}{9} < c \]

The stability region of the equilibria are summarized in Figure 3.1.

**Note 3.4.1.** 1. As discussed in the paper by Takada [6], in the case of \( c = c' \), when varying \( \alpha \) and \( c \), we find that \( c \) has no effect on the dynamics which depend only on the weighting parameter \( \alpha \). See Figure 3.2.

2. The stability of the coexistence equilibrium in the Takada-Nakajema case depends on the contribution of \( \alpha \) and \( \beta \) in the weighted sums \( M \) and \( N \).
Secondly, we consider the density dependent function as a Ricker-type non-linearity \[ f = \exp(-cM), \quad g = \exp(-c'N) \]

Hence we have

\[ f' = -c\exp(-cM^*), \quad g' = -\exp(M^*), \quad M^* = f^{-1} = \frac{\ln(f^*)}{-c}, \quad N^* = f^{-1} = -\ln(g^*). \]
So the existence conditions for each equilibrium become:

i) \((x^*, 0)\) always exists since \(M^* = \frac{0.5108}{c} > 0\) is always true.

ii) \((0, z^*)\) always exists since \(g^* = 1.6094 > 0\) is always true.

iii) \((x', z')\): The same argument, as above, yields the existence region

\[ \alpha c < 0.3174 < c \quad \text{OR} \quad c < 0.3174 < \alpha c. \]

The stability conditions for these equilibria are:
a) \((x^*, 0)\): The condition is

\[
0 < k < \frac{7}{6} \quad \text{and} \quad p + g(N^*) < 0.6
\]

But

\[
k = -Ex^* f'(M^*) = -\frac{\ln(f^*)}{\| (I - A)^{-1} D \|_1} = 0.1916 < \frac{7}{6}.
\]

So for stability we need only to satisfy \(p + g(N^*) < f^* = 0.6\). This gives

\[
c < 0.3174
\]

b) \((0, z^*)\): The stability condition of this equilibrium is

\[
0 < k' < \frac{7}{6} \quad \text{and} \quad \alpha c > 0.3174.
\]

The first condition is automatically satisfied. So the stability condition is

\[
\alpha c > 0.3174
\]

c) \((x', z')\): In this case it is difficult to use either the general formula (3.9) or analysing the corresponding characteristic equation since both yield tedious calculations. Therefore we will rely on simulation to determine the stability region. Simulations suggest that the region is given as

\[
\alpha c < 0.3174 < c
\]

See Figure (3.3).
3. Thirdly, we choose the density dependent function as a modified version of Beverton-Holt [32] as follows:

\[ f = \frac{1}{c + M} \quad \text{and} \quad g = \frac{1}{\ell' + N}. \]

Here we change the value of \( p = 0.4 \) to \( p = 0.1 \) to have clearer graphs using Matlab. Hence \( g^* \) will change to \( g^* = 0.5 \).

Again doing the same steps as above we get the existence conditions:
i) \((x^*, 0)\) exists for all \(c\) satisfying the condition of \(c < 1.6667\).

ii) \((0, z^*)\) exists always because \(g^* < 1\) always true.

iii) \((x', z')\) exists if we have

\[
\alpha c < 1.4168 < c \quad \text{OR} \quad \alpha c > 1.4168 > c
\]

To check stability we need \(f'\) and \(g'\). In this case

\[
f' = -f^2 \quad \text{and} \quad g' = -g^2
\]

a) For \((x^*, 0)\) the necessary condition for the stability is

\[
k > 0, \quad \text{and} \quad c < 0.6667
\]

For this density dependence,

\[
k = -f'Ex^* = (f^*)^2M^*G_{DE}(1) = 0.0191 - 0.0147c
\]

and \(k > 0\) if \(c < 1.2993\). This is true since we already have \(c < 0.6667\).

For this example, we know the root locus departs the unit circle at \(-1\) when \(k = 7/6\). Since \(c > 0\), \(k < 0.0191 < 7/6\). Therefore the stability condition of the equilibrium is

\[
c < 0.6667
\]

b) \((0, z^*)\) the necessary stability condition is:
\[ k' > 0 \quad \text{and} \quad f(M^*) > \frac{1}{G_E D(1)} \]

Here \( f(M^*) = \frac{1}{c + M^*} = \frac{1}{c + \alpha N^*} = c + \alpha \), and \( k' = g^*(g^* - 1) = 0.25 > 0 \) is always true. As before, the necessary and sufficient condition reduces to:

\[ c + \alpha > 1.6668 \]

c) \((x', z')\): Again we rely on simulation to determine the stability region which gives the stability region as

\[ \alpha < 1.6667 - c < 1 \]

See figure (3.4).
Figure 3.4: The graph shows the region of existence for the coexistence equilibrium is \( \alpha < 0.6668 \) or \( c < 0.6668 \) or \( \alpha < c \). The the stability of the coexistence equilibrium is \( \alpha c < 0.6668 \) or \( c < \alpha c \). Similarly the stability region of the \( x \)-axis equilibrium, which means the resident type wins, is the region when \( c < 0.6668 \), while the stability region of the \( z \)-axis equilibrium, which means the invader type will win, is when \( \alpha + c > 0.6668 \).

### 3.4.2 A 5 × 5 Numerical Examples

This example is a modified version adapted from [32]. It is typical of stage-structured models of fish, e.g. Chinook Salmon. It has 5 stage classes with stages 3 through to 5 representing adult fish which reproduce. The linear part
of the transition matrix in (3.2) is given by

\[
A = \begin{bmatrix}
0 & 0 & 15 & 16 & 17 \\
0.0131 & 0 & 0 & 0 & 0 \\
0 & 0.8 & 0 & 0 & 0 \\
0 & 0 & 0.7896 & 0 & 0 \\
0 & 0 & 0 & 0.6728 & 0
\end{bmatrix}
\]

with structure

\[
E = C = \begin{bmatrix} 0 & 0 & 1 & 0 & 0 \end{bmatrix},
D = B = \begin{bmatrix} 0 \\ 1 \\ 0 \\ 0 \\ 0 \end{bmatrix};
\]

\[
c' = 1, p = 0.2, a = \begin{bmatrix} 1 & 1 & 1 & 1 \end{bmatrix}, M^* = |x'| + \alpha |z'|, N^* = |x'| + |z'|.
\]

Using Matlab we found:

\[
f^* = 0.7697 \quad \text{and} \quad g^* = 0.5697
\]

1. First assume that \( f = 2 - cM \) and \( g = 2 - c'N \).

Then the conditions of existence of equilibria are

i) \((x^*, 0)\) always exists because \( f^{-1}(f^*) = \frac{2 - f^*}{c} > 0 \) always hold.

ii) \((0, z^*)\) always exists because \( g^{-1}(g^*) = (2 - g^*) > 0 \) always hold.

iii) \((x', z')\) exists when
\[ \alpha c < 0.8232 < c \quad \text{OR} \quad c < 0.8232 < \alpha c \]

The stability regions of equilibria are given as follows:

a) \((x^*, 0)\). In the necessary condition we need

\[ k > 0 \quad \text{and} \quad 0 < c < 0.8232 \]

But in this case we have \( k = -f'EU_{x^*} = 0.0306 \).

Based on the root locus technique we found that the first eigenvalue of \( A + f^*DE + f'E_x^*Da^T \) goes out of the unit circle at the point \((-1, 0)\).

So the corresponding value of \( k \) is determined by

\[ -TFk = -\frac{1}{G_{a^rD}(-1)} = 0.0529 \]

where \( G_{a^rD}(-1) = a^T(-I - A - f^*DE)D \).

Clearly \( k < -TFk \). So the necessary and sufficient condition for stability is determined solely from the \((2, 2)\) block of \( J \) and is:

\[ c < 0.8232. \]

See Figure (3.5).
3.5.1: Root locus for \( x \)-axis equilibrium with unlimited range of \( k \)

3.5.2: Root locus for \( x \)-axis equilibrium with \( k = 0.0306 \)

Figure 3.5: Figures (1), (2) shows the root locus of \((x^*, 0)\) equilibrium inside the unit circle, as (1) gives the root locus graph before adding the range of \( k \) and (2) gives the graph with the range of \( k \).
b) For \((0, z^*)\) we need:

\[
  k' > 0 \quad \text{and} \quad \alpha c < 0.6333
\]

Again using root locus techniques we found that the eigenvalues escape out of the unit circle through \(-1\). So the critical \(k'\) is given by

\[
  -TFk' = 0.0529. \quad \text{But} \quad k' = 0.0249 < -TFk'. \quad \text{So the necessary and sufficient condition for stability becomes simply}
\]

\[
  \alpha c < 0.8232.
\]

c) \((x', z')\): The same can be said here. The simulations gives a condition of stability as:

\[
  \alpha c < 0.8232 < c
\]

2. The second density dependent functions are:

\[
  f = \exp(-cM), \quad \text{and} \quad g = \exp(-c'N)
\]

Calculating the first derivative and the inverse of the functions \(f\) and \(g\) we obtain:

\[
  f' = -c \exp(-cM^*), \quad g' = -\exp(N^*), \quad M^* = f^{-1} = \frac{\ln(f^*)}{-c}, \quad N^* = g^{-1} = -\ln(g^*)
\]

The conditions of existence for equilibria:

i) \((x^*, 0)\): always exists because \(f^* = \frac{-0.2618}{-c} > 0\) is true.

ii) \((0, z^*)\): always exists because \(g^* = -(-0.5627) > 0\) is true.
iii) \((x', z')\): exist when

\[
\alpha c < 0.4652 < c \quad \text{or} \quad c < 0.4652 < \alpha c
\]

We obtain the stability conditions as follows:

a) \((x^*, 0)\). Here the necessary condition is

\[
k > 0 \quad \text{and} \quad c < 0.4652
\]

But in this case \(k = -f'Ex^* = 0.005\). Using the root locus technique we found that the first eigenvalue goes out of the unit circle from the point \((-1, 0)\). As before we compute

\[
-TFk = -\frac{1}{G_{aD}(-1)} = 0.0529
\]

But \(k < 0.0529\). So the stability condition of this equilibrium is:

\[
c < 0.4652
\]
3.6.1: Root locus for $x$-axis equilibrium with unlimited range of $k$

3.6.2: Root locus for $x$-axis equilibrium with $k \in (0, 0.0529)$

Figure 3.6: (1), (2) shows the root locus of $(x^*, 0)$ equilibrium inside the unit circle, as (1) gives the root locus graph before adding the range of $k$ and (b) gives the graph with the range of $k$. 
b) \((0, z^*)\) we need:

\[
 k' < 0 \quad \text{and} \quad \alpha c < 0.4652
\]

But \(k' = 0.008\), and \(-TFk' = 0.0529\). So the stability condition is simply

\[
\alpha c < 0.4652
\]

c) \((x', z')\): Using simulations we obtain a stability condition

\[
\alpha c < 0.4652 < c
\]

2. With the same PPM \(A\) with \(D, B, C,\) and \(E\), the third density dependent function is

\[
f = \frac{1}{c + M} \quad g = \frac{1}{c' + N}
\]

Again, we calculate the first derivative and the inverse of each density dependent function:

\[
M^* = f^{-1}(f^*) = \frac{1}{f^*} - c \quad \text{and} \quad N^* = g^{-1}(g^*) = \frac{1}{g^*} - c'
\]

and

\[
f' = \frac{-1}{(c + M)^2} \quad g' = \frac{-1}{(c' + N)^2}
\]

The existence regions of each equilibria are:

i) \((x^*, 0)\) exists when \(M^* > 0\) that is \(c < 1.2992\).

ii) \((0, z^*)\) always exists as \(N^* > 0\) that is \(g^* < 1\).
iii) \((x', z')\) exists when

\[
\alpha c < 0.5439 < c \quad \text{and} \quad \alpha c > 0.5439 > c
\]

The stability conditions for each equilibrium:

a) For \((x^*, 0)\) we need

\[
k > 0 \quad \text{and} \quad 0 < c < 0.5439
\]

Here \(k = -f^*(c - f^*)EU_x = 0.0147 - 0.0192c\). Then \(k\) is positive when \(c < 0.7656\). Gathering this it with the \(2, 2\)-block matrix condition we have:

\[
c < 0.5439
\]

We know that the first escape out of the unit circle is through \((-1, 0)\) and \(-TFk' = 0.0529\). But \(c\) is positive and so \(k < 0.0147\). So the stability condition is:

\[
c < 0.5439
\]

b) For \((0, z^*)\) we need:

\[
k' < 0 \quad \text{and} \quad c > 1.2992 - 0.7553\alpha
\]

But here \(k' = -g' Ez^* = 0.0061\). So the stability condition is simply

\[
c > 1.2992 - 0.7553\alpha
\]
c) \((x', z')\): From simulations we have stability when

\[ c < 1.2992 - 0.7553 \alpha < c \]

3.5 Conclusion

In this chapter we introduced a new invasion model and we used a transfer function approach to analyse it. Conditions for existence and stability of the possible equilibria have been obtained in the general case. We showed that the model introduced is actually a general version of the one introduced in [6]. A special case of \(2 \times 2\) has been considered with specific structure. Here we obtained simple necessary and sufficient stability conditions for axial equilibria. We also discussed stability conditions for the coexistence equilibrium in the special \(2 \times 2\) case. Due to difficulties of obtaining informative analytical conditions of stability, we rely on simulations to visualise the region of stability. A detailed analytical study for this case would be a good for future work.
3.7.1: Root locus for $x$-axis equilibrium with unlimited range of $k$

3.7.2: Root locus for $x$-axis equilibrium with $k \in (0, 0.0529)$

Figure 3.7: (1), (2) shows the root locus of $(x^*, 0)$ equilibrium inside the unit circle, as (1) gives the root locus graph before adding the range of $k$ and (b) gives the graph with the range of $(k)$. 
Chapter 4

Basins of Attraction of Non-zero Equilibria

4.1 Introduction

The basin of attraction $\mathcal{B}_{x_e}$ of an equilibrium $x_e$ is the totality of initial states whose states trajectories converge to the equilibrium [33]. Basins of attraction are useful in that they indicate how sensitive is a system to disturbances away from equilibrium: if the basin of attraction is relatively large, then small disturbances return back to equilibrium; if the basin of attraction is relatively small, then small perturbations take the system away from the equilibrium under focus and cause large deviations in system behaviour [34]. Loosely speaking, the larger the basin of attraction the more robust (i.e. insensitive) is the system to small disturbances. It is important to know the basin of attraction $\mathcal{B}_{x_e}$ of an equilibrium $x_e$ in the context of population dynamics [34]. However, finding or even estimating basins of attraction is difficult [35]. Even when a system is well parameterised, the calculations involved are complicated. But in the case
of population dynamics, models are rarely well parameterised. One approach to estimating basins of attraction is to use a Lyapunov function approach \cite{36}. As we will see, this is particularly useful in the context of population dynamics because our models are readily broken down into linear and non-linear parts.

In chapter \cite{3} we investigate the convergence of multiple equilibria (all possible stable equilibria: \((x', z'), (x^*, 0), (0, z^*)\)) of the System \((3.2)\). Here, we examine the robust stability properties of each equilibrium by estimating the basin of attraction of each equilibrium or, a region with guaranteed stability for the perturbed system. The results obtained are applied to given examples and computer simulations are used for more illustration.

### 4.2 Global Asymptotic Stability, Basin of Attraction and Lyapunov Analysis

We will use Taylor expansions, with highly structured terms, to estimate the basin of attraction of each non-zero equilibrium. To do this we first require some definitions and theorems. The definitions and theorems used in this section are taken from \cite{36, 37}.

#### 4.2.1 A Lyapunov Function Approach

Consider an arbitrary non-linear discrete-time system:

\[
x(t + 1) = F(x(t)), \quad F : \mathbb{R}^n \rightarrow \mathbb{R}^n.
\]

The point \(x_e \in \mathbb{R}^n\) is an equilibrium point of \((4.1)\), and without loss of generality is assumed to be zero.
Definition 4.2.5. The system (4.1) is called asymptotically stable around the equilibrium at the origin if it satisfies the following two conditions:

1. Given any $\varepsilon > 0$; there exists $\delta_1 > 0$ such that:
   
   \[ \text{if } ||x(t_0)|| < \delta_1, \text{ then } ||x(t)|| < \varepsilon; \text{ for all } t > t_0: \]

2. There exists $\delta_2 > 0$ such that if $||x(t_0)|| < \delta_2$, then $x(t) \to 0$ as $t \to \infty$.

Theorem 4.2.4. Consider the discrete-time system (4.1). If there exists a continuous function $V(x)$ such that

1. $V$ is positive definite, i.e. $V(x) > 0$ for all $x$;

2. $\Delta V(x) < 0$ for all $x$, where

   \[ \Delta V = V(F(x)) - V(x). \]

3. $V(x) \to \infty$ as $||x|| \to \infty$ (V is radially unbounded).

Then $x = 0$ is globally asymptotically stable i.e. $B_0 = \mathbb{R}^n$.

Example 4.2.3. This example is taken from [37]. Consider the system:

\[ x(t+1) = \frac{ax(t)}{1+x^2(t)} \]

\[ z(t+1) = \frac{bx(t)}{1+z^2(t)} \]

with $|a| \leq 1$ and $|b| \leq 1$. The only equilibrium is $x = z = 0$. Choose the quadratic Lyapunov function:

\[ V(x) = x^2 + z^2. \]
Clearly $V$ is continuous and radially unbounded and:

1. $V(x, z) > V(0) = 0$ for all $x \neq 0$,

2. 
\[
\Delta V(x(t)) = -\left(1 - \frac{b^2}{(1 + z^2)^2}\right)x^2 - \left(1 - \frac{a^2}{(1 + x^2)^2}\right)z^2 \leq 0.
\]

Hence $(0, 0)$ is globally asymptotically stable equilibrium if $|a|, |b| < 1$.

**Theorem 4.2.5.** The following are equivalent:

1. The origin in $\mathbb{R}^n$ is an asymptotically stable equilibrium point for the system:
\[
x(t + 1) = Ax(t).
\]

2. All eigenvalues of $A$ have modulus strictly less than one.

3. For each positive definite matrix $Q$, there exist a positive definite matrix $P$ such that:
\[
A^T PA - P = -Q.
\]

**Example 4.2.4.** Let $A = \begin{bmatrix} 0 & 1 \\ 0 & 0 \end{bmatrix}$. Then the eigenvalues of $A$ are both zero and so by using the above theorem, for a chosen positive definite matrix $Q$, there exist a positive definite matrix $P$ such that:
\[
A^T PA - P = -Q.
\]

Let
\[
Q = \begin{bmatrix} q_1 & q_2 \\ q_2 & q_3 \end{bmatrix} \quad \text{and} \quad P = \begin{bmatrix} p_1 & p_2 \\ p_2 & p_3 \end{bmatrix}.
\]
Then

$$A^TPA - P = -\begin{bmatrix} p_1 & p_2 \\ p_2 & p_3 - p_1 \end{bmatrix} = -\begin{bmatrix} q_1 & q_2 \\ q_2 & q_3 \end{bmatrix}. $$

Hence

$$P = \begin{bmatrix} q_1 & q_2 \\ q_2 & q_1 + q_3 \end{bmatrix}. $$

If $Q > 0$ then $q_1 > 0, q_3 > 0$ and $\text{Det}(Q) > 0$. Then $\text{Det}(P) = \text{Det}(Q) + q_1^2 > 0$ and so $P$ is positive definite.

**Definition 4.2.6.** The Basin of attraction $\mathcal{B}_0$ of an equilibrium point $x = 0$ say, is the set of all initial conditions $x(0)$ for which $x(t) \to 0$ as $t \to \infty$:

$$\mathcal{B}_0 = \{ x : \text{if } x(0) = x, \text{then } \lim_{t \to \infty} x(t) = 0 \}.$$ 

Every asymptotically stable equilibrium has a basin of attraction.

**Example 4.2.5.** In the example (4.2.3) if we choose $a = b = 1$ then

$$\Delta V(x_k) = -V(x_k) \left(1 - \frac{1}{(1 + z_k^2)^2}\right) \leq 0.$$ 

Hence $(0,0)$ is globally asymptotically stable and therefore the basin of attraction will be $\mathcal{B}_0 = \mathbb{R}^n$. 
CHAPTER 4. BASIN OF ATTRACTION

4.3 The Basins of Attraction of inclusive and Coexistence Equilibria

4.3.1 Preliminaries

In this Section we use Taylor expansion formula to rewrite the right hand sides of the system (3.2) as an expanded function around each equilibrium. First we rewrite the system (3.2) as:

\[ x(t + 1) = F(M_t)x(t) \]
\[ z(t + 1) = G(N_t)z(t), \]

where

\[ F(M) = (A + f(M)DE) \]
\[ G(N) = (A + pBC + g(N)DE). \]

Here \( F \) and \( G \) are both differentiable functions at \((x_e, z_e)\). The Taylor expansions of \( F \) and \( G \) around the \((x_e, z_e)\) equilibrium are:

\[ F(x_e, z_e) + \Delta F = F(x_e, z_e) + \frac{\partial F}{\partial x}|_{(x_e, z_e)}(x' + \Delta x) + \frac{\partial F}{\partial z}|_{(x_e, z_e)}(z_e + \Delta z) + \text{HOT} \]
\[ G(x_e, z_e) + \Delta G = G(x_e, z_e) + \frac{\partial G}{\partial x}|_{(x_e, z_e)}(x_e + \Delta x) + \frac{\partial G}{\partial z}|_{(x_e, z_e)}(z_e + \Delta z) + \text{HOT}. \]
which can be written as the sum of linear and non-linear parts:

\[
\begin{align*}
    f(M) &= f(M) + f'(M)\Delta M + \phi(\Delta M) \\
    g(N) &= g(N) + g'(N)\Delta N + \psi(\Delta N). \\
\end{align*}
\] (4.4)

Now, we rebuild the system equations into linear and non-linear terms using the Taylor series as shown above. Then we use this Taylor approximation to obtain a Lyapunov function of each equilibrium. The next three sections show the system at each equilibrium written as a combination of linear and non-linear terms.

**Taylor Expansion around the** \( x \)-axis equilibrium \((x^*, 0)\)

We apply the formula [4.3] to the system [4.2] at the equilibrium \((x^*, 0)\). Let

\[
x = x^* + \Delta x = x^* + w, \quad z = u \quad \text{and} \quad W = \begin{bmatrix} w \\
                             u \end{bmatrix},
\]

and \( M^* = N^* = ||x^*||. \)

Then we split \( f(M) \) and \( g(N) \) into linear and non-linear parts so that

\[
    f(M) = f(M^*) + f'(M^*)\Delta M + \phi(\Delta M);
\]

and

\[
    g(N) = g(N^*) + g'(N^*)\Delta N + \psi(\Delta N).
\]

Here \( \phi \) and \( \psi \) represent the non-linear terms of \( f \) and \( g \) respectively. The variables \( \Delta M = M - M^* \) and \( \Delta N = N - N^* \) are the increments.
Then using the Formula (4.3) we have:

\[
x^* + w_{t+1} = (A + f^* DE + f'(M^*) \Delta MDE + \phi(\Delta M)DE)(x^* + w)
\]

\[
= (A + f^* DE)x^* + (A + f^* DE)w + f'(M^*) \Delta MDE x^* + f'(M^*) \Delta MDE w \cdot \
+ \phi(\Delta M)DE x^* + \phi(\Delta M)DE w.
\]

But

\[
x^* = (A + f^* DE)x^*, \quad \text{and} \quad \Delta M = a^Tw + \alpha a^Tu.
\]

Then

\[
w_{t+1} = (A + f^* DE + f'Ex^*Da^T)w_t + f'Ex^*Da^Tu_t + f'DEw_t a^Tw_t + \alpha f'(M^*)DEw_t a^Tu_t 
+ \phi(\Delta M_t)DE x^* + \phi(\Delta M_t)DE w
\]

Then we can rewrite the vector \( w_{t+1} \) as follows:

\[
w_{t+1} = L_{11}w_t + L_{12}u_t + f'(N^*)DEw_t(a^Tw_t + \alpha a^Tu_t) + \phi(\Delta N_t)(x^* + w_t) \quad (4.5)
\]

where

\[
L_{11} = A + f^* DE + f'(M^*)Ex^*Da^T \\
L_{12} = f'(M^*)Ex^*Da^T.
\]

Now we turn attention to the \( z_{t+1} \) equation of the system (4.2). With similar
techniques:

\[ u_{t+1} = (A + pBC + g^*DE + g'(N^*)\Delta NDE + \psi(\Delta N)DE)u. \]  \( (4.6) \)

Rearranging and gathering together (4.5) and (4.6), we have:

\[ w_{t+1} = [L_{11} \, L_{12}]W_t + f'(M^*)DE_0W_tE_1W_t + \phi(E_1W_t)D(Ex^* + E_0W_t) \]
\[ u_{t+1} = L_{22}u + g'(N^*)DE_\tilde{E}_0W_tE_1W_t + \psi(E_2W_t)DE_0W_t. \]  \( (4.7) \)

Now, we know \( W = \begin{bmatrix} w \\ u \end{bmatrix} \) so we can rewrite (4.7) as

\[ W_{t+1} = \begin{pmatrix} L_{11} & L_{12} \\ 0 & L_{22} \end{pmatrix}W_t + f'(M^*)D_1(E_0W_t)(E_1W_t) + \phi(E_1W_t)D_1(Ex^* + E_0W_t) \]
\[ + g'(N^*)D_2(E_\tilde{E}_0W_t)(E_2W_t) + \psi(E_2W_t)D_2E_0W_t. \]  \( (4.8) \)

Here

\[ L_{22} = A + pBC + g^*DE, \quad D_1 = \begin{bmatrix} D \\ 0 \end{bmatrix}, D_2 = \begin{bmatrix} 0 \\ D \end{bmatrix}, E_0 = \begin{bmatrix} E & 0 \end{bmatrix}; \]

\[ E_1 = \begin{bmatrix} a^T & \alpha a^T \end{bmatrix}, E_2 = \begin{bmatrix} a^T & \beta a^T \end{bmatrix}, \Delta M = E_1W, \Delta N = E_2W, E_\tilde{E}_0 = \begin{bmatrix} 0 & E \end{bmatrix}. \]

The main point of this analysis is to rewrite the system (3.2) at the x-axis equilibrium as a sum of linear and non-linear parts. Then the problem of constructing a Lyapunov function for (4.8) becomes relatively easy.
Taylor Expansion around the $z$-axis equilibrium $(0, z^*)$

We apply the formula (4.3) on the system (4.2) at the equilibrium $(0, z^*)$. Let

\[ x = \Delta x = w, \quad z = z^* + \Delta z = z^* + u \quad \text{and} \quad W = \begin{bmatrix} w \\ u \end{bmatrix}; \]

and \( M^* = \alpha \| z^* \| \) whilst \( N^* = \beta \| z^* \| \).

We again split \( f(M) \) and \( g(N) \) into linear and non-linear parts so that

\[ f(M) = f(M^*) + f'(M^*) \Delta M + \phi(\Delta M) \]
\[ g(N) = g(N^*) + g'(N^*) \Delta N + \psi(\Delta N). \]

Here \( \phi \) and \( \psi \) represent the non-linear terms of \( f \) and \( g \) respectively and \( \Delta M = M - M^* \) and \( \Delta N = N - N^* \) are the increments.

Then using the Formula (4.3), and following the same procedure as above, we have:

\[
W_{t+1} = \begin{pmatrix} L_{11} & 0 \\ L_{21} & L_{22} \end{pmatrix} W_t + g'D_2(\tilde{E}_0 W_t)(E_2 W_t) + \phi(E_1 W_t)D_1(E_0 W_t) \\
+ f'D_1(E_0 W_t)(E_1 W_t) + \psi(E_2 W_t)D_2(E z^* + \tilde{E}_0 W_t) \tag{4.9}
\]

where

\[
L_{11} = A + f^* DE, \quad L_{21} = g'D E z^* a^T, \quad L_{22} = A + pBC + g^* DE + \beta E z^* g'D a^T;
\]
\[ D_1 = \begin{bmatrix} D & 0 \\ 0 & D \end{bmatrix}, D_2 = \begin{bmatrix} 0 & E \\ E & 0 \end{bmatrix}, E_0 = \begin{bmatrix} 0 & E \end{bmatrix}, E_1 = \begin{bmatrix} a^T & \alpha a^T \end{bmatrix}, E_2 = \begin{bmatrix} a^T & \beta a^T \end{bmatrix}; \]

\[ \Delta M = E_1 W, \Delta N = E_2 W. \]

The formula (4.9) is a new version of the system (3.2) at the z-axis equilibrium using Taylor expansion formula. The reason behind using the Taylor expansion formula is to rebuild the system (3.2) as a sum of linear and non-linear parts. This makes it easier to construct a Lyapunov function of the new version (4.8) of the system.

**Taylor Expansion around the Coexistence Equilibrium \((x', z')\)**

We apply the formula (4.3) on the system (4.2) at the equilibrium \((x', z')\). Let \(x = x' + w, \ z = z' + u\) and \(W = \begin{bmatrix} w \\ u \end{bmatrix}\).

\[ M^* = \|x'\| + \alpha \|z^*\| \text{ whilst } N^* = \|x'\| + \beta \|z^*\|. \]

Split \(f(M)\) and \(g(N)\) into linear and non-linear parts so that

\[ f(M) = f(M^*) + f'(M^*) \Delta M + \phi(\Delta M) \]
\[ g(N) = g(N^*) + g'(N^*) \Delta N + \psi(\Delta N). \]

Again, using the Formula (4.3) and applying the same techniques as above, we have:
\[ W_{t+1} = \begin{pmatrix} L_{11} & L_{12} \\ L_{21} & L_{22} \end{pmatrix} W_t + f'(M*)D_1(E_0W_t)(E_1W_t) + \phi(E_1W_t)D_1(Ex' + E_0W_t) \\
+ g'(N*)D_2(\tilde{E}_0W_t)(E_2W_t) + \psi(E_2W_t)D_2(Ez' + \tilde{E}_0W_t) \]

(4.10)

where,

\[ L_{11} = A + f^*DE + f'DEx'a^T, L_{12} = \alpha f'DEx'a^T, L_{21} = g'DEz'a^T, L_{22} = A + pBC + g^*DE + \beta g'DEz'a^T; \]

\[ D_1 = \begin{bmatrix} D \\ 0 \end{bmatrix}, D_2 = \begin{bmatrix} 0 \\ D \end{bmatrix}, E_0 = \begin{bmatrix} E & 0 \end{bmatrix}, \tilde{E}_0 = \begin{bmatrix} 0 & E \end{bmatrix}, E_1 = \begin{bmatrix} a^T & \alpha a^T \end{bmatrix}; \]

\[ E_2 = \begin{bmatrix} a^T \\ \beta a^T \end{bmatrix}, \Delta M = E_1W_t, \Delta N = E_2W_t. \]

The formula (4.10) represents the system (3.2) as sum of linear and non-linear parts. Constructing a Lyapnov function using this new formula is then much easier.

In summary, we have the Taylor expansion formulas for each equilibria:

- Taylor expansion for the x-axis equilibrium \((x^*, 0)\):

\[ W_{t+1} = \begin{pmatrix} L_{11} & L_{12} \\ 0 & L_{22} \end{pmatrix} W_t + f'D_1(E_0W_t)(E_1W_t) + \phi(E_1W_t)D_1(Ex' + E_0W_t) + \]

\[ \phi \times \text{affine linear} \]

\[ \phi(E_1W_t)D_1(Ex^* + E_0W_t) \]

- Taylor expansion for z-axis equilibrium \((0, z^*)\):
CHAPTER 4. BASIN OF ATTRACTION

\[
W_{t+1} = \begin{pmatrix}
L_{11} & 0 \\
L_{21} & L_{22}
\end{pmatrix} W_t + \begin{pmatrix}
\text{Linear part} & \text{quadratic non-linear} \\
\phi \times \text{linear} & \psi \times \text{affine linear}
\end{pmatrix}
\begin{align*}
&f'(E_0 W_t)(E_1 W_t) + g'(E_0 W_t)(E_2 W_t) + \\
&\phi(E_1 W_t)D_1(E_0 W_t) + \psi(E_2 W_t)D_2(Ez^* + \tilde{E}_0 W_t)
\end{align*}
\]

- Taylor expansion for coexistence equilibrium \((x', z'):\)

\[
W_{t+1} = \begin{pmatrix}
L_{11} & L_{12} \\
L_{21} & L_{22}
\end{pmatrix} W_t + \begin{pmatrix}
\text{Linear part} & \text{quadratic non-linear} \\
\phi \times \text{affine linear} & \psi \times \text{affine linear}
\end{pmatrix}
\begin{align*}
&f'(E_0 W_t)(E_1 W_t) + g'(E_0 W_t)(E_2 W_t) + \\
&\phi(E_1 W_t)D_1(Ez' + E_0 W_t) + \psi(E_2 W_t)D_2(Ez' + \tilde{E}_0 W_t)
\end{align*}
\]

**Remark 4.3.3.** Each formula above has the form of a linear part and highly structured non-linear part. In each case the non-linear part is made up from quadratic terms plus higher degree functions (\(\phi\) and \(\psi\)) multiplied by a linear/affine linear term.

In this section we use the Lyapunov technique to estimate the basin of attraction of all the possible equilibria. The basin of attraction is expected to be small as we have mentioned earlier. Of course finding the region of attraction is only applicable to the locally asymptotically stable equilibrium points such as \((x^*, z^*), (x', 0), (0, z')\).

To obtain the conditions for the existence of a Lyapunov function for each equilibrium we apply the next steps on each equilibrium:

To proceed, we consider an equilibrium \((x_e, z_e)\) (representing \((x^*, 0), (0, z^*)\)
and \((x', z')\). Set \(W = (x - x_e, z - z_e)\). Separating to linear and non-linear terms the system \([4.2]\) yields:

\[
W_{t+1} = L_{xx} W_t + [f'(E_0 W_t E_1 W_t) + \phi(E_1 W)(E x_e + E_0 W_t)] D_1 +
\left[g'(E_0 W_t)(E_2 W_t) + \psi(E_2 W)(E z_e + E_0 W_t)\right] D_2
\]

where

\[
L_{xx} = \begin{pmatrix}
L_{11} & L_{12} \\
L_{21} & L_{22}
\end{pmatrix},
D_1 = \begin{pmatrix}
D \\
0
\end{pmatrix},
D_2 = \begin{pmatrix}
0 \\
D
\end{pmatrix}.
\]

### 4.3.2 Main Theorem

**Theorem 4.3.6.** Consider the system \([4.2]\) at the general equilibrium point \((x_e, z_e)\) with functions \(F\) and \(G\) defined as in \([4.4]\) and \(\phi\) and \(\psi\) are the non-linear terms such that:

\[
\frac{|\phi(E_1 W)|}{|E_1 W|} \to 0 \quad \text{and} \quad \frac{|\psi(E_2 W)|}{|E_2 W|} \to 0 \quad \text{as} \quad |W| \to 0
\]

i.e.

for all \(\varepsilon > 0\) there exist \(\delta_{\phi,\varepsilon} > 0, \delta_{\psi,\varepsilon} > 0\) such that

\[
|\phi(E_1 W)| < \varepsilon |W|, \quad \text{if} \quad |W| < \delta_{\phi,\varepsilon} \quad \text{and} \quad |\psi(E_2 W)| < \varepsilon |W| \quad \text{if} \quad |W| < \delta_{\psi,\varepsilon}.
\]

Define

\[
\rho = \min\left(\frac{\mu_2}{k_3} \sqrt{\frac{\mu_1 q_1}{k_1}}, \frac{\mu_3}{k_5} \sqrt{\frac{\nu_1 q_1}{k_2}}, \delta_{\phi,\varepsilon}, \delta_{\psi,\varepsilon}\right).
\]

(4.11)
One substitutes the epsilon below into the constants $\delta_{\phi, \varepsilon}, \delta_{\psi, \varepsilon}$ above to obtain the estimate of the basin.

\[
\varepsilon = \min \left( \frac{v_2}{k_4 ||E_1||} \sqrt{\frac{\mu_1 q}{k_1}}, \frac{v_3}{k_6 ||E_2||} \sqrt{\frac{v_1 q}{k_2}} \right);
\]

and

\[\mu_1, v_1, \mu_2, v_2, \mu_3, v_3 > 0, \mu_1 + v_1 < \frac{1}{2} \quad \text{and} \quad \mu_2 + v_2 + \mu_3 + v_4 < 1.\]

**Note 4.3.2.** $k_1, k_2, k_3$ and $k_5$ do not depend on the specific equilibria, while $k_4, k_6$ and $\varepsilon$, and hence $\rho$, do.

Then using the Lyapunov function method we have:

- For the $x$-axis equilibrium $(x^*, 0)$, when the stability condition holds:

  Then

  \[
  B_{(x^*, 0)} \supset \{ (x_0, z_0) : ||(x_0 - x^*, z_0)|| < \rho \},
  \]
where \( \rho \) is given by (4.11) with:

\[
  k_4 = |Ex'| + ||E_0||
\]

\[
  k_6 = ||E_0||;
\]

- For the \( z \)-axis equilibrium \((0, z^*)\), when the stability condition holds:

  Then

  \[
  B_{(0,z^*)} \supset \{(x_0, z_0) : ||(x_0, z_0 - z^*)|| < \rho\}
  \]

  where \( \rho \) is given by (4.11) with:

  \[
  k_4 = ||E_0||
  \]

  \[
  k_6 = |Ez'| + ||E_0||;
  \]

- For the equilibrium \((x', z')\), when stability condition holds:

  Then

  \[
  B_{(x',z')} \supset \{(x_0, z_0) : ||(x_0 - x', z_0 - z')|| < \rho\}
  \]

  where \( \rho \) is given by (4.11) with:

  \[
  k_4 = |Ex'| + ||E_0||
  \]

  \[
  k_6 = |Ez'| + ||E_0||.
  \]
Proof. This is obtained immediately from applying Theorem 4.2.4 on the system (4.11) at each equilibrium. For \( Q > 0 \), let \( P > 0 \) be such that

\[
L^T P L - P = -Q.
\]

Define a Lyapunov function

\[
V(W) = W^T P W.
\]

Note that different choices of \( Q \) will determine different estimates of the basin of attraction. With \( V \) determined by the above, we seek estimates so that

\[
\Delta V = V(W^T)PV(W) - W^T PW < 0.
\]

For full details see Appendix B.

4.3.3 Examples

A 2 \times 2 Example

This theoretical example is taken from Takada et. al. Consider the perturbed, stage structure population model (3.2) with:

\[
A = \begin{bmatrix} 0 & 2 \\ 0.5 & 0.7 \end{bmatrix}, E = C = \begin{bmatrix} 0 & 1 \end{bmatrix}, D = B = \begin{bmatrix} 1 \\ 0 \end{bmatrix}, f = -cM, g = -c'N,
\]

\[
c' = 1, p = 0.4, a = \begin{bmatrix} 1 & 1 \end{bmatrix}, M = |x'| + \alpha|z'|, N = |x'| + |z'|,
\]
Then \( f' = -c, f'' = f''' = \ldots = 0, g' = -1, g'' = g''' = \ldots = 0, \) and \( f^{-1} = \frac{f^*}{-c}, g^{-1} = -g^*. \)

In this case, \( \phi \) and \( \psi \) are both zero.

Then

\[
L_{11} = \begin{bmatrix} 0 & 0.6 \\ 0.5 & 0.7 \end{bmatrix}, L_{12} = \begin{bmatrix} \alpha c[0 1]x^* & \alpha c[0 1]x^* \\ 0 & 0 \end{bmatrix}, L_{21} = \begin{bmatrix} -[0 1]z^* & -[0 1]z^* \\ 0 & 0 \end{bmatrix}, L_{22} = \begin{bmatrix} 0 & 0.6 \\ 0.5 & 0.7 \end{bmatrix}.
\]

An estimate of the basin of attraction of each equilibrium is:

1. At \((x^*, 0)\) we have

\[
W_{t+1} = \begin{pmatrix} L_{11} & L_{12} \\ 0 & L_{22} \end{pmatrix} W_t - cD_1(E_0W_t)(E_1W_t) - D_2(\tilde{E}_0W_t)(E_2W_t).
\]

Now using Theorem[4.2.4] we have:

\[
\rho = 0.0022 \text{ with } \varepsilon < 6.0314 \times 10^{-4}.
\]
2. At \((0, z^*)\) we have

\[
W_{t+1} = \begin{pmatrix} L_{11} & 0 \\ L_{21} & L_{22} \end{pmatrix} W_t - D_2(\tilde{E}_0 W_t)(E_2 W_t) - cD_1(E_0 W_t)(E_1 W_t).
\]

Using the Theorem \([4.2.4]\) we obtain:

\[
\rho = 8.9719 \times 10^{-4} \text{ with } \varepsilon < 8.0397 \times 10^{-5}
\]

3. At \((x', z')\) we have

\[
W_{t+1} = \begin{pmatrix} L_{11} & L_{12} \\ L_{21} & L_{22} \end{pmatrix} W_t - cD_1(E_0 W_t)(E_1 W_t) - D_2(\tilde{E}_0 W_t)(E_2 W_t).
\]

Then using Theorem \([4.2.4]\) we have

\[
\rho = 8.9719 \times 10^{-4} \text{ with } \varepsilon < 8.0397 \times 10^{-5}
\]

A 5 × 5 Example

In this example we estimate the basin of attraction for Example\([3.4.2]\). Recall that the density dependent function used is the exponential function \(f(M) = \exp(-cM), g(N) = \exp(-c'N)\) and

\[
A = \begin{bmatrix}
0 & 0 & 15 & 16 & 17 \\
0.0131 & 0 & 0 & 0 & 0 \\
0 & 0.8 & 0 & 0 & 0 \\
0 & 0 & 0.7896 & 0 & 0 \\
0 & 0 & 0 & 0.6728 & 0
\end{bmatrix}
\]

and
$c = 0.1, E = C = \begin{bmatrix} 0 & 0 & 1 & 0 & 0 \end{bmatrix}; D = B = \begin{bmatrix} 0 \\ 1 \\ 0 \\ 0 \\ 0 \end{bmatrix}$

$c' = 1, p = 0.2, a = \begin{bmatrix} 1 & 1 & 1 & 1 \end{bmatrix}, M^* = |x'| + \alpha |z'|, N^* = |x'| + |z'|.$

This corresponds to a resident-invader system with interactions determined via a Ricker-type density dependence [38].

Then

$f' = -c \exp(-cM^*), g' = -\exp(N^*), M^* = f^{-1} = \frac{\ln(f^*)}{-c}, N^* = g^{-1} = -\ln(g^*).$

Analysing this model we obtain:

$f^* = 0.7697$ and $g^* = 0.5697.$

The estimate of the basin of attraction of each equilibrium is:

1. $(x^*, 0): \rho = 1.1722 \times 10^{-6}$ with $\varepsilon < 1.9487 \times 10^{-7}$

2. $(0, z^*): \rho = 4.8438 \times 10^{-19}$ with $\varepsilon < 6.6670 \times 10^{-2}$

3. $(x', z'): \rho = 1.4444 \times 10^{-7}$ with $\varepsilon < 2.9846 \times 10^{-8}$

Remark 4.3.4. Among the huge amount of literature studying basins of attraction of system equilibria, we note that there are many ways of enlarging
the basin of attraction of a system equilibria - for instance using backstepping and CLFs with singularities and Zubov’s method [34], [35]. The importance of studying these ways is that enlarging the basin of attraction of equilibrium of a system is of way of showing how robust is the system. In other words the bigger the basin of attraction of an equilibrium, the more robust is the system around this equilibrium.

4.4 Conclusion

We apply the Lyapunov method on the system (3.2) to estimate the basin of attraction of all non-zero equilibrium. To do that, we rebuild the system using Taylor series to make a systems that is highly structured. This allows us to make estimates in Lyapunov function arguments. We applied the estimates to two examples.
Chapter 5

Harvesting Efforts

5.1 Introduction

The problem of keeping an environment in desired circumstances is a key challenge. In ecosystems which are exposed to streams of alien invasions this issue is of particular importance where we have seen many ecosystems collapse as a consequence of ignoring the impact of alien invaders [14]. Deploying the right management policy could play a significant role in avoiding such disasters. In this chapter, the main issue we explore is the effect of harvesting in coupled resident-invader systems. In some circumstances, eradicating one of the species from the ecosystem is one of the objectives, since the invader (or the resident) could be a harmful pest and this might have adverse effects, for instance, causing economic damage or one species to out-compete the other species and so drive them to extinction [2].
5.2 Harvesting a Single Population

Before we consider harvesting a two population, resident-invader model, to motivate a number of key ideas we first consider the harvesting of a single, stage-structured population. So we start with a single population with harvesting effort $H$ described as follows:

$$x_{t+1} = (I - H) [A + f(Ex_t)DE] x_t. \quad (5.1)$$

In equation $5.1$, $I$ is the identity matrix of appropriate dimension, $E$ and $D$ are non-negative row and column vectors, $f$ is a non-linear, non-increasing, density dependent function, and $H$ is a diagonal matrix with diagonal elements $h_i$ that determine the proportion of individuals removed from stage $i$ at time $t$. The diagonal entries of $H$ satisfy the condition

$$0 \leq h_i < 1.$$

In subsequent analysis we will extend the model to other situations, e.g. where $f(\cdot)$ is not assumed to be a function of $Ex$.

We borrow some ideas from [32] on a trichotomy of stability for density dependent population models. One of the ingredients of this approach is to assume that the matrix $A + pDE$ is primitive for some positive $p$. But to use the ideas from [32] we actually need this to be true with $A$ replaced by $(I - H)A$ and $D$ replaced by $(I - H)D$.

**Lemma 5.2.1.** When $0 < h_i < 1$ for each $i$, then primitivity of $A + pDE$ is inherited by $(I - H)(A + pDE)$.

**Proof.** The edge connections in the life cycle graph of $(I - H)(A + pDE)$ are
the same as those of $A + pDE$ because the diagonal entries of $I - H$ are non-zero. Also $(I - H)(A + pDE)$ is non-negative because the entries of $(I - H)$ are non-negative. Hence $(I - H)(A + pDE)$ is primitive when $A + pDE$ is.

A second key assumption in [32] is that the dominant eigenvalue of $A$ is less than one. Again this is inherited by the harvesting system (5.1).

**Lemma 5.2.2.** When $0 < h_i < 1$, then the dominant eigenvalue of $(I - H)A$ is less than or equal to the dominant eigenvalue of $A$.

For each harvesting matrix $H$ we can associate with (5.1) the “steady state gain”

$$g(H) = E(I - (I - H)A)^{-1}(I - H)D,$$

and define

$$\rho(H) = \frac{1}{g(H)}.$$

For any $H$, $\rho(H)$ is finite and positive because of the assumed primitivity and because $D$ and $E$ are non-zero, see Lemma 2.1 in [32]. We associate with the non-linearity $f$ the “non-linear gains”

$$f_0 = \lim_{y \to 0^+} f(y) \in (0, \infty] \quad \text{and} \quad f_\infty = \lim_{y \to \infty} f(y) \in [0, f_0).$$

For illustration of the last line of equations above see Figure 5.1 for a plot of the function $yf(y) = y(8 + y)/(1 + y)$ with the values of $f_0 = 8$ and $f_\infty = 1$. 
Figure 5.1: The blue line shows the non-linear function $yf(y) = (8 + y)y/(1 + y)$, the line with slope $f_0 = 8$ is in green and the line with slope $f_\infty = 1$ is in red.

An equilibrium $x^*$ of (5.1) is *globally asymptotically stable* if $x_t \rightarrow x^*$ for every $x_0 \geq 0$. We show that the global dynamics of the harvested system (5.1) exhibit a trichotomy of stability which is completely characterised in terms of the steady state gain of the harvested system, or its reciprocal $\rho(H)$, and the quantities $f_0$ and $f_\infty$. We recall, from [32], a result we restate here in terms of the system $((I - H)A, (I - H)D, E)$.

**Lemma 5.2.3.** If $p < \rho(H)$, then the spectral radius $r((I - H)A + p(I - H)DE) < 1$ whilst if $p > \rho(H)$ then $r((I - H)A + p(I - H)DE) > 1$.

**Theorem 5.2.7.** Consider the non-linear (density dependent) system (5.1) under the following assumptions $A1 - A4$:
(A1) $A$ is non-negative with spectral radius $r(A) < 1$;

(A2) the vectors $D$ and $E$ are non-negative, non-zero row and column vectors respectively;

(A3) the density dependence $yf(y)$ is non-negative, continuous on $\{y \geq 0\}$ vanishes at $y = 0$ and $f(y)$ is decreasing for $y > 0$ and

\[
 f_0 = \lim_{y \to 0^+} f(y) \in (0, \infty] \quad \text{and} \quad f_{\infty} = \lim_{y \to \infty} f(y) \in [0, f_0).
\]

(A4) $A + pDE$ is primitive for some $p \geq 0$, i.e. $(A + pDE)^k$ is a positive matrix for some $p \geq 0$ and $k \in \mathbb{N}$. Since the di-graph of $A + pDE$ is the same for all positive $p$, it follows that $A + pDE$ is, in fact, primitive for all non-negative $p$.

Let $H$ be diagonal with diagonal entries strictly between 0 and 1. Then the following trichotomy of stability holds:

1. If $f_0 < \rho(H)$, then 0 is a globally asymptotically stable equilibrium of the harvested system [5.1].

2. If $f_{\infty} > \rho(H)$, then 0 is unstable and if $x_0$ is non-negative and non-zero, then $x_t$ is strongly divergent so that

\[
 \lim_{t \to \infty} (\min(x_t)) = \infty \quad \text{for all non negative} \quad x_0.
\]

3. Suppose in addition that the function $y \mapsto yf(y)$ is non-decreasing on $\mathbb{R}^+$. If $f_{\infty} < \rho^*(H) < f_0$, then there exists $y^* > 0$ so that

\[
 y^* f(y^*) = \rho(H)y^*
\]
and for all $x_0 \in \mathbb{R}_+^n$

$$
\lim_{t \to \infty} x_t = x^*,
$$

(5.2)

where the limit $x^*$ is given by

$$x^* := (I - (I - H)A)^{-1}(I - H)d\rho^*y^*.$$

Remark 5.2.5. 1. This result follows directly from the corresponding result in [32]. The proof is essentially the same since the required assumptions on (5.1) hold.

2. The key ingredient of Theorem 5.2.7 is that the conclusion of the trichotomy depends on $H$. Determining the values of $h_i$ so that $\rho(H)$ lies in the range of $(f_\infty, f_0)$ will tell us acceptable harvesting rates without losing stability of $x^*$. On the other hand, if we have unwanted species, then our choice of $h_i$ will allow us to force the species to die out. As we vary the diagonal entries in $H$ so one of

$$\rho(H) < f_\infty, \quad f_\infty < \rho(H) < f_0, \quad \rho(H) > f_0$$

will hold. This will determine partitioning hyper-surfaces in the $(h_1, \ldots, h_n)$ space for which we have extinction, explosion or convergence to a positive steady state. Figure 5.3 shows a sketched graph illustrating the result of the Theorem 5.2.7.
Figure 5.2: This graph depicts the region in the harvesting parameter space for which we have extinction \( x(t) \to 0 \), explosion \( x(t) \to \infty \) or convergence to a positive steady state.

To obtain the trichotomy of stability result, and in particular its characterisation in terms of \( \rho(H) \), \( f_0 \) and \( f_\infty \), we used the fact that the density dependence has the special form

\[
f(y)y, \ \text{with} \ y = c^T x.\]

Whilst this sort of density dependence is common, see the discussion in [32], a more general set up would be to assume a density dependence of the form

\[
f(a^T x)Ex\]

in which \( f \) is non-negative, continuous and bounded. This is the model as-
sumptions used in Chapter 3. In this case, establishing the trichotomy is not as easy although general, abstract results exist [39]. Even when existence of the trichotomy can be proved, it is then more difficult to describe the trichotomy via something like $\rho(H)$ and the nonlinear gains $f_0$ and $f_\infty$. However, partial results are possible as described in the proposition to follow. First set

$$
 f_{\text{min}} = \min_{y \geq 0} f(y) \geq 0 \quad \text{and} \quad f_{\text{max}} = \max_{y \geq 0} f(y).
$$

We can rewrite the system (5.1) as follows:

$$
 x_{t+1} = (I - H) \left( Ax_t + f(a^T x_t)DEx_t \right).
$$

(5.3)

where $a$ is a positive vector (e.g. $a^T = (1 \cdots 1)$) would make $f$ a function of population density $\|x_t\|_1$.

**Proposition 5.2.2.** Consider the system (5.3) with the assumptions (A1), (A2) and (A4). Then

1. If $f_{\text{max}} < \rho(H)$, then (5.3) has a unique equilibrium at $x = 0$ which is globally asymptotically stable.

2. If $f_{\text{min}} > \rho(H)$, then $x = 0$ is unstable and every non-zero solution diverges.

**Proof.**

1. If $f_{\text{max}} < \rho(H)$, then

$$
 x_{t+1} = (I - H) \left[ Ax_t + Df(a^T x_t)Ex_t \right] \leq (I - H) [Ax_t + pDEx_t]
$$
for some \( p < \rho(H) \). It follows that
\[
\|x_t\| \leq \|(I - H)(A + pDE))^t x_0\|.
\]

But \( r((I - H)A + p(I - H)DE) < 1 \).

So \( x = 0 \) is globally asymptotically stable.

2. Suppose \( f_\infty > p^*_c \). Then
\[
x_{t+1} = (I - H) [Ax_t + bf(a^T x_t)Ex_t] \geq (I - H) [Ax_t + pDEx_t], \quad (5.4)
\]
for some \( p > \rho(H) \). Let \( v^T \) and \( w \) be the positive left and right eigenvectors of \((I - H)(A + pDE)\) corresponding to the dominant eigenvalue \( \lambda = r((I - H)(A + pDE)) > 1 \). Then, using an eigenmode expansion in the right hand side of the inequality (5.4) we have
\[
\lim_{t \to \infty} \lambda^{-t} x_t \geq \lim_{t \to \infty} \lambda^{-t}((I - H)(A + pDE))^t x_0 = \frac{v^T x_0}{v^T w} w.
\]

But \( x_0 \) is non-zero and non-negative. It follows that \( x = 0 \) is an unstable equilibrium and all solutions diverge to \( \infty \).

\[
\]

5.2.1 Examples

We consider a trichotomy of stability for a Chinnook Salmon model (3.4.2) when we add the effect of fishing/harvesting. In this example, the density dependence has the form
\[
yf(y)
\]
CHAPTER 5. HARVESTING EFFORTS

and so we do obtain the trichotomy of stability as given by Theorem 5.2.7. In the second example we consider a hypothetical model in which we relax the form of the density dependence so that it has the form \( f(a^T x)Ex \) with \( a \neq E \). In this case we only obtain partial results determining sufficient conditions for \( x = 0 \) to be globally asymptotically stable or for all non-zero solutions to diverge.

**Example 5.2.6.** Consider the model (5.3) with a population projection matrix for Chinook Salmon. The model is structured with 5 stage classes with stages 3 – 5 representing adult fish which spawn. The population projection model has the form

\[
A = \begin{pmatrix}
0 & 0 & 0 & 0 & 0 \\
0.0131 & 0 & 0 & 0 & 0 \\
0 & 0.8 & 0 & 0 & 0 \\
0 & 0 & 0.7896 & 0 & 0 \\
0 & 0 & 0 & 0.6728 & 0
\end{pmatrix}, \quad D = \begin{pmatrix}
1 \\
0 \\
0 \\
0 \\
0
\end{pmatrix}, \quad E = \begin{pmatrix}
0 \\
0 \\
0.3262 \\
5.0157 \\
39.6647
\end{pmatrix}.
\]

In this example, density dependence affects fecundity.

In this case \((I - H)(A + pDE)\) is primitive for all positive \( p \) and the smallest power so that \(((I - H)(A + pDE))^k\) is a positive matrix is \( k = 8 \).

We assume a density dependence \( f(y)y, y = Ex \), with the function \( f \) defined as follows:

\[
f(y) = \frac{V}{K + y} \quad \text{with } V > 0 \text{ and } K > 0.
\]

For this \( f \) we have

\[
f_0 = \frac{V}{K} \quad \text{whilst } \quad f_\infty = 0.
\]

So for this specific function we only have a dichotomy of stability in that either
CHAPTER 5. HARVESTING EFFORTS

\( x = 0 \) is globally asymptotically stable or there is a positive steady state that is globally asymptotically stable.

We consider a harvesting/fishing effort with arbitrary choice:

\[
H = \begin{pmatrix}
0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 \\
0 & 0 & h_1 & 0 & 0 \\
0 & 0 & 0 & h_2 & 0 \\
0 & 0 & 0 & 0 & h_1 \\
\end{pmatrix},
\]

where \( 0 < h_1, h_2 < 1 \).

Suppose first that harvesting is fixed with, for example, \( h_1 = 0.005 \) and \( h_2 = 0.003 \). Then

\[
\rho(H) = \frac{1}{e^T(H - A)^{-1}(I - H)D} = 3.8088.
\]

It follows that:

1. \( 0 \) is globally asymptotically stable if \( f_0 = \frac{V}{K} < 3.8088 \) and
2. there is a positive, globally asymptotically stable equilibrium if \( 3.8088 < f_\infty = \frac{V}{K} \).

For arbitrary harvesting, the dichotomy of stability partitions the 2-dimensional harvesting parameter set \((h_1, h_2)\) depending on whether \( x = 0 \) is globally asymptotically stable or \( x = x^* \neq 0 \) is globally asymptotically stable. Obviously, this depends also on our choice of \( V \) and \( K \). This is depicted in Figure 5.3.
CHAPTER 5. HARVESTING EFFORTS

Figure 5.3: This curve partitions the harvesting values so that either \( x = 0 \) is globally asymptotically stable or there is a positive, globally asymptotically stable equilibrium. In these calculations \( V = 8 \) and \( K = 4 \).

Example 5.2.7. Consider the system (5.3) for a simple \( 2 \times 2 \) population projection model with harvesting factor \( H \). The model is described as follows:

\[
A = \begin{pmatrix} 0 & 0 \\ 0.5 & 0.7 \end{pmatrix}, \quad E = \begin{pmatrix} 0 & 1 \end{pmatrix}, \quad D = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad a = \begin{pmatrix} 1 & 1 \end{pmatrix},
\]

and the diagonal harvesting matrix:

\[
H = \begin{pmatrix} h_1 & 0 \\ 0 & h_2 \end{pmatrix}
\]
and density dependence \( f(a^T x)Ex \) and \( f(y) \) is given as above. In this case

\[
f_{\text{min}} = 0 \quad \text{and} \quad f_{\text{max}} = \frac{V}{K}.
\]

With \( h_1 = 0.005, h_2 = 0.003 \) we have:

\[
\rho(H) = \frac{1}{G_{ED}} = 0.6
\]

Then \( x = 0 \) is globally asymptotically stable if

\[
\frac{V}{K} < 0.6.
\]

*See Figure 5.4.*

---

Figure 5.4: Above the curve the higher harvesting values force the equilibrium \((0,0)\) to be globally asymptotically stable obtained by varying the values of \( h_1 \) and \( h_2 \) between zero and one. Here \( V = 8, K = 14 \).
5.3 Harvesting Effort in a Resident-Invader System

In this section we extend the work in Section 5.2 to the case of two populations structured as in the matrix model of (3.2). We incorporate harvesting effort $H$ in both the resident and the invader dynamics and derive sufficient conditions for the coupled resident-invader ecosystem to exhibit at most one non-zero equilibrium.

Assume that we have a species of resident $x(t)$ and invasive pest $z(t)$ which both feed from the same resource, and we harvest each species so that at each time we take a proportion $H_1x(t)$ and $H_2z(t)$ from the resident and the pest respectively. Adding such harvesting to the coupled model (3.2) yields a harvested resident-invader system:

$$
\begin{align*}
    x(t+1) &= (I - H_1)(A + f(M(t))DE)x(t) \\
    z(t+1) &= (I - H_2)(A + pBC + g(N(t))DE)z(t).
\end{align*}
$$

We make the following assumptions:

(B1) The non-negative transition matrix $A$ stable i.e. $r(A) < 1$;

(B2) the vectors $D, B, C$ and $E$ are non-negative and non-zero. The quantities of $M$ and $N$ are functions of $a_1^T x, a_2^T z$ and $a_3^T z$ where $a_1$ is a row vector of 1’s, $a_2 = \alpha a_1$ and $a_3 = \beta a$ so that:

$$
M = a_1^T x + a_2^T z, \quad N = a_1^T x + a_3^T z.
$$

(B3) $H_1 = diag((h_{1i}))$, and $H_2 = diag((h_{2i}))$ are the harvesting rates for each of the two populations.
(B4) The density dependence functions \( f \) and \( g \) are both continuous positive and bounded.

(B5) \( A + fDE \) is primitive for some \( f \geq 0 \), i.e. \((A + fDE)^k\) is a positive matrix for some \( f \geq 0 \) and \( k \in \mathbb{N} \). Since the di-graph of \( A + fDE \) is the same for all positive \( p \), it follows that \( A + fDE \) is, in fact, primitive for all non-negative \( f \).

We assume that \( A + pBC + gDE \) is primitive for some \( g, p \geq 0 \), i.e. \((A + pBC + gDE)^k\) is a positive matrix for some \( g, p \geq 0 \) and \( k \in \mathbb{N} \). Since the di-graph of \( A + pBC + gDE \) is the same for all positive \( p \) and \( g \), it follows that \( A + pBC + gDE \) is, in fact, primitive for all non-negative \( p \) and \( g \).

Our goal is to find threshold harvesting rates which guarantee the desired population of Equation (5.1) model grows with harvesting or forces the unwanted species to go extinct.

### 5.3.1 Harvesting State

At equilibrium, the model (5.1) has a resident-only steady state: \((x^*, 0)\) given by

\[
x^* = (I - H_1)(A + f^*DE)x^*.
\]

Here \( f^* = f(M^*) \) and \( M^* = a^T x^* \). Rearranging this as before yields

\[
x^* = (I - (I - H_1)A)^{-1}(I - H_1)f^DE x^*
\]
or simply

\[ x^* = ((I - H_1)^{-1} - A)^{-1} f^* D E x^*. \]

Multiplying on both sides by \( E \) gives

\[ E x^* = E((I - H_1)^{-1} - A)^{-1} f^* D E x^* \]

so that

\[ 1 = E((I - H_1)^{-1} - A)^{-1} f^* D. \]

Define

\[ \rho_1(H_1) := \frac{1}{G_{ED}} = \frac{1}{E((I - H_1)^{-1} - A)^{-1} D} \]

where

\[ \tilde{G}_{ED} = E(\tilde{H}_1 - A)^{-1} D \text{ and } \tilde{H}_1 = (I - H_1)^{-1}. \]

The key question is: With harvesting, do we have a non-zero steady state?

According to the approach developed above the answer is yes if, and only if

\[ \rho_1(H_1) < f_{\text{max}} \quad (5.2) \]

where \( f_{\text{max}} \) is the maximum value of \( f \).

Hence, if \( f_{\text{max}} > \rho_1(H_1) \), then \( f^* \) exist. Whereas, if \( f_{\text{max}} < \rho_1(H_1) \) then \( f^* \) does not exist and. In fact, when \( f_{\text{max}} < \rho_1(H_1) \), then the zero equilibrium is globally asymptotically stable as shown in the Proposition 5.3.3 below.

We can then vary the harvesting matrix \( H_1 \) so that (5.2) holds.

**Proposition 5.3.3.** Consider the system (5.1) with hypothesis (B1) to (B5).

If

\[ f_{\text{max}} < \rho_1(H_1), \]
then for all $x(0) \neq 0$, 

$$\lim_{t \to \infty} x(t) = 0$$

**Proof**

We know from (5.2) that $f(M)$ is bounded. That is

$$|f(M)| < f_{\text{max}}.$$ 

This guarantees

$$x_{t+1} = (I - H_1)(A + f_{M_1}DE)x_t \leq (I - H_1)(A + f_{\text{max}}DE)x_t.$$ 

But

$$f_{\text{max}} \hat{G}_{ED}(1) < 1$$

so

$$\lambda((I - H_1)(A + f_{\text{max}}DE)) < 1.$$ 

Then

$$x(t) \leq ((I - H_1)(A + f_{\text{max}}DE))^t x(0) \to 0.$$ 

So $x = 0$ is globally asymptotically stable.

If the target population is the invader then we look at the invader only equilibrium $(0, z^*)$. Then

$$z^* = (I - H_2)(A + pBC + g^*DE)z^*$$
and analysing as above we obtain

\[ z^* = ((I - H_2)^{-1} - A - pBC)^{-1}g^*DEz^* \]

and multiplying on both sides by \( E \) and simplifying

\[ Ez^* = E((I - H_2)^{-1} - A - pBC)^{-1}g^*DEz^* \]

or

\[ 1 = E((I - H_2)^{-1} - A - pBC)^{-1}g^*D \, . \]

Define

\[ \rho_2(H_2) := \frac{1}{E((I - H_2)^{-1} - A - pBC)^{-1}D}. \]

Rearranging we have:

\[ \rho_2(H_2) = \frac{1}{\tilde{G}_{ED} + p\tilde{G}_{EB}(1 - p\tilde{G}_{CB})^{-1}\tilde{G}_{CD}} \]

where \( \tilde{G}_{EB} = E(\tilde{H}_2 - A)^{-1}B \), \( \tilde{G}_{CB} = C(\tilde{H} - A)^{-1}B \), \( \tilde{G}_{CD} = C(\tilde{H}_2 - A)^{-1}D \) and \( \tilde{H}_2 = (I - H_2)^{-1} \).

In this case the harvesting condition that guarantees extinction of the invader is

\[ \rho_2(H_2) > g_{\text{max}} \quad (5.3) \]

where \( g_{\text{max}} \) is the maximum value of \( g \). Again we can say that:

if \( g_{\text{max}} > \rho_2(H_2) \), then \( g^* \) exist. Whereas, if \( g_{\text{max}} < \rho_2(H_2) \) then \( g^* \) does not exist and in fact \( z(t) \to 0 \) and harvesting forces the invader to die out as shown in the Proposition 5.3.4.
Proposition 5.3.4. If
\[ g_{\text{max}} < \rho_2(H_2), \]
then for all \( z(0) \neq 0 \),
\[ \lim_{t \to \infty} z(t) = 0 \]

Remark 5.3.6. Proposition 5.3.3 and Proposition 5.3.4 give conditions under which either \( x_t \) or \( z_t \) go extinct.

5.3.2 Examples

Example 5.3.8. Here we re-examine Example 3.3 in the presence of a harvesting factor.

The 2 \( \times \) 2 invasion model is then:

\[
A = \begin{pmatrix} 0 & 0 \\ 0.5 & 0.7 \end{pmatrix}, \quad E = C = \begin{pmatrix} 0 & 1 \end{pmatrix}, \quad D = B = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad a = \begin{pmatrix} 1 & 1 \end{pmatrix}, \quad c' = 1,
\]

\[ p = 0.4, M^* = |x^*| + |z^*|, N^* = |x^*| + \alpha |z^*|, \]

with density dependent functions defined as follows:

\[
f = \begin{cases} 
2 - cm & m \leq \frac{c}{2} \\
0 & \text{otherwise}
\end{cases}
\]
and
\[
g = \begin{cases} 
2 - c'n & n \leq \frac{c'}{2} \\
0 & \text{otherwise}.
\end{cases}
\]

The diagonal harvesting matrix \( H \) (equal to \( H_1 \) or \( H_2 \)) is given by:
\[
A = \begin{pmatrix} h_1 & 0 \\
0 & h_2 \end{pmatrix}.
\]
The functions \( f \) and \( g \) are both bounded by 2. In fact:
\[
f_{\text{max}} = f_0 = 2 \quad \text{and} \quad f_{\text{min}} = 0.
\]
and
\[
g_{\text{max}} = g_0 = 2 \quad \text{and} \quad g_{\text{min}} = 0.
\]
For the calculation we choose \( h_1 = 0.5 \) and \( h_2 = 0.3 \) (in \( H_1 \) or \( H_2 \)). So we have:
\[
\rho_1(H) = \frac{1}{G_{ED}} = 5.8286
\]
and
\[
\rho_2(H) = \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} = 5.0286.
\]
For general harvesting we have:

- For the population \( x_t \), \( \lim_{t \to \infty} x(t) = 0 \) when

\[
\rho_1(H_1) > 2.
\]

See Figure 5.5.
CHAPTER 5. HARVESTING EFFORTS

Harvesting State

\[ H \]

The entry \( h_1 \) of the harvesting matrix \( H \)

The entry \( h_2 \) of the harvesting matrix \( H \)

\[ \begin{array}{ccccccc}
0.1 & 0.2 & 0.3 & 0.4 & 0.5 & 0.6 & 0.7 & 0.8 & 0.9 \\
0.1 & & & & & & & \\
0.2 & & & & & & & \\
0.3 & & & & & & & \\
0.4 & & & & & & & \\
0.5 & & & & & & & \\
0.6 & & & & & & & \\
0.7 & & & & & & & \\
0.8 & & & & & & & \\
0.9 & & & & & & & \\
\end{array} \]

Harvesting State

\[ \begin{array}{ccccccc}
\text{The entry } h_1 \text{ of the harvesting matrix } H \\
\text{The entry } h_2 \text{ of the harvesting matrix } H \\
\end{array} \]

Figure 5.5: Above the curve gives the harvesting values which force the resident population \( x(t) \) to tend to zero.

- For the population \( z_t \) we have \( g \) bounded by 2 and when

\[ \rho_2(H_2) > 2 \]

we have that \( \lim_{t \to \infty} z(t) = 0 \). Hence the invading population will eventually go extinct. See Figure 5.6.
Figure 5.6: Above the curve gives the harvesting values which force the resident population $z(t)$ to tend to zero.

Example 5.3.9. We reconsider Example 3.4.2 with harvesting factor $H_1$ and $H_2$. Here $\lambda_{max}(A) < 1$. We assume density dependent functions $f(M) = \exp(-0.1M)$ and $g(N) = \exp(-N)$ with range $(0, 1]$. The $5 \times 5$ invasion model is:

$$A = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 \\
0.0131 & 0 & 0 & 0 & 0 \\
0 & 0.8 & 0 & 0 & 0 \\
0 & 0 & 0.7896 & 0 & 0 \\
0 & 0 & 0 & 0.6728 & 0 \\
\end{bmatrix}, D = B = \begin{bmatrix} 1 \\
0 \\
0 \\
0 \\
0 \\
\end{bmatrix}.$$
\[ E = C = \begin{bmatrix} 0 & 0 & 0.3262 & 5.0157 & 39.6647 \end{bmatrix}, p = 0.2, a = \begin{bmatrix} 1 & 1 & 1 & 1 \end{bmatrix}, \]

and,

\[ M^{*} = |x^{*}| + \alpha|z^{*}|, \quad N^{*} = |x^{*}| + |z^{*}|. \]

We assume a diagonal harvesting matrix \( H \) (equal to \( H_1 \) or \( H_2 \)) by:

\[
A = \begin{bmatrix}
h_1 & 0 & 0 & 0 & 0 \\
0 & h_2 & 0 & 0 & 0 \\
0 & 0 & h_1 & 0 & 0 \\
0 & 0 & 0 & h_2 & 0 \\
0 & 0 & 0 & 0 & h_1 \\
\end{bmatrix},
\]

The function \( f \) and \( g \) are bounded by 1. In fact:

\[ f_{\text{max}} = f_0 = 1 \text{ and } f_{\text{min}} = 0, \]

and

\[ g_{\text{max}} = g_0 = 1 \text{ and } g_{\text{min}} = 0. \]

For the calculation we choose \( h_1 = 0.005 \) and \( h_2 = 0.003 \) (in \( H_1 \) or \( H_2 \)).

So we have:

\[ \rho_1(H) = \frac{1}{G_{ED}} = 3.8588 \]

and

\[ \rho_2(H) = \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} = 3.6578. \]

We obtain the following:
CHAPTER 5. HARVESTING EFFORTS

• For the population $x_t$, $\lim_{t \to \infty} x(t) = 0$ when

$$\rho_1(H_1) > 1.$$ 

See Figure 5.7.

Figure 5.7: Above the curve gives the harvesting values which force the resident population $x(t)$ to tend to zero.

• For the population $z_t$, $\lim_{t \to \infty} z(t) = 0$ when

$$\rho_2(H_2) > 1.$$ 

See Figure 5.8.
5.4 Conclusion

In this Chapter we have added harvesting to our models. To motivate our analysis we first considered the case of a single, stage structured population. Building on results in [32], we show that harvesting forces a trichotomy of stability and this trichotomy partitions the harvesting parameter space into three regions: extinction; global convergence to a positive steady state and population explosion. The trichotomy only holds when the density dependence has a special structure. When we relax the restrictions on the density dependence, we can show that when zero is the only steady state then it is GAS. We then extend these results to the case of harvesting a resident-invader system. We
characterise regions in the harvesting parameter space in which either the resident or the invader is forced into extension. We illustrate the results with a number of examples.
Chapter 6

Population Momentum, System Robustness and Biological Invasion

6.1 Introduction

The work in this chapter builds on work initiated in [40]. It considers the interplay between population momentum, system robustness and biological invasion. Specifically it explores whether population transients in an invader can facilitate successful invasion when the long term dynamics would suggest otherwise. If we introduce neglected non-linear effects, such as an Allee effect [1], in a highly non-normal system, then linearisation may or may not give the correct prediction of invasion; in other words the invasion exponent may give misleading indications of a species’ ability to invade [40]. We will not study this problem comprehensively. Instead, our purpose is merely to point to alternative mechanisms by which an invader may become established.
The invasion exponent, \( \theta = \log(\lambda) \), is the logarithm of the dominant eigenvalue of the linearised invasion matrix \( A_{\text{inv}} \). It is obtained by linearising the non-linear dynamics of the resident-invader system around a steady state, in which the invader is at zero density and the resident is at carrying capacity \([5]\). If the invasion exponent is negative, then invasion is predicted to fail \([41]\). In fact for the model, linear stability theory guarantees that the invasion fails when the density of the invader is “small enough” and the resident does not deviate “too far away” from carrying capacity. If the invasion exponent is positive, then linear stability also guarantees that the “resident only” equilibrium is not locally stable and in this case, invasion is possible \([41]\). In such situations, with sufficiently small perturbations, the invasion exponent does capture the behaviour of the system correctly. In the previous chapters we used such linearisation arguments to study the stability of resident-only, invader-only and co-existing equilibria. We also estimated the basins of attraction of stable equilibria which can help to quantify when such linearisation techniques are valid. However, such basins of attraction calculations are complicated and our estimates produced regions which were very small.

To properly understand the fate of an invasion attempt requires a deeper understanding of the underlying dynamics, and especially in determining whether an invasion will fail, requires us to understand the caveats above concerning “small enough” and “too far away”. Unfortunately, whilst such detailed analysis might be possible for systems whose models are well understood and properly parameterised, for the ecological models arising in a context of biological invasions, it is very unlikely that such detailed information will be
readily available. Indeed, it is unlikely that there will be sufficient data available to parameterise the dynamics of a novel invasive species in anything but the crudest terms. The lack of data and the resulting uncertainty attached to any modelling conclusion is just one issue; there are many more. Putting to one side the complexities surrounding the computation of basins of attraction, the computation of invasion exponents is not sensitive to whether or not the linearised PPMs are normal - all that matters is the value of \( \log(\lambda) \). We will therefore arrive at the same prediction of invasion irrespective of whether the linearised invasion matrix is highly normal and well behaved or whether it is very non-normal and badly behaved. However, the population dynamics of natural systems tend to have more complicated, and especially more non-normal behaviour. This is due to many factors, but primarily because reproductive effort tends to be skewed across age or stage classes. Such non-normal behaviour produces large transient dynamics. These transients are commonplace in stage-structured populations and are now becoming recognised as a source of less predictable dynamics. Further complications arise when one is forced to make over-simplifying assumptions about the dynamics of the invader. Here unmodelled density dependence could be an additional problem.

In summary, the modelling and prediction of biological invasion is problematic because of (i) model uncertainty (ii) transient dynamics (iii) unmodelled density dependence and (iv) an over-reliance on infinitesimal analyses requiring disturbances away from a steady state to be “small”.

Engineers and numerical analysts have, for many years, recognised the im-
portance of the issues (i) - (iv) above [13], [20]. In the context of numerical analysis, Dahlquist [42], [43] introduced the notion of initial growth to capture transients in numerical schemes. Control engineers have developed tools of robust control to combine optimality and uncertainty within a common modelling framework. Each of these approaches attempts to retain the simplifying and appealing features of linearisations and eigenvalues and, in the case of robust control, quadratic cost performance, but recognise, either directly or indirectly, the importance of capturing model uncertainty. Such principles of robustness and uncertainty are central to the development of pseudo-spectrum techniques. Pseudo-spectrum tools can be used to explain an apparent mismatch between predictions based on models and real observations, highlighted especially in determining the transition from plane to turbulent flow in hydrodynamic stability theory [44]. Here the main result is that it is not the transition of eigenvalues, but rather the transition of pseudo-eigenvalues into instability that captures the transition to unstable, turbulent flow. These issues of model uncertainty and disturbances are gaining traction in mainstream ecological modelling, where asymptotic eigenvalue-based techniques are being complemented with other quantitative tools based around population momentum and inertia, indices of transient dynamics and transfer function analyses of asymptotic and transient dynamics. But these recent developments are mostly for single populations or for linear models of meta populations. To what extent can these robustness approaches be carried over to the analysis and prediction of density dependent biological invasions? Can we appeal to an analogy with transition to turbulent flow - i.e as we increase the fitness of an invasive demography, is the success of an invasion captured by something akin to pseudo-invasion? Or can we attribute successful biological invasion to
some measure of transients or population momentum?

Biological invasions are complex processes with density dependence, spatial components and stochastic effects [15]. Here we will not present a comprehensive modelling framework. Instead our focus is to highlight in the simplest terms the way in which transients, model non-normality and neglected density dependence interact to promote invasion success. We use a simple three-stage model of the resident and invader dynamics [40]. We manipulate the non-normality or proneness to transients by adjusting the fecundity of each stage class. The density dependent dynamics of the invader are identical except for one transition where a density independent transition is replaced by a density dependent Allee-type transition rate [45]. We show that as we increase the population momentum of the linearised invasion matrix so the strength of the Allee effect needed for invasion decreases. We show similar, though weaker association for other transient measures. The key message is that to assess the likelihood of invasion success, one should pay attention to the population momentum of the invader; even if the invasion exponent is negative, a large value of population momentum will suggest that biological invasion is likely.

The aim of this chapter is to introduce a new indicator of a successful invasion in terms of a robustness threshold. We can use this to indicate the likelihood of successful invasion in the case of non-normal systems with a negative invasion exponent. When the robustness is high and the Allee effect is weak, then we can rely on the invasion exponent to predict the invasion establishment. However, in the short time scale (transient), as robustness decreases and the strength of the Allee effect increases, so invasion becomes more likely.
It is the interplay between Allee effects and short time scale transients that produces results at odds with results obtained on long time scales. Throughout this chapter all our analysis will be in a short time scale. Note that the success of the invasion is also dependent on which life stage the invader is in. Stages with high transient responses can be invaded at lower Allee effect thresholds.

The chapter is organized as follows: In Section 6.2 we reconsider the invasion model (3.2) with the perturbation element $p$ as a non-linear density dependent function $\alpha(N_z(t))$ where $N_z(t)$ is the invader density. Then we illustrate with examples some related issues, such as Allee effects and the invasion exponent. Other related themes, such as non-normality of PPMs, transient dynamics and population momentum are discussed with examples in Section 6.3. Section 6.4 is devoted to the main part of this chapter, a simulation study based on 100 different PPMs. Discussion and conclusions are given in Section 6.5 and Sections 6.6.

### 6.2 System Set-Up

In previous chapters, we considered the model (3.2) where the difference between the resident dynamics and those of the invader is a linear perturbation element defined by the constant parameter $p$ and structure matrices $B$ and $C$. Here, we replace this constant term with a density dependent term $\alpha(N_z)$ depending on the density $N_z$ of the invader. This is meant to capture a potential advantage for the invader dynamics. In other words, the only difference between the resident and the invader PPMs assumed here is that the invader has a density dependent Allee effect $\alpha(N_z(t))$. 
Therefore, the stage-structured, density dependent model of the resident-invader system is given by:

\[
x(t + 1) = (A_R + f(N(t))DE_{fec})x(t)
\]
\[
z(t + 1) = (A_I + \alpha(N_z)BC + f(N(t))DE_{fec})z(t).
\]

Here,

- $A_R$ and $A_I$ are the density independent parts of the resident and invader PPMs;
- $E_{fec}$ is a fecundity row and represents the distribution of reproductive effort across ages/stages;
- $f$ is a density dependent function in both the resident and the invader demography;
- $\alpha$ is a non-linear Allee effect;
- $N(t) = |x|_1 + |z|_1$ is the total density of the resident and the invader population;
- $N_z$ is the total population of the resident and $N_z$ the total population of the invader;

Early chapters supposed no Allee-type effect in the invader dynamics and only considered density dependent functions that decrease with increasing density of the population, i.e.

\[z(t + 1) = F(z(t)),\]

with

\[F(z_1) \leq F(z_2) \iff z_1 \geq z_2.\]

However, with the Allee effect, this monotonicity no longer holds.
6.2.1 Allee Effect

The key new ingredient of Model (6.1) compared to models in previous chapters is the term $\alpha(N_z)BC$. When the density of the invader is low and the resident is near to carrying capacity, then we assume that the density dependent PPM of the invader is less than or equal to (in the sense of non-negative matrices) the density dependent PPM of the resident. As density of the invader increases, the term $\alpha(N_z)$ crosses a threshold above which reproduction, growth or survival of the invader is promoted. However, as density grows further, so a second threshold is crossed and for all higher density, the density dependent invader PPM is less than the resident PPM at carrying capacity. The threshold is determined by a value $\alpha^*$ and characterises an Allee effect: when $\alpha(N_z)$ exceeds this threshold then reproduction, growth or survival of the invader is promoted, whereas when $\alpha$ is below this threshold growth is not promoted. Figure 6.1 shows $\alpha^* = 1$ as a threshold value. At very low densities, the Allee effect is not helpful. At low to medium densities, the Allee effect is helpful. At medium to higher and higher densities, the Allee effect fades away. It is the low-medium densities that are promoted by transients and perhaps why transients and Allee effects combine to produce results at odds with the longer time scale results. So in the short time scale, starting from a low density, the Allee effect has negligible effect on population growth because of the difficulty of finding a mate at low densities. When the density of the invader is higher, then the chances of meeting a mate increase and there is the possibility of a window of invader density through which $\alpha(N_z) > \alpha^*$. However, for much higher density, competition effects increase and $\alpha(N_z) < \alpha^*$ for all sufficiently large $\alpha(N_z)$. This process, whereby, between population density thresholds, population growth has a positive relationship with population density, was
suggested by Allee [1]. The Allee effect phenomenon is naturally associated with invasion models, as invasions usually begin with low invader densities. Allee effects can be strong or weak (See Figure 6.1) and these differences in strength can cause significant differences in population dynamics, especially in stage-structured PPMs [45].

\[
a(N) = \frac{N^{\delta - 1}}{1 + bN^\delta}
\]

Figure 6.1: Allee effects. The Allee effect function is \( a(N) = \frac{N^{\delta - 1}}{1 + bN^\delta} \) as a function of invader density with \( b = 0.3 \) and \( \delta = 2.5 \). The left graph shows a weak Allee effect with \( 0.5a(N) \). The right graph represents a strong Allee effect with \( 1.5a(N) \).
6.2.2 Invasion Exponent

If the dynamics of the resident and invader are described by the linear time-invariant PPMs $A_R$ and $A_I$, then the invader will be established at the expense of the resident if

$$\lambda_{\text{max}}(A_I) > \lambda_{\text{max}}(A_R).$$

For density-dependent resident and invader PPMs, the invasion exponent is usually used to check the invadability. The invasion exponent for an invasion process is the logarithm of the maximum eigenvalue $\log(\lambda_{\text{max}}(A_{\text{inv}}))$. Here $A_{\text{inv}}$ is the matrix obtained by linearising the invader dynamics around the resident at carrying capacity and the invader at zero density [5].

The next example shows how the invasion exponent can predict invasion perfectly.

Example 6.2.10. The example based on Example(3) in [40]. Here we simulate a $3 \times 3$ system of resident-invader:

$$RM = A_1 + pB_{\text{fec}}, \quad IM = A_2 + pB_{\text{fec}}.$$  

Here $A_1$ and $A_2$ are randomly generated, but relatively normal matrices scaled to have $\lambda_{\text{max}} < 1$. (To check the non-normality of a matrix using matlab we just check that $A^*A - A^*A$ is small.) The matrices are structured as:

$$A_1, A_2 = \begin{pmatrix} 0 & 0 & 0 \\ v_1 & 0 & 0 \\ 0 & v_2 & v_3 \end{pmatrix},$$

where $v_1, v_2$ and $v_3$ scaled to have values such that $0 < v_1, v_2, v_3 < 1$. The
matrix $B$ is given by

$$ B = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix}, $$

and $E_{fec}$ is randomly generated $1 \times 3$ row, then $RM$ scaled so that $\lambda_{\text{max}}(RM) = 1$. Then the value of $A_2$ rescaled to have slightly bigger or smaller values. So we achieve that at equilibrium the resident is at carrying capacity with chosen value $N^*_x = 1$ and invader supposed to start from the negligible density, say $N^*_z = 0.1$. The density dependent multiplier $p(N)$ is given by:

$$ p(N) = \exp(-0.1N). $$

We run the simulation code twice such that for the first time we choose the parameters so that the invasion exponent is positive and for the second time the parameters has been chosen such that the invasion exponent has a negative value. As we can see from Figure 6.2 the invasion exponent accurately predicts successful invasion. Also, in Figure 6.3 the invasion exponent accurately predicts failed invasion.
Figure 6.2: Invasion exponent predicts successful invasion. The left-hand graph shows the invader growing in density from small density of 0.005, while the one on the right shows the decline of the resident from high density of 1 down to 0.
6.2.3 Motivating Example

In Example 6.2.10 the linear parts of the resident and the invader matrices were normal, and there is no Allee effect considered. Hence the prediction is precisely captured by the invasion exponent. To motivate the idea that system non-robustness and Allee effects can combine to produce surprising results at odds with invasion exponent calculations we consider two simple examples. The model describes interacting populations of resident and invader based on (6.1). Both populations have three-stage structures.

Using the model given by (6.1), we assume that the constant part of the resident is the same as the constant part of the invader except at the entry
(2, 1) which has a value of 0.1 in the resident transient matrix and 0 in the invader transient matrix. The column matrix D specifies that we put the fecundity in the top row of the matrices $A_I$ and $A_R$. The matrices $B$ and $C$ define the place of Allee effect in the entry (2, 1). Specifically, we have:

$$A_R = \begin{pmatrix} 0 & 0 & 0 \\ 0.1 & 0 & 0 \\ 0 & 0.1 & 0.1 \end{pmatrix}, \quad A_I = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0.1 & 0.1 \end{pmatrix}, \quad D = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}$$

$$B = \begin{bmatrix} 0 \\ 0.08 \\ 0 \end{bmatrix}, \quad C = \begin{bmatrix} 1 & 0 & 0 \end{bmatrix}$$

$N_z(t) = \|z(t)\|_1$ (invader density).

The density dependent multiplier $f(N)$ is given by:

$$f(N) = \exp(-N) \quad \text{with} \quad N = \|x\|_1 + \|z\|_1$$

The Allee effect function $\alpha$ is assumed to have the form:

$$\alpha(N_z(t)) = 1 + s \left( \frac{N_z^{\delta-1}}{1 + \delta N_z^\delta} \right), \quad s \in [0, 2]$$

In the first example we assume a fecundity row

$$E_{fec} = \begin{bmatrix} 5 & 2 & 0.1 \end{bmatrix}$$
whilst in the second we assume a fecundity row

\[ E_{fec} = \begin{bmatrix} 0.3 & 4.2 & 10.2 \end{bmatrix} \]

For both fecundity choices we have the same resident carrying capacity \( N^*_x = 1 \) so that

\[ f(1)E_{fec}(I - A_R)^{-1}D = 1 \]

We now make a succession of invasion attempts at times \( t = 0, 100, 200, \ldots \) with initial invader density of \( N^*_z = 0.1 \) but with increasing Allee effect strength achieved by increasing the parameter \( s \) in the function \( \alpha(N_x) \).
The only difference between the two models above is in the fecundity row. The fecundity row in the first example describes a population with high reproduction in early stages but with reproduction declining strongly in latter stages. Conversely, in the second example, fecundity is low in early stages but increases strongly in higher stages. In both PPMs the invasion exponent has a negative sign, indicating no invasion. However the right-hand graph in Figure 6.4 shows that there is invasion when the Allee effect is strong enough.

So why do we have invasion when the invader exponent is negative? Why do we see a significant difference in the success or failure of invasion between
the two PPMs when they differ only in the fecundity row? As we will see, transients and non-robustness are somehow the cause.

6.3 Transients and System Non-Normality

In the simple example described in Section 6.2.3 both systems had comparable invasion exponents but quite different dynamics. So the linearisations are failing to capture essential ingredients of the dynamics. One possible explanation is that whilst the eigendata (eigenvalues, eigenvectors) of a system give all the information concerning the asymptotic dynamics of the system behaviour, the short-term behaviour of the system could be completely different. Because of this, transient behaviour of ecological systems has received much interest in recent years, e.g. [46], [47], and [48].

6.3.1 Transient Dynamics

A population in asymptotically stable steady state does not necessarily settle to this state immediately after being perturbed. Such disturbances could be caused by various factors. Food resources could dwindle rapidly as a result of desertification, or populations could decline rapidly as a result of industrial pollution. Models will return to steady state asymptotically - but what does this mean? What time scales are involved - days, years? Or maybe decades, even centuries. This means the stability may not be useful over timescales when it is wanted, for example, an asymptotically extinct population may show significant (destabilising) growth from a short time scale perspective. All these aspects lead us to a study of transient dynamics. Such transients could persist across the whole time frame of interest.
One of the first ideas of transient dynamics in ecological models can be found in the work of Neubert and Caswell [49]. They introduced the notion of reactivity [49]. It refers to the maximum rate, over all disturbances, at which a population grows, see [49]. For discrete-time models

\[ x(t + 1) = Ax(t) \]

where reactivity is the 1-norm of the transition matrix \( A \). For continuous time models

\[ \dot{x}(x) = Ax(t) \]

where reactivity is the largest eigenvalue of \( A + A^T \). Numerical analysts call this initial growth [42].

Consider a hypothetical size-classified population transition matrix [50]:

\[ A = \begin{pmatrix} .3763 & 0 & .8431 & 8.4312 \\ .1939 & .5421 & 0 & 0 \\ 0 & .1177 & .524 & 0 \\ 0 & 0 & .1291 & .5254 \end{pmatrix} \]

with initial condition \( n_0 = (0 \ 0 \ 0 \ 1)^T \). The maximum eigenvalue of \( A \) is \( \lambda_{\text{max}} = 0.9211 \) which means that asymptotically this population is declining. However we can clearly see from the left-hand graph of Figure 6.5 that the population will face growth before it declines. So the transient dynamics in this example are completely different from the eventual, asymptotic dynamics of the population. The right-hand graph of Figure 6.5 represents the transient
dynamics of a tropical fruit tree population [26] with PPM:

\[
A = \begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 16 & 34 & 59 & 9 \\
.52 & .1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & .02 & .52 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & .16 & .57 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & .3 & .91 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & .05 & .93 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & .05 & .95 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & .03 & .94 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & .04 & .98 \\
\end{pmatrix}
\]

with initial population \( n_0 = (0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 1)^T \). In contrast, the asymptotic behaviour of this population is to grow at a geometric rate \( \lambda_{\text{max}} = 1.0196 \) but the graph shows declining short term transient dynamics.
6.3.2 Population Momentum

Population momentum can be defined in various equivalent ways. For the purpose of this thesis we used the following definition. The stage-specific population momentum $M$, depending on initial population structure $x_0$, is:

$$M(x_0) = \lim_{t \to \infty} \lambda^{-t} \frac{\|x(t)\|}{\|x_0\|},$$

where $\lambda = \lambda_{\text{max}}(A)$. We can also talk of maximum and minimum values of population momentum by maximising and minimising $M(x_0)$ over all possible $x_0$. 

Figure 6.5: The values of $\|A^t\|_1$ over time for the hypothetical PPM (Left), and the tropical fruit tree PPM (Right).
When $x_0$ is a stable stage structure, then $M(x_0) = 1$. The case $M > 1$ means that the population will settle at a size larger than the one at $t = 0$ whereas in the case $M < 1$ it settles at a size smaller than the one at $t = 0$ [5].

6.3.3 System Robustness

The robustness of a system is its ability to tolerate perturbations. To study the future behaviour of a natural population we need to build a model that mimics the real population. The inaccuracy of building such models could lead to very different from reality, and so we need to account for model uncertainty. Model uncertainty is essentially the mismatch between the the mathematical model parameters set-up and the real parameter values. This can be ascribed to many reasons such as imprecise knowledge of model parameters, lack of understanding of the dynamics and simplifications of models...etc [12]. Results obtained from such uncertain models are often deceptive [12].

To overcome of this problem of model uncertainty, robustness theory was developed. In this approach, we study the effect of perturbations, i.e. changes in PPMs parameters, on the behaviour of the system. For example, the collection of all possible spectra calculated from the perturbed systems could have at least one close enough to the real system spectra.

6.3.4 Non-Normality

The asymptotic (long term) behaviour of any model can be captured by the eigenvalues of its Jacobian matrix. The eigendata (eigenvalues and eigenvectors) of a normal matrix can be described in terms of its orthogonal eigen-
vectors. If the Jacobian matrix is normal, then the eigenvalues also actually capture the short term (transient behaviour). This is not the case for non-normal matrices which do not have an orthogonal basis of eigenvectors. A system governed by a non-normal stable matrix could exhibit transient instability behaviour due to the skewness of its eigenvectors. Recent literature \[44\] suggests that attention should be given to the non-normality of the operators governing any dynamic under consideration. If the linearised matrix (Jacobian matrix) is non-normal, then we cannot rely on the eigenvalues to capture the transient behaviour of the system.

**Definition 6.3.7.** A matrix $A$ is called normal whenever:

$$A^* A = AA^*$$

where $(A^*)_j = \tilde{A}_{jk}$.

This means, $A$ is diagonalisable by an orthogonal matrix transformation. Which in turn means that:

$$||A^t||_2 = \lambda_{\text{max}}^t$$

Here $||A||_2$ is the induced 2-norm of $A$.

A matrix is called non-normal if it fails to satisfy the definition of normality i.e.:

$$A^* A \neq AA^*.$$  

We can talk loosely of $A$ being non-normal when we need a large constant $c > 1$ in the bound:

$$||A^t|| \leq c\lambda_{\text{max}}^t,$$

being deliberately vague on choice of matrix norm.
A few well known facts about normal and non normal matrices.\[14\]

1. A stable reactive matrix is a simple example of non-normal matrices. \(A\) is reactive if \(\|A\| >> 1\). Obviously when the PPM is not normal the system is reactive.

2. For any \(n \times n\) matrix \(A\), the following are equivalent:

   - \(A\) is normal.
   - \(A\) has a complete set of orthogonal eigenvectors.
   - \(A\) is unitarily diagonalisable.

3. One way to measure the non-normality of a matrix \(A\) is how much \(A\) fails to satisfy the properties of normal matrices.

   From this point of view Pseudo-spectra are pivotal.

**Definition 6.3.8.** Let \(M\) be an \(n \times n\) matrix and \(\varepsilon\) be a positive number. The \(\varepsilon\)-pseudo-spectrum, \(\Lambda_\varepsilon(M)\), of \(M\) is the set of all eigenvalues of all matrices that lie within \(\varepsilon\) of \(M\):

\[
\Lambda_\varepsilon(M) = \{z \in \mathbb{C} | z \ is \ an \ eigenvalue \ of \ M + P \ for \ some \ P \ with \ \|P\| < \varepsilon\}.
\]

In fact:

\[
\Lambda_\varepsilon(A) = \{\lambda \in \mathbb{C} : \|(\lambda I - A)^{-1}\| \geq \varepsilon^{-1}\}.
\]

so \(\Lambda_\varepsilon(M)\) can be computed using Matlab codes `inv` and `contour`\[44\].

Using Pseudo-spectra we can quantify from the linearised invasion matrix how robust the non-invasion of species is, based purely on approximate models derived from poor data. We can use the Pseudo-spectra as an indicator of non-normality. The non-normality is captured by the size and the shape of the
pseudo-spectra. The normal matrix shows a small shape of bubbles whereas the non-normal matrices show big bubbles. Figure 6.6 shows the pseudo-spectra of two PPMs. It is easy to recognise that the left-hard graph is for a normal matrix while the right graph is for a non-normal matrix.

![Figure 6.6: We depict the pseudo-spectra of two different PPMs. The left-hard graph shows the pseudo-spectrum of a normal matrix. The right-hard graph shows the pseudo-spectrum of a non-normal matrix.](image)

facts.

1. The eigenvalues of a matrix can be quite sensitive to perturbations.

2. The pseudo-spectrum of a matrix is quite robust to perturbations.

3. Pseudo-spectra can be used to quantify transient dynamics.
4. Pseudo-spectra can capture the effects of perturbed dynamics

\[ x(t + 1) = (A + \Delta A)x(t). \]

5. Pseudo-spectra can be refined to handle structured perturbation and stage-structured disturbances. For details see [44].

### 6.4 The Interplay in the Motivating Example

The key matrix is the matrix

\[ A_{inv} = A_I + \alpha(0)BC + f(1)DE_{fec}. \]

The quantity \( \theta = \log(\lambda_{max}(A_{inv})) \) is the invasion exponent. The invasion exponent plays a key role in invasion exponent theory and in determining evolutionarily stable strategies. When the invasion exponent is positive, then rare mutants can invade. When the invasion exponent is negative, then invasion by rare mutants fails. Here, rare means in low enough density that linearisation yields a unstable approximation. But is this ‘rare mutant’ approximation valid? How rare is rare? Do we have enough data to properly parameterise the models so as to be confident in the computations of ‘rare’? This depends strongly on, amongst other things, the behaviour of the linearised matrix, in particular its transients and of neglected nonlinearities. Motivated by the analysis of transition, we expect a strong interplay between transients of this linearised matrix and the strength of neglected/unmodelled density dependence, in particular the strength of the Allee effect \( \alpha(N_z) \). Unlike linearised stability, which is determined simply by the dominant eigenvalue, transients are not described by a single number. Amongst a plethora of measures of transients we focus on four:
• **Invasion Non-normality.** This is measured by $\|A_{inv}A_{inv}^T - A_{inv}^T A_{inv}\|;

• **Invasion Reactivity.** This is the one-time step gain/amplification and is $\|A_{inv}\|;$

• **Maximum Invasion Momentum.** This is $\lim_{t \to \infty} \| (A_{inv}/\lambda_{max}(A_{inv}))^t \|$

• **Invasion Gain.** This is the steady state gain $\|(I - A_{inv})^{-1}\|$

Each of these transient measures will depend on survival and growth parameters and on the fecundity vector $E_{fec}$. For some choices of $E_{fec}$, the transients (non-normality, reactivity, momentum and/or gain) will be large and for others they will be small. We hypothesise that even when the invasion exponent is negative (rare mutants cannot invade), invasion by small in density but not ‘rare’ mutants can succeed when the combined effects of neglected non-linearity, transients and invader density are large enough. We further expect and hypothesise:

1. for a fixed initial density of invader, that there will be a monotone decreasing relationship between magnitude of transient and strength of neglected density dependence;

2. even when the density of the invasion attempt is small, invasion will succeed once the transient exceeds a threshold, e.g. if invasion momentum is large enough this will allow an asymptotically unfit population to invade.

Based on Subsection 6.2.3 and the hypothesis given above, we consider the same example but instead of just two fecundity matrices

\[
E_{fec} = \begin{bmatrix}
5 & 2 & 0.1
\end{bmatrix}
\quad \text{and} \quad
E_{fec} = \begin{bmatrix}
0.3 & 4.2 & 10.2
\end{bmatrix}
\]
we set up one hundred random fecundity matrices. For each fecundity matrix we have an invasion matrix $A_I$. We then order this set of fecundity matrices in four ways according to increases in: non-normality of $A_I$; population momentum; reactivity or invasion gain. The matrices were chosen such that $\lambda_{\text{max}}(A_{\text{inv}})$ is in the range between 0.96 and 0.98, which ensures that the invasion exponent is negative. To ensure throughout that the carrying capacity for the resident in the absence of the invader is set to a density $N_x = 1$, we normalise the fecundity matrices so that

$$f(1)E_{\text{fec}}(I - AR)^{-1}D = 1.$$ 

In the simulation study, the one hundred fecundity matrices resulted in invasion non-normality between 0-300, invasion reactivity between 0-20, invasion momentum between 0-15 and invasion gain between 0-500.

We choose an Allee effect with the special structure

$$\alpha(N_z) = 1 + s \left( \frac{1.1N_z}{0.1(1 + 50(1.1N_z^2)))} \right), s \in [0, 4].$$

The total density $N$ in the density dependent term $f(N)$ is actually chosen such that $N = \|x\| + 2\|z\|$. In this case, if the invader replaces the resident then it does so at a density of 0.5. We needed to do this because of the form of $\alpha(N_z)$ and so that the graphs looked clearer.

We varied the parameter $s$ in the Allee effect and, for each choice of fecundity, recorded the minimum $s$ so that in a time-series simulation we observed a successful invasion. More precisely, in the simulations an invasion was considered successful when

$$N_z(500) > 0.25.$$
In the first case we assume that the invader initial condition is given as

\[ z_0 = \delta \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix} \]

where \( \delta > 0 \) is the invader species initial density which, according to the structure of the vector, is in stage class three.

Figure 6.7 shows clearly how the population momentum exhibits the clearest (smoohest) and most monotone decreasing graph, followed by invasion reactivity, then non-normality, and finally invasion gain.

Apparently, according to Figure 6.7, invasion momentum is the best predictor for the invasion. However, the simulation is based on the assumption that the invader starts initially in stage class three. To further the analysis we perform simulations with other invader initial density regimes, namely, invaders with initial density in stage classes one and two. Figure 6.8 shows the critical Allee effect plotted against stage specific invasion momentum for invasion in each of the three stage classes. So, invasion momentum in stage class one would be

\[ \frac{v^T}{v^T w} \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix} \cdot \]

Whilst the plots of the critical Allee effect against momentum are less smooth, we still see the same pattern. When stage specific momentum is high, so the critical Allee effect is low. Loosely speaking, if transients of the invader are high, then this gives the invader a chance to overcome density thresholds and then invade, even when, according to linearised asymptotic rates of growth,
Figure 6.7: Plots of “transient strength” of the invasion demography ($x$-axis) and minimum strength of Allee effect required for successful invasion ($y$-axis) for four different measures of non-normality: Top Left: Non-normality of $A_{inv}$; Top Right: Reactivity of $A_{inv}$; Bottom Left: Population Momentum of $A_{inv}$; Bottom Right: Steady State Gain of $A_{inv}$. Each sub-plot has four different magnitudes of initial density of invader: 5%, 1%, 0.5% and 0.1% of the density of the resident at carrying capacity in the absence of an invader.
Figure 6.8: These three plots show the invasion stage specific momentum according to initial invader density. The top plot shows the invasion stage class momentum with initial invader density $\delta (0 \ 0)^T$. The middle and the bottom plots show the invasion stage specific momentum with initial invader density at stage two and three, respectively.

invasion would fail.
6.5 Discussion

When the invasion exponent is negative, then \((x^*, 0)\) is an asymptotically stable equilibrium of the density dependent, resident-invader system. This means that if \(x(0)\) is close enough to \(x^*\) and the density of the invader is small, so that \(N_z(0)\) is sufficiently small, then according to linearised stability theory \((x(t), z(t))\) will tend to the equilibrium \((x^*, 0)\) and the invasion attempt fails. In dynamical systems terms, if \((x(0), z(0))\) lies in the basin of attraction of \((x^*, 0)\), then invasion fails. The basin of attraction is rather difficult to compute and even then, such computations have limited use, especially when the state space has dimension greater than 2, as is necessary here. What we can say for certain is that the basin of attraction depends on two key factors: the strength of the nonlinearities \(f\) and, especially, \(\alpha\) and the extent to which \(A_R\), and particularly, \(A_I\) are non-normal. When any one of these is large, then the basin of attraction will be small. If we fix a density for the invasion attempt, then as either the Allee effect or non-normality is increases, so a threshold is reached where \(z(0)\) is no longer in the basin of attraction, and so we cannot guarantee failure of invasion based on stability arguments. Such arguments and calculations based on basins of attraction, whilst fine in theory, are difficult if not impossible to apply to population models. Population models are usually derived from time series data, which are rarely long enough or accurate enough to create more than a crude model. Instead, we require qualitative and quantitative tools which reflect this underlying model uncertainty. In this simplified study we find that population momentum is a good indicator of the potential for successful invasion. This is not surprising because proneness to transients, as reflected by any one of the transient measures taking on large
values, will be closely associated with basins of attraction being smaller.

Based on the short time scale, and due to the interaction between beneficial Allee effects at low-medium densities and the boosting of density by transients, and using these ideas of non-normality we can suggest the following qualitative predictions for invasion:

- For a given density of invasion attempt, if the Allee effect is small (enough), then, independently of the strength of the non-normality, then $z(0)$ lies in the basin of attraction and the invasion fails;

- For a given density of invasion attempt, if the Allee effect is large (enough), then invasion succeeds if robustness is below a certain threshold.

### 6.6 Conclusion

In this chapter we investigated the reliability of the invasion exponent in accurately predicting invasion outcomes. Then we introduced a new indicator to predict invasion. The results are summarised in Figure 6.7. In each of the sub-panels of the figure we see a common trend: as the transient measure increases, so the critical value of the Allee effect parameter $s$ decreases. In the case of population momentum, there is a clear monotone decreasing relationship between Allee effect strength and momentum.
Chapter 7

Conclusion

Throughout this thesis we present some tools as powerful techniques to analyse invasion models. A Transfer Function Approach is emerging as an alternative to the established sensitivity approaches for analysing stage-structured population projection models. This TFA is well suited to ecological models that are parametrically uncertain with non-infinitesimal uncertainty. The model of stage-structured resident-invasion has been introduced in Chapter. Then robust control-based TFA is extended to study the model and obtain the existence and local stability conditions. We demonstrate some of the advantages of using TFA compared to previous studies by Takada and Nakajima, who use sensitivity analysis to determine parameter ranges for when invasion attempts can succeed when the difference between resident and mutant demographies are small but highly structured. The TFA approach turns the resulting high-dimensional, multi-parameter eigenvalue problem into a much more tractable $3 \times 3$ problem. Studying this lower-dimensional eigenvalue problem then yields checkable criteria for the existence and stability of ‘resident wins’, ‘invader wins’ and co-existence equilibria. To complete the
analysis we use classical control systems tools based on root locus methods.

Chapter 4 is essentially a further study (analysis) of system (3.2). A parameter-based characterisation of the stability of all the possible equilibria is obtained. A detailed Lyapunov analysis has been performed for all the equilibria. We write both the resident and the invader dynamics in Taylor expansion around each equilibria and define a quadratic Lyapunov function \((w^T P w)\) on the system state space. The goal behind this is the estimation of the basin of attraction for each equilibrium. For each case we found that the state disturbance has to be within a distance less than or equal to \(\rho\) (depending on the system parameters). More precisely, for each equilibrium \((x_e, z_e)\) under concern we compute \(\rho\), so that if disturbances \((x_0, z_0)\) satisfy

\[
\|(x_0 - x_e, z_0 - z_e)\| < \rho
\]

then

\[
\|(x_t - x_e, z_t - z_e)\| \rightarrow 0 \quad \text{as} \quad t \rightarrow \infty
\]

We used Examples 4.3.3 for illustration.

**Future Work 1:**

Usually mathematical systems aim to have enough robustness (large enough basin of attraction) to capture the behaviour of natural systems. As can be seen in our case, the basin of attraction we obtained is likely to be small; this can ascribed to the sequence of approximations we have made. Literature suggests that there are many clever ways to get around this deficiency; for instance, back steeping, Common Lyapunov functions and Zubov’s method can
be utilised for this purpose. Time limitations are the main reason that have prevented us from exploring these issues and we leave it as a suggestion for future work.

In Chapter 5, the effect of harvesting/fishing efforts is considered. The theorem in [32] has been extended and applied to a single species population model. A trichotomy of the system stability properties has been observed. This trichotomy feature is crucially dependent on harvesting efforts (the harvesting matrix \( H \)). More precisely, a desired state of the system can be achieved by suitable tuning of the harvesting matrix entries. This simple observation opened our eyes to applying the same principle in controlling invasion regimes, where we can incorporate harvesting as desired, to force the system to behave as wanted. This principle has been used to further analyse the invasion system introduced in the previous chapter. Harvesting has been incorporated in both the invader and resident dynamics. We design the system hypothesis in Theorem 5.1 to split the harvesting parameter space into two distinct regions - one where the resident goes extinct and the other where the invader does (see Examples 5.2.1).

In Chapter 6, a new indicator for invadability, namely invasion momentum, has been introduced. We showed by Example 6.4 that the invasion exponent \( \log(\lambda_{\text{max}}) \), the traditional indicator for invader establishment, is inconclusive when the underlying PPM is non-normal or incorporates an Allee effect. We considered a simulation study based on one hundred matrices with different
fecundities of the form

\[ A_{inv} = A_I + f(1)DE_{fec}, \]

chosen so that \( \lambda_{max}(A_{inv}) < 1 \), to ensure that the invasion exponent has a negative sign. The matrices are ordered according to their degree of non-normality, population momentum, invasion gain and reactivity.

The simulations in Figure 6.7 show how regions of invasion succession vary in four different parameter spaces. In the subplots, non-normality, invasion momentum, invasion gain and reactivity are plotted against a critical Allee effect. We find that as population momentum increases, so the critical (smallest) Allee effect decreases, even though the invasion exponent is negative and random.

**Future Work 2:**

Throughout this chapter we shed a light on the possibility of developing a more trustworthy measures for invasion. An application of this indicator to other kinds of invasion would be worthy of further study.
Appendix A

Appendices of Chapter 3

A.1 Derivation of forms (3.3), (3.4), (3.5) and (3.6)

Suppose the System 3.2 at general equilibrium \((x_e, z_e)\) then:

\[
\begin{align*}
x_e &= (A + f(M_e)DE)x_e \\
z_e &= (A + pBC + g(N_e)DE)z_e
\end{align*}
\]  
(A.1)

A.1.1 The \(x\)-axis equilibrium \((x^*, 0)\)

At this equilibrium the system (A.1) becomes:

\[
x^* = (A + f(M^*)DE)x^* \]

since \(z_e = 0\), and we have

\[
M^* = |x^*|_1, \quad N^* = |x^*|_1
\]  
(A.2)
and \( f^* = f(M^*) \), so
\[
x^* = f^*(I - A)^{-1} D E x^*.
\] (A.3)

Multiplying both sides of the last equation by \( E \) from the left and simplifying yields
\[
E x^* = f^* E (I - A)^{-1} D E x^*.
\]

Now \( E x^* \neq 0 \) since otherwise \( x^* = 0 \). So
\[
1 = f^* E (I - A)^{-1} D E.
\]

Rearranging gives
\[
f^* = \frac{1}{E (I - A)^{-1} D E}.
\]

Setting \( G_{ED} = E (I - A)^{-1} D \), this becomes
\[
f^* = \frac{1}{G_{ED}}.
\] (A.4)

A.1.2 The z-axis equilibrium \((0, z^*)\)

At this equilibrium the system \([A.1]\) becomes:
\[
z^* = (A + pBC + g^* D E) z^*
\] (A.5)

where \( g^* = g(N^{**}) \). Since \( x_e = 0 \), we have
\[
M^{**} = \alpha |z^*|_1, \quad \text{and} \quad N^{**} = \beta |z^*|_1.
\]
Applying the same steps as above yields:

\[ z^* - Az^* - pBCz^* = g^* DEz^*. \]

Rearranging we have:

\[ z^* = g^*(I - A - pBC)^{-1} DEz^*. \] (A.6)

Multiplying both sides by \( E \) from the left and simplifying yields

\[ g^* = \frac{1}{E(I - A - pBC)^{-1} D}. \]

To simplify the dominator of the last equation \( (I - A - pBC)^{-1} \), we use the Sherman-Morrison-Woodbury formula:

\[(T + UV)^{-1} = T^{-1} - T^{-1}U(I + VT^{-1}U)VT^{-1}.\]

Applying this formula with \( T = (I - A), U = -pB, V = C \), we obtain

\[(I - A - pBC)^{-1} = (I - A)^{-1} + p(I - A)^{-1} B(1 - pC(I - A)^{-1} C(I - A)^{-1}).\]

Then

\[ E(I - A - pBC)^{-1} D = E(I - A)^{-1} D + pE(I - A)^{-1} B(1 - pC(I - A)^{-1}) C(I - A)^{-1} D, \]

or, with the \( G_{ED} \) notation introduced above,

\[ E(I - A - pBC)^{-1} D = G_{ED} + pG_{EB}(1 - pC(I - A)^{-1}) G_{CD}. \]
Therefore
\[ g^* = \frac{1}{G_{ED} + pG_{EB}(1 - pC(I - A)^{-1})G_{CD}}. \] (A.7)

### A.1.3 Coexistence Equilibrium \((x', z')\)

At the coexistence equilibrium the system \([A.1]\) we have:

\[
x' = (A + f'DE)x',
\]

\[
z' = (A + pBC + g'DE)z'
\]

so from the first equation we have:

\[ x' = (A + f'DE)x' \]

then

\[ x' = f'(I - A)^{-1}DEx' \] (A.8)

which by compare it with the calculation done for the \(x\)-axis equilibrium led to:

\[ f' = \frac{1}{G_{ED}}. \] (A.9)

Doing the same for the second equation and compare it with the \(z\)-axis equilibrium we have:

\[ z' = g'(I - A - pBC)^{-1}DEz'. \] (A.10)

\[ g' = \frac{1}{G_{ED} + pG_{EB}(1 - pGCB)^{-1}G_{CD}}, \] (A.11)

both happen simultaneously.

We now use these to find the corresponding values of \(M', N', x'\) and \(z'\).
Using (A.9) and (A.11) we have

\[ M' = |x'|_1 + \alpha |z'|_1 = f^{-1}(f') = f^{-1} \left( \frac{1}{G_{ED}} \right) \]  \hspace{1cm} (A.12)

and

\[ N' = |x'|_1 + \beta |z'|_1 \
= g^{-1}(g') \
= g_1^{-1} \left( \frac{1}{G_{ED} + pG_{EB}(1-pG_{CB})^{-1}G_{CD}} \right) \].  \hspace{1cm} (A.13)

The last two equations imply

\[ (\alpha - \beta) |z'|_1 = f^{-1} \left( \frac{1}{G_{ED}} \right) - g^{-1} \left( \frac{1}{G_{ED} + pG_{EB}(1-pG_{CB})^{-1}G_{CD}} \right) \]

so that

\[ |z'|_1 = \frac{1}{\alpha - \beta} \left( f^{-1} \left( \frac{1}{G_{ED}} \right) - g^{-1} \left( \frac{1}{G_{ED} + pG_{EB}(1-pG_{CB})^{-1}G_{CD}} \right) \right) \].  \hspace{1cm} (A.14)

From (A.12) we have

\[ |x'|_1 = f^{-1}(f') - \alpha |z'|_1, \]

which using (A.14) becomes:

\[ |x'|_1 = f^{-1}(f') - \frac{\alpha}{\alpha - \beta} \left( f^{-1} \left( \frac{1}{G_{ED}} \right) - g^{-1} \left( \frac{1}{G_{ED} + pG_{EB}(1-pG_{CB})^{-1}G_{CD}} \right) \right) \]

Simplifying we obtain

\[ |x'|_1 = \frac{1}{\beta - \alpha} \left( \beta f^{-1} \left( \frac{1}{G_{ED}} \right) - \alpha g^{-1} \left( \frac{1}{G_{ED} + pG_{EB}(1-pG_{CB})^{-1}G_{CD}} \right) \right), \]
that is
\[ |x'|_1 = \frac{1}{\beta - \alpha} \left( \beta f^{-1}(f') - \alpha g^{-1}(g') \right). \]  
(A.15)

Now, from (A.8) we have that
\[ x' = y f'(I - A)^{-1} D, \]
where \( y = Ex' \).

**Note A.1.3.** Because of our assumptions on the system (3.2) that \( \lambda(A) < 0 \)
and the density dependent functions are non-negative so we grantee that \( |x| \) and \( |z| \) are both positive so we can say for both that \( |x| = a^T x \) and \( |z| = a^T z \) where \( a^T \) is row of 1’s with the same dimension as \( x, z \).

Taking the 1-norm on both sides gives
\[ |x'|_1 = y f'|(I - A)^{-1}D|. \]
(A.16)

From (A.15) and (A.16)
\[ y f'|(I - A)^{-1}| = \frac{1}{\beta - \alpha} \left( \beta f^{-1}(f') - \alpha g^{-1}(g') \right) \]
so that
\[ y = \left( \frac{1}{f'|(I - A)^{-1}D|} \right) \left[ \frac{1}{\beta - \alpha} \left( \beta f^{-1}(f') - \alpha g^{-1}(g') \right) \right]. \]

Hence
\[ x' = \frac{1}{\beta - \alpha} \left( \beta f^{-1}(f') - \alpha g^{-1}(g') \right) U(I - A)^{-1} D \]
(A.17)
Where
\[ U_{(I-A)^{-1}D} = \frac{(I - A)^{-1}D}{|(I - A)^{-1}D|}. \]

Similarly, from (A.10) we have
\[ z' = y'g'(I - A - pBC)^{-1}D, \]
where \( y' = Ez' \).

Again taking the 1-norm on both sides gives:
\[ |z'|_1 = y'g'|(I - A - pBC)^{-1}D|_1. \]

From (A.14)
\[ y'g'|(I - A - pBC)^{-1}D|_1 = \frac{1}{\alpha - \beta} \left( f^{-1}(f') - g^{-1}(g') \right), \]
so that
\[ y' = \frac{1}{(\alpha - \beta)g'|(I - A - pBC)^{-1}D|_1} \left( f^{-1}(f') - g^{-1}(g') \right). \]

Then
\[ z' = \frac{1}{(\alpha - \beta)g'|(I - A - pBC)^{-1}D|_1} \left( f^{-1}(f') - g^{-1}(g') \right) g'(I - A - pBC)^{-1}D, \]
or simply
\[ z' = \frac{1}{\alpha - \beta} \left( f^{-1}(f^*) - g^{-1}(g^*) \right) U_{(I-A-pBC)^{-1}D}. \quad (A.18) \]

Here
\[ U_{(I-A-pBC)^{-1}D} = \frac{(I - A - pBC)^{-1}D}{|(I - A - pBC)^{-1}D|_1}. \]
A.2 Derivation of Conditions for Existence of Equilibria

A.2.1 Existence of the \( x \)-axis equilibrium \((x^*, 0)\)

At equilibrium
\[ |x^*| > 0 \quad \text{and} \quad |z_e| = 0. \]

and at equilibrium these values become:
\[ M^* = N^* = |x^*|. \]

But
\[ f(M^*) = f^*. \]

This means that
\[ M^* = |x^*| = f^{-1}(f^*) = f^{-1}\left(\frac{1}{E(I - A)^{-1}D}\right). \]

Then the existence condition for the \( x \)-axis equilibrium is:
\[ M^* = f^{-1}(f^*) > 0. \]

A.2.2 Existence of \( z \)-axis equilibrium \((0, z^*)\)

At this equilibrium:
\[ |z^*| > 0 \quad \text{and} \quad |x_e| = 0 \]

and
\[ M^{**} = \alpha |z^*|, \quad \text{and} \quad N^{**} = \beta |z^*|. \]

But \[ g(N^{**}) = g^*. \]

This means that \[ N^{**} = \beta |z^*| = \beta g^{-1}(g^*) = g^{-1} \left( \frac{1}{E(I - A - pBC)^{-1}D} \right). \]

Then the existence condition for the \( z \)-axis equilibrium is:

\[ N^{**} = g^{-1}(g^*) > 0. \]

### A.2.3 Existence of the coexistence equilibrium \((x', z')\)

For this we need the formulas above for \( x' \) and \( z' \) to yield non-negative vectors so that \[ |x'| > 0 \quad \text{and} \quad |z'| > 0. \]

So we need

\[ |x'|_1 = \frac{1}{\beta - \alpha} \left( \beta f^{-1} \left( \frac{1}{G_{ED}} \right) - \alpha g^{-1} \left( \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} \right) \right) > 0, \]

and

\[ |z'|_1 = \frac{1}{\alpha - \beta} \left( f^{-1} \left( \frac{1}{G_{ED}} \right) - g^{-1} \left( \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} \right) \right) > 0. \]
For $|x| > 0$ we require

$$\frac{1}{\beta - \alpha} \left( \beta f^{-1}\left( \frac{1}{G_{ED}} \right) - \alpha g^{-1}\left( \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} \right) \right) > 0,$$

which means that either both

$$\frac{1}{\beta - \alpha} > 0,$$

and

$$\left( \beta f^{-1}\left( \frac{1}{G_{ED}} \right) - \alpha g^{-1}\left( \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} \right) \right) > 0,$$

or

$$\frac{1}{\beta - \alpha} < 0,$$

and

$$\left( \beta f^{-1}\left( \frac{1}{G_{ED}} \right) - \alpha g^{-1}\left( \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} \right) \right) < 0.$$

Suppose $\frac{1}{\beta - \alpha} > 0$. Then $\alpha < \beta$ i.e. $\frac{\alpha}{\beta} < 1$ and

$$\beta f^{-1}\left( \frac{1}{G_{ED}} \right) - \alpha g^{-1}\left( \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} \right) > 0.$$

That is

$$f^{-1}\left( \frac{1}{G_{ED}} \right) > \frac{\alpha}{\beta} g^{-1}\left( \frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}} \right)$$

So the first condition for $|x'| > 0$ is

$$\frac{\alpha}{\beta} < 1$$
together with

\[ f^{-1}(\frac{1}{G_{ED}}) > \frac{\alpha}{\beta} g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}}). \]

Now suppose \( \frac{1}{\beta - \alpha} < 0 \), i.e. \( \frac{a}{\beta} > 1 \) and

\[ \beta f^{-1}(\frac{1}{G_{ED}}) - \alpha g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}}) < 0. \]

Then we obtain the condition for \(|x'| > 0\):

\[ f^{-1}(\frac{1}{G_{ED}}) > \frac{\alpha}{\beta} g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}}), \frac{\alpha}{\beta} > 1. \]

Secondly, \(|z'| > 0\) if

\[ \frac{1}{\alpha - \beta} \left( f^{-1}(\frac{1}{G_{ED}}) - g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}}) \right) > 0. \]

This means either both

\[ \frac{1}{\alpha - \beta} > 0, \]

and

\[ (f^{-1}(\frac{1}{G_{ED}}) - g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}})) > 0, \]

or

\[ \frac{1}{\alpha - \beta} < 0, \]

and

\[ (f^{-1}(\frac{1}{G_{ED}}) - g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}})) < 0. \]
Suppose $\frac{1}{\beta - \alpha} > 0$. Then $\alpha > \beta$ i.e. $\frac{\alpha}{\beta} > 1$ and

$$(f^{-1}(\frac{1}{G_{ED}}) - g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}})) > 0.$$ 

That is we require

$$(f^{-1}(\frac{1}{G_{ED}}) > g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}})).$$

We can rewrite this as

$$(f^{-1}(\frac{1}{G_{ED}}) > g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}}), \frac{\alpha}{\beta} > 1.$$ 

Now suppose that $\frac{1}{\beta - \alpha} < 0$. Then $\alpha < \beta$ i.e. $\frac{\alpha}{\beta} < 1$ and

$$(f^{-1}(\frac{1}{G_{ED}}) < g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}})).$$

This gives the condition

$$(f^{-1}(\frac{1}{G_{ED}}) < g^{-1}(\frac{1}{G_{ED} + pG_{EB}(1 - pG_{CB})^{-1}G_{CD}}), \frac{\alpha}{\beta} < 1.$$ 

The condition for the coexistence equilibrium are summarised shown in the Table [A.1].
Table A.1: Existence Conditions for the Coexistence Equilibria

| \( \frac{\alpha}{\beta} \leq 1 \) | \( |x'| > 0 \) | \( |z'| > 0 \) |
|---|---|---|
| \( \frac{\alpha}{\beta} < 1 \) | \( f^{-1}(f^*) > \frac{\alpha}{\beta} g^{-1}(g^*) \) | \( f^{-1}(f^*) < g^{-1}(g^*) \) |
| \( \frac{\alpha}{\beta} > 1 \) | \( f^{-1}(f^*) < \frac{\alpha}{\beta} g^{-1}(g^*) \) | \( f^{-1}(f^*) > g^{-1}(g^*) \) |

Summarising we have that \((x', z')\) exists when

\[ 1 < \frac{f^{-1}(f^*)}{g^{-1}(g^*)} < \frac{\alpha}{\beta} \quad \text{OR} \quad 1 > \frac{f^{-1}(f^*)}{g^{-1}(g^*)} > \frac{\alpha}{\beta} \]

### A.3 Derivation of Local Stability Conditions

#### A.3.1 The \( x \)-axis Equilibrium

Here differentiation \( F(x_t, z_t) \) and \( G(x_t, z_t) \) with respect of \( x \) and \( z \) gives:

\[
\frac{\partial F}{\partial x_t}(x^*, 0) = A + fDE + f'DEx_ta^T = A + fDE + Ex^*f'Da^T.
\]
\[
\frac{\partial F}{\partial z_t}(x^*, 0) = Ex^*f'Db^T.
\]
\[
\frac{\partial G}{\partial x_t}(x^*, 0) = 0.
\]
\[
\frac{\partial G}{\partial z_t}(x^*, 0) = A + pBC + gDE.
\]
so the Jacobian matrix $J$ matrix will be

$$J = \begin{pmatrix} A + fDE + Ex^* f'Da^T & Ex^* f'Db^T \\ 0 & A + pBC + gDE \end{pmatrix}$$

or simply:

$$J = \begin{pmatrix} A + fDE + p_1 Da^T & p_1 Db^T \\ 0 & A + pBC + gDE \end{pmatrix}$$

where $p_1 = Ex^*$.

Now $J$ can be written as:

$$J = AA + P$$

where

$$D_1E_1 + D_2E_2 + D_3E_3$$

and

$$AA = A \begin{pmatrix} I & 0 \\ 0 & I \end{pmatrix} ; D_1 = \begin{pmatrix} D \\ 0 \end{pmatrix} ; D_2 = \begin{pmatrix} 0 \\ B \end{pmatrix} ; D_3 = \begin{pmatrix} 0 \\ D \end{pmatrix}$$

and

$$E_1 = \begin{pmatrix} fE + p_1 a^T & \alpha p_1 a^T \end{pmatrix} ; E_2 = \begin{pmatrix} 0 \\ pC \end{pmatrix} ; E_3 = \begin{pmatrix} 0 \\ gE \end{pmatrix} .$$

Using Theorem 4.3 (stuart et al 2006 [20]) we can say $\lambda$ is an eigenvalue of $J$ if and only if 1 is an eigenvalue of $JJ$ where $JJ$ is:
\[ JJ = \begin{pmatrix}
G_{11} & G_{12} & G_{13} \\
G_{21} & G_{22} & G_{23} \\
G_{31} & G_{32} & G_{33}
\end{pmatrix} \]

where

\[ G_{ij} = E_i(\lambda I - AA)^{-1}D_j. \]

So calculating the values of \( G_{ij} \) we obtain:

\[ G_{11} = E_1(\lambda I - AA)^{-1}D_1 = \left( fE + p_1a^T \quad \alpha p_1a^T \right) \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} D \\ 0 \end{pmatrix} = fG_{ED} + p_1G_{a^T D}. \]

and

\[ G_{12} = E_1(\lambda I - AA)^{-1}D_2 = \left( fE + p_1a^T \quad \alpha p_1a^T \right) \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ B \end{pmatrix} = \alpha p_1G_{a^T B}. \]

Also

\[ G_{13} = E_1(\lambda I - AA)^{-1}D_3 = \left( fE + p_1a^T \quad \alpha p_1a^T \right) \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ D \end{pmatrix} = \alpha p_1G_{a^T D}. \]

\[ G_{21} = E_2(\lambda I - AA)^{-1}D_1 = \begin{pmatrix} 0 & pC \\ 0 & R \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & D \end{pmatrix} = 0, \]
\[ G_{22} = E_2(\lambda I - AA)^{-1}D_2 = \begin{pmatrix} 0 & \alpha pC \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ B \end{pmatrix} = pG_{CB}, \]

\[ G_{23} = E_2(\lambda I - AA)^{-1}D_3 = \begin{pmatrix} 0 & pC \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ D \end{pmatrix} = pG_{CD}, \]

\[ G_{31} = E_3(\lambda I - AA)^{-1}D_1 = \begin{pmatrix} 0 & gE \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} D \\ 0 \end{pmatrix} = 0, \]

\[ G_{32} = E_3(\lambda I - AA)^{-1}D_2 = \begin{pmatrix} 0 & gE \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} D \\ 0 \end{pmatrix} = gG_{EB}, \]

\[ G_{33} = E_3(\lambda I - AA)^{-1}D_3 = \begin{pmatrix} 0 & gE \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ 0 \end{pmatrix} = gG_{ED}. \]

Then the \( JJ \) matrix becomes:

\[
JJ = \begin{pmatrix}
  fG_{CB} + p_1 G_{aT_D} & \alpha p_1 G_{aT_B} & \alpha p_1 G_{aT_D} \\
  0 & pG_{CB} & pG_{CD} \\
  0 & gG_{EB} & gG_{ED}
\end{pmatrix}.
\]

Computing \( I - JJ \) we have:
\( I - JJ = \begin{pmatrix} 1 - fG_{CB} - p_1G_{aT_D} & -\alpha p_1G_{aT_B} & -\alpha p_1G_{aT_D} \\ 0 & 1 - pG_{CB} & -pG_{CD} \\ 0 & -gG_{EB} & 1 - gG_{ED} \end{pmatrix} \) the general

stability condition is:

\[
(1 - fG_{ED} - f'Ex^*G_{aT_D}) (1 - pG_{CB} - gG_{ED} + pgG_{CB}G_{ED} - pgG_{EB}G_{CD}) \\
\neq 0, \text{ for all } |\lambda| \geq 1
\]

This yields the condition for the stability of the \( x \) axis equilibrium.

### A.3.2 \( z \)-axis Equilibrium

Differentiation the functions \( F(x_t, z_t) \) and \( G(x_t, z_t) \) with respect of \( x \) and \( z \) gives:

\[
\frac{\partial F}{\partial x_t}(0, z^*) = A + fDE.
\]

\[
\frac{\partial F}{\partial z_t}(0, z^*) = 0.
\]

\[
\frac{\partial G}{\partial x_t}(0, z^*) = Ez^*g'Da^T.
\]

\[
\frac{\partial G}{\partial z_t}(0, z^*) = A + pBC + gDE + Ez^*g'Dc^T.
\]

so the \( J \) matrix will be

\[
J = \begin{pmatrix} A + fDE & 0 \\ Ez^*g'Da^T & A + pBC + gDE + Ez^*g'Dc^T \end{pmatrix}
\]
or simply:

\[
J = \begin{pmatrix}
A + fDE & 0 \\
p_2Da^T & A + pBC + gDE + \beta p_2Da^T
\end{pmatrix}
\]

where \( p_2 = Ex^* \).

So the matrix can be written as

\[
J = AA + P.
\]

where

\[
P = D_1E_1 + D_2E_2 + D_3E_3.
\]

and

\[
AA = A \begin{pmatrix}
I & 0 \\
0 & I
\end{pmatrix};
D_1 = \begin{pmatrix}
D \\
0
\end{pmatrix};
D_2 = \begin{pmatrix}
0 \\
B
\end{pmatrix};
D_3 = \begin{pmatrix}
0 \\
D
\end{pmatrix}
\]

and

\[
E_1 = \begin{pmatrix}
fE & 0
\end{pmatrix};
E_2 = \begin{pmatrix}
0 & pC
\end{pmatrix};
E_3 = \begin{pmatrix}
p_2a^T & gE + \beta p_2a^T
\end{pmatrix}
\]

Again using Theorem 4.3 (stuart et al 2006 [20]) we can say \( \lambda \) is an eigenvalue of \( J \) if and only if 1 is an eigenvalue of \( JJ \) where \( JJ \) is:
\[ JJ = \begin{pmatrix}
G_{11} & G_{12} & G_{13} \\
G_{21} & G_{22} & G_{23} \\
G_{31} & G_{32} & G_{33}
\end{pmatrix}. \]

Here

\[ G_{ij} = E_i(\lambda I - AA)^{-1}D_j. \]

So calculating the values of \( G_{ij} \) we obtain:

\[ G_{11} = E_1(\lambda I - AA)^{-1}D_1 = \begin{pmatrix}
fE \\
R \\
0
\end{pmatrix}
\begin{pmatrix}
R & 0 \\
0 & R \\
0 & 0
\end{pmatrix}
\begin{pmatrix}
D \\
0 \\
0
\end{pmatrix} = fG_{ED}; \]

and

\[ G_{12} = E_1(\lambda I - AA)^{-1}D_2 = \begin{pmatrix}
fE \\
R \\
0
\end{pmatrix}
\begin{pmatrix}
R & 0 \\
0 & R \\
0 & B
\end{pmatrix}
\begin{pmatrix}
0 \\
0 \\
B
\end{pmatrix} = 0; \]

also

\[ G_{13} = E_1(\lambda I - AA)^{-1}D_3 = \begin{pmatrix}
fE \\
R \\
0
\end{pmatrix}
\begin{pmatrix}
R & 0 \\
0 & R \\
0 & D
\end{pmatrix}
\begin{pmatrix}
0 \\
0 \\
D
\end{pmatrix} = 0; \]

\[ G_{21} = E_2(\lambda I - AA)^{-1}D_1 = \begin{pmatrix}
0 & pC \\
R & 0 \\
0 & R
\end{pmatrix}
\begin{pmatrix}
D \\
0 \\
0
\end{pmatrix} = 0; \]
\[ G_{22} = E_2(\lambda I - AA)^{-1}D_2 = \begin{pmatrix} 0 & pC \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ B \end{pmatrix} = pG_{CB}; \]

\[ G_{23} = E_2(\lambda I - AA)^{-1}D_3 = \begin{pmatrix} 0 & pC \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ 0 \\ D \end{pmatrix} = pG_{CD}; \]

\[ G_{31} = E_3(\lambda I - AA)^{-1}D_1 = \begin{pmatrix} p_2a^T & gE + \beta p_2a^T \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} D \\ 0 \end{pmatrix} = p_2G_{aT_D}; \]

\[ G_{32} = E_3(\lambda I - AA)^{-1}D_2 = \begin{pmatrix} p_2a^T & gE + \beta p_2a^T \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ B \end{pmatrix} = gG_{EB} + \beta p_2G_{aT_B}; \]

\[ G_{33} = E_3(\lambda I - AA)^{-1}D_3 = \begin{pmatrix} p_2a^T & gE + \beta p_2a^T \\ R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ D \end{pmatrix} = gG_{ED} + \beta p_2G_{aT_D}. \]

Then the JJ matrix becomes:
Then

\[
J J = \begin{pmatrix}
  f G_{ED} & 0 & 0 \\
  0 & p G_{CB} & p G_{CD} \\
  p_2 G_{aT_D} & g G_{EB} + \beta p_2 G_{aT_B} & g G_{ED} + \beta p_2 G_{aT_D} \\
\end{pmatrix}
\]

Then

\[
I - J J = \begin{pmatrix}
  1 - f G_{ED} & 0 & 0 \\
  0 & 1 - p G_{CB} & -p G_{CD} \\
  -p_2 G_{aT_D} & -g G_{EB} - \beta p_2 G_{aT_B} & 1 - g G_{ED} - \beta p_2 G_{aT_D} \\
\end{pmatrix}
\]

and

\[
(1 - f G_{ED}) [(1 - p G_{CB})(1 - g G_{ED} - \beta g'E z^* G_{aT_D}) - p G_{CD}(g G_{EB} + \beta g'E z^* G_{aT_B})] \\
\neq 0, \text{ for all } |\lambda| \geq 1.
\]

This gives the condition of stability for the z axis equilibrium.

### A.3.3 Coexistence equilibrium

To study the local stability of the system around this equilibrium we linearise the system around this equilibrium. Now

\[
x' = (A + f(a^T x' + b^T z') DE)x' \\
z' = (A + p BC + g(a^T x' + c^T z' DE) z'.
\]

Here we set \(|x'| = a^T x', \alpha|x'| = b^T z', \text{ and } \beta|z'| = c^T z', \text{ a} = (1 \cdots 1), b^T = \alpha a^T \text{ and } c^T = \beta a^T. \]
APPENDIX A. APPENDICES OF CHAPTER 3

Let
\[ F(x', z') := (A + f(a^T x_t + b^T z')D E)x'; \]

and
\[ G(x', z') := (A + pBC + g(a^T x' + c^T z')D E)z'. \]

Then
\[
\begin{align*}
\frac{\partial F}{\partial x_t}(x', z') &= A + fD E + f'D E x_t a^T = A + fD E + E x' f'D a^T. \\
\frac{\partial F}{\partial z_t}(x', z') &= E x' f'D b^T. \\
\frac{\partial G}{\partial x_t}(x', z') &= E z' g'D a^T. \\
\frac{\partial G}{\partial z_t}(x', z') &= A + pBC + gD E + g'D E z_t c^T = A + pBC + gD E + E z' g'D c^T.
\end{align*}
\]

So we have the linearisation
\[
J \begin{pmatrix}
A + fD E + E x' f'D a^T & E x' f'D b^T \\
E z' g'D a^T & A + pBC + gD E + E z' g'D c^T
\end{pmatrix}
\]

This can be written as follows:
\[ J = A \begin{pmatrix} I & 0 \\ 0 & I \end{pmatrix} + \begin{pmatrix} 0 \\ B \end{pmatrix} \begin{pmatrix} 0 & pC \\ D & 0 \end{pmatrix} \begin{pmatrix} fE + yf' a^T & \alpha yf' a^T \\ 0' g' a^T & \alpha gE + \beta y' g' a^T \end{pmatrix} + \begin{pmatrix} 0 \\ D \end{pmatrix}. \]

Let

\[ \begin{align*}
AA &= A \begin{pmatrix} I & 0 \\ 0 & I \end{pmatrix} ; D_1 = \begin{pmatrix} 0 \\ B \end{pmatrix} ; D_2 = \begin{pmatrix} D \\ 0 \end{pmatrix} ; D_3 = \begin{pmatrix} 0 \\ D \end{pmatrix}; \\
E_1 &= \begin{pmatrix} 0 & pC \end{pmatrix} ; E_2 = \begin{pmatrix} fE + yf' a^T & \alpha yf' a^T \\ 0' g' a^T & \alpha gE + \beta y' g' a^T \end{pmatrix} ; E_3 = \begin{pmatrix} y' g' a^T & \alpha gE + \beta y' g' a^T \end{pmatrix}. 
\end{align*} \]

Then

\[ J = AA + D_1 E_1 + D_2 E_2 + D_3 E_3 \]

or simply

\[ J = AA + P \]

where \( P \) is the perturbation matrix:

\[ P = D_1 E_1 + D_2 E_2 + D_3 E_3 \]

Again using Theorem 4.3 from in (Hodgson and Townley 2006 [20]) we can
say:

λ is an eigenvalue of \( J \) if and only if 1 is an eigenvalue of \( JJ \), where:

\[
JJ = \begin{pmatrix}
G_{11} & G_{12} & G_{13} \\
G_{21} & G_{22} & G_{23} \\
G_{31} & G_{32} & G_{33}
\end{pmatrix}
\]

where

\[
G_{ij} = E_i(\lambda I - AA)^{-1}D_j
\]

and

\[
(\lambda I - AA)^{-1} = \begin{pmatrix}
I - A & 0 \\
0 & I - A
\end{pmatrix}^{-1}
\]

Now

\[
(\lambda I - AA)^{-1} = \begin{pmatrix}
(I - A)^{-1} & 0 \\
0 & (I - A)^{-1}
\end{pmatrix}
\]

For simplicity put \( R = (I - A)^{-1} \).

Calculating the values of \( G_{ij} \) we obtain:

\[
G_{11} = E_1(\lambda I - AA)^{-1}D_1 = \begin{pmatrix}
0 & pC
\end{pmatrix}
\begin{pmatrix}
R & 0 \\
0 & R
\end{pmatrix}
\begin{pmatrix}
0 \\
B
\end{pmatrix} = pG_{CB}
\]
and

\[ G_{12} = E_1(\lambda I - AA)^{-1}D_2 = \begin{pmatrix} 0 & pC \\ R & 0 \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} D \\ 0 \end{pmatrix} = 0. \]

Also

\[ G_{13} = E_1(\lambda I - AA)^{-1}D_3 = \begin{pmatrix} 0 & pC \\ R & 0 \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ D \end{pmatrix} = pG_{CD} \]

\[ G_{21} = E_2(\lambda I - AA)^{-1}D_1 = \begin{pmatrix} fE + p_1a^T & \alpha p_1a^T \\ R & 0 \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ B \end{pmatrix} = \alpha p_1G_{a^TB} \]

\[ G_{22} = E_2(\lambda I - AA)^{-1}D_2 = \begin{pmatrix} fE + p_1a^T & \alpha p_1a^T \\ R & 0 \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} D \\ 0 \end{pmatrix} = f + p_1G_{CB} \]

\[ G_{23} = E_2(\lambda I - AA)^{-1}D_3 = \begin{pmatrix} fE + p_1a^T & \alpha p_1a^T \\ R & 0 \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ D \end{pmatrix} = \alpha p_1G_{a^TD} \]
\[ G_{31} = E_3(\lambda I - AA)^{-1}D_1 = \begin{pmatrix} ga^T & gE + \beta p_1a^T \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ B \end{pmatrix} = gG_{EB} + \beta p_1 G_{a^TB} \]

\[ G_{32} = E_3(\lambda I - AA)^{-1}D_2 = \begin{pmatrix} ga^T & gE + \beta p_1a^T \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} D \\ 0 \end{pmatrix} = p_1 G_{a^TD} \]

\[ G_{33} = E_3(\lambda I - AA)^{-1}D_3 = \begin{pmatrix} ga^T & gE + \beta p_1a^T \end{pmatrix} \begin{pmatrix} R & 0 \\ 0 & R \end{pmatrix} \begin{pmatrix} 0 \\ D \end{pmatrix} = gG_{ED} + \beta p_1 G_{a^TD} \]

where

\[ G_{CB} = C(I - A)^{-1}B, G_{CD} = C(I - A)^{-1}D, G_{a^TB} = a^T(I - A)^{-1}B, \]

\[ G_{ED} = E(I - A)^{-1}D, G_{a^TD} = a^T(I - A)^{-1}D, G_{EB} = E(I - A)^{-1}B. \]

Then the \( JJ \) matrix can be written as:
\[ JJ = \begin{pmatrix}
    pG_{CB} & 0 & pG_{CD} \\
    \alpha yf'G_{aTB} & fG_{ED} + yf'G_{aTD} & \alpha yf'G_{aTD} \\
    gG_{EB} + \beta y'g'G_{aTB} & y'g'G_{aTD} & gG_{ED} + \beta y'g'G_{aTD}
\end{pmatrix} \]

where
\[ G_{CB} = B(\lambda I - A)^{-1}C, \quad G_{aTB} = a^T(\lambda I - A)^{-1}B, \quad G_{ED} = E(\lambda I - A)^{-1}D, \quad G_{aTD} = a^T(\lambda I - A)^{-1}D, \quad G_{EB} = E(\lambda I - A)^{-1}B. \]

So
\[ I - JJ = \begin{pmatrix}
    1 - pG_{CB} & 0 & -pG_{CD} \\
    -\alpha yf'G_{aTB} & 1 - fG_{ED} - yf'G_{aTD} & -\alpha yf'G_{aTD} \\
    -gG_{EB} - \beta y'g'G_{aTB} & -y'g'G_{aTD} & 1 - gG_{ED} + \beta y'g'G_{aTD}
\end{pmatrix} \]

which can be simplified to \( I - JJ = \).
\[
\begin{pmatrix}
1 - p G_{CB} & 0 & 0 \\
-\alpha p_1 G_{aTB} & 1 - f G_{ED} - p_1 G_{aTD} & -\alpha p_1 G_{aTD} - \frac{\alpha p_1 G_{aTB}}{1 - p G_{CB} (p G_{CD})} \\
-g G_{EB} - \beta p_2 G_{aTB} & -p_2 G_{aTD} & 1 - g G_{ED} + \beta p_2 G_{aTD} - \frac{(g G_{EB} + \beta p_2 G_{aTB}) p G_{CD}}{1 - p G_{CB}}
\end{pmatrix}
\]

where

\[
y = E x', y' = E z', p_1 = y f', p_2 = y' g'.
\]

Then, for stability we require

\[
det(I - J J) = (1 - p G_{CB}) [(1 - f G_{ED} - f' E x' G_{aTD}) \\
(1 - g G_{ED} - \beta E z' g' G_{aTD} - \frac{(g G_{EB} + \beta E z' g' G_{aTD}) p G_{CD}}{1 - p G_{CB}}) - E z' g' G_{aTD} (\alpha E x' f' G_{aTD} \\
+ \frac{\alpha E x' f' G_{aTB} G_{CD}}{1 - p G_{CB}})] 
eq 0, \text{ for all } |\lambda| \geq 1.
\]
Appendix B

Appendices of Chapter 4

Proof of Theorem (4.3.6)

Part One: Lyapunov Function Analysis of the equilibrium at \((x^*, 0)\)

Recall that

\[
W_{t+1} = \begin{pmatrix} L_{11} & L_{12} \\ 0 & L_{22} \end{pmatrix} W_t + f'(M^*)D_1(E_0 W_t)(E_1 W_t) + \phi D_1(E_1 W_t)(E x^* + E_0 W_t)
\]

\[
+ g'(N^*)D_2(E_0 W_t)(E_2 W_t) + \psi D_2 E_2 W_t E_0 W_t.
\]

For simplicity let

\[
L_x = \begin{pmatrix} L_{11} & L_{12} \\ 0 & L_{22} \end{pmatrix};
\]

\[
s_1 = f'(M^*) (E_0 W_t)(E_1 W_t) + \phi (E_1 W_t)(E x^* + E_0 W_t), \text{ and}
\]

\[
s_2 = g'(N^*) D_2 (E_0 W_t)(E_2 W_t) + \psi D_2 E_2 W_t E_0 W_t.
\]
Then
\[ W_{t+1} = L_x W + s_1 D_1 + s_2 D_2. \]

Since \( L_x \) is stable we can, for each positive definite \( Q \) find a positive definite \( P \) so that
\[ L_x^T P L_x - P = -Q. \]

Define \( V(W) = W^T P W \). In the Lyapunov analysis we need to compute
\[ \Delta V = V(W_{t+1}) - V(W_t) \]
\[ = W_{t+1}^T P W_{t+1} - W_t^T P W_t \]
\[ = (L_x W + s_1 D_1 + s_2 D_2)^T P (L_x W + s_1 D_1 + s_2 D_2) - W^T P W \] (dropping the \( t \)'s)
\[ = (W^T + s_1 D_1^T + s_2 D_2^T) P (L W + s_1 D_1 + s_2 D_2) - W^T P W. \]

Expanding we have
\[ \Delta V = W^T L^T P L W + W^T L^T P s_1 D_1 + W^T L^T P s_2 D_2 \]
\[ + s_1 D_1^T P L W + s_1 D_1^T P s_1 D_1 + s_1 D_1^T P s_2 D_2 \]
\[ + s_2 D_2^T P L W + s_2 D_2^T P s_1 D_1 + s_2 D_2^T P s_2 D_2 \]
\[ - W^T P W \]

But
\[ W^T L^T P L W - W^T P W = -W^T Q W. \]
Then

\[ \Delta V = -W^TQW + 2s_1W^TLPD_1 + 2s_2W^TLPD_2 + s_1^2D_1^TPD_1 + 2s_1s_2D_1^TPD_2 + s_2^2D_2^TPD_2 \]  

\begin{equation} 
(B.1) 
\end{equation}

Obviously we can rewrite the last equation as:

\[ \Delta V = -W^TQW + HOT \]

and we need to make estimates in the $HOT$ so as to satisfy

\[ \Delta V < 0. \]

So we need to prove that

\[ -W^TQW + HOT < 0. \]

We need to make estimates on the terms in $[B.1]$. Completing squares we have:

\[ 2s_1W^TLPD_1 \leq \frac{q}{4}||W||^2 + \frac{1}{q}||s_1L^TPD_1||^2 \]

where we choose $q = \min(eig(Q))$. Next we have

\[ 2s_2W^TLPD_2 \leq \frac{q}{4}||W||^2 + \frac{1}{q}||s_2L^TPD_2||^2 \]
\[ 2s_1s_2D_1^T PD_2 = D_1^T PD_2 (2s_1s_2) \]

\[ \leq D_1^T PD_2 (s_1^2 + s_2^2) \]

and

\[ W^T Q W > q ||W||^2. \]

So \( \Delta V \) becomes:

\[-W^T Q W + \text{HOT} \leq -q ||W||^2 + \frac{q}{4} ||W||^2 + \frac{4}{q} ||s_1 L^T PD_1||^2 + \frac{q}{4} ||W||^2 + \frac{4}{q} ||s_2 L^T PD_2||^2 + s_1^2 D_1^T PD_1 + s_2^2 D_2^T PD_2 + (s_1^2 + s_2^2) D_1^T PD_2. \]

Rearranging we have:

\[-W^T Q W + \text{HOT} \leq -\frac{q}{2} ||W||^2 + K_1 s_1^2 + K_2 s_2^2, \]

where

\[ K_1 = \frac{4}{q} ||L^T PD_1||^2 + D_1^T PD_2 + D_1^T PD_1; \]

\[ K_2 = \frac{4}{q} ||L^T PD_2||^2 + D_2^T PD_2 + D_1^T PD_2; \]

Now, recall the values of \( s_1 \):

\[ s_1 = f'(M^*)(E_0 W_t)(E_1 W_t) + \phi(E_1 W_t)(Ex^* + E_0 W_t) \]
we can write:

\[
|s_1| = |f'(M^*)(E_0W_t)(E_1W_t) + \phi(E_1W_t)(Ex^* + E_0W_t)|
\]

\[
\leq |f'(M^*)| ||E_0|| ||W|| ||E_1|| ||W|| + ||\phi(E_1W_t)|| (||Ex^*|| + ||E_0|| ||W_t||)
\]

we know \( |W| \leq \min(1, \delta) \) for some \( \delta > 0 \) to be defined later. Then

\[
|s_1| \leq |f'(M^*)|||E_0||||E_1||||W||^2 + ||\phi(E_1W_t)|| (||Ex^*|| + ||E_0||)
\]

or simply:

\[
|s_1| \leq K_3||W||^2 + K_4||\phi(E_1W_t)||
\]

where

\[
K_3 = |f'(M^*)|||E_0||||E_1||, \quad \text{and} \quad K_4 = ||Ex^*|| + ||E_0||
\]

Now, for all \( \varepsilon > 0 \) there exist \( \delta_1 \) such that

\[
|\phi| \leq ||E_1|| \varepsilon ||W||, \quad \text{(B.2)}
\]

so that

\[
|s_1| \leq (K_3||W|| + K_4||E_1||\varepsilon) ||W||
\]

Doing the same for the value of \( s_2 \):

\[
s_2 = g'(N^*)(E_0W_t)(E_2W_t) + \psi(E_2W_t)E_0W_t,
\]
then we can write:

\[ |s_2| = |g'(N^*)(E_0W_i)(E_2W_i) + \psi(E_2W_i)E_0W_i| \]

\[ \leq |g'| ||E_0|| ||W|| ||E_2|| ||W|| + |\psi(E_2W)| ||E_0|| ||W|| \]

we know \(|W| \leq \min(1, \delta)\) for some \(\delta > 0\) (to be defined later). Then

\[ |s_2| \leq |g'| ||E_0|| ||E_2|| ||W||^2 + |\psi(E_2W)| ||E_0|| ||W|| \]

or simply:

\[ |s_2| \leq (K_5||W|| + K_6||\psi(E_2W)||) ||W|| \]

where, \(K_5 = |g'| ||E_0|| ||E_2||\) and \(K_6 = ||E_0||\), but for all \(\varepsilon > 0\) there is \(\delta_2 > 0\) such that:

\[ |\psi(E_2W)| < \varepsilon |E_2W| \quad \text{if} \quad E_2W < \delta_2. \quad (B.3) \]

Then,

\[ |s_2| \leq (K_5||W|| + K_6||E_2||\varepsilon) ||W||. \]

Back to the value of \(\Delta V\):

\[ \Delta V \leq -\frac{q}{2} ||W||^2 + K_1||W||^2 (K_3||W|| + K_4||E_1||\varepsilon)^2 + K_2||W||^2 (K_5||W|| + K_6||E_2||\varepsilon)^2. \]

that is:

\[ \Delta V \leq \left[ -\frac{q}{2} + K_1 (K_3||W|| + K_4||E_1||\varepsilon)^2 + K_2 (K_5||W|| + K_6||E_2||\varepsilon)^2 \right] ||W||^2. \]
So to have $\Delta V < 0$ we need:

$$K_1 (K_3\|W\| + K_4\|E_1\|\varepsilon)^2 + K_2 (K_5\|W\| + K_6\|E_2\|\varepsilon)^2 < \frac{q}{2}$$

We can split this inequality to two different inequalities:

$$K_1 (K_3\|W\| + K_4\|E_1\|\varepsilon)^2 < \mu q \quad (B.4)$$

and

$$K_2 (K_5\|W\| + K_6\|E_2\|\varepsilon)^2 < \nu q \quad (B.5)$$

where $\mu, \nu > 0$ and $\mu + \nu < 0.5$. So using (B.4) and rearranging we have

So we need

$$K_3\|W\| + K_4\|E_1\|\varepsilon < \sqrt{\mu q / K_1}$$

We can achieve this inequality in lots of ways. One way is to make

$$K_3\|W\| < \mu_2 \sqrt{\mu q / K_1} \quad \text{and} \quad K_4\|E_1\|\varepsilon < \nu_2 \sqrt{\mu q / K_1}$$

with $\mu_2, \nu_2 > 0$ and $\mu_2 + \nu_2 = 1$. So we choose $\varepsilon_1$ such that

$$\varepsilon < \nu_2 \sqrt{\mu q / K_1} / (K_4\|E_1\|) := \varepsilon_1 \quad (B.6)$$

then we re-choose $\delta_1$ above, call it $\delta_3$, so that

$$\delta_3 = \min \left( \delta_1, \mu_2 \sqrt{\mu q / K_1} / K_3 \right).$$

Then we repeat the argument for the term:

$$K_5\|W\| + K_6\|E_2\|\varepsilon < \sqrt{\nu q / K_2}$$
So we need to choose the \( \varepsilon \) so that

\[
\varepsilon < \nu_3 \sqrt{\frac{\nu_1 q/K_2}{(K_6 ||E_2||)}} := \varepsilon_2 \tag{B.7}
\]

and then re-choose \( \delta_2 \), call it \( \delta_4 \) so that

\[
\delta_4 = \min \left( \delta_2, \mu_3 \sqrt{\nu_1 q/K_2/K_5} \right)
\]

Then we choose \( \varepsilon = \min (\varepsilon_1, \varepsilon_2) \) with \( \varepsilon_1 \) and \( \varepsilon_2 \) given by (B.6) and (B.7).

Finally, now choose \( \delta_1 \) and \( \delta_2 \) to ensure (B.2) and (B.3) hold for this \( \varepsilon \) and then use

\[
\delta = \min \left( \delta_1, \mu_2 \sqrt{\mu_1 q/K_1/K_3}, \delta_2, \mu_3 \sqrt{\nu_1 q/K_2/K_5} \right).
\]

**Part 2 and Part 3**

Doing the same for the other equilibria we obtained the conditions of stability for \((0, z^*)\) and \((x', z')\) equilibria. In summary we obtain:

- For \( x \)-axis equilibrium the Lyapunov function exists under the following condition:

\[
\delta = \min \left( \delta_1, \mu_2 \sqrt{\mu_1 q/K_1/K_3}, \delta_2, \mu_3 \sqrt{\nu_1 q/K_2/K_5} \right)
\]

Where

\[
\mu_1, \mu_2, \mu_3, \nu_1, \nu_2, \nu_3 > 0, \quad \mu_1 + \nu_1 < 0.5;
\]

\[
K_1 = \frac{4}{q} \| M^T P D_1 \|^2 + |D_1^T P D_2| + |D_1^T P D_1|;
\]

\[
K_2 = \frac{4}{q} \| M^T P D_2 \|^2 + |D_2^T P D_2| + |D_2^T P D_2|;
\]
\[ K_3 = |f'||E_0||E_1|; \]
\[ K_4 = ||Ex^*|| + ||E_0||; \]
\[ K_5 = |g'||E_0||E_2|; \]
\[ K_6 = ||E_0||; \]

and
\[ \varepsilon < \min \left( \frac{\nu_2}{K_4||E_1||} \sqrt{\frac{\mu_1 q}{K_1}}, \frac{\nu_3}{K_6||E_2||} \sqrt{\frac{\nu_1 q}{K_2}} \right). \]

- For z-axis equilibrium the Lyapunov function exists under the following condition:
\[ \delta = \min \left( \delta_1, \mu_2 \sqrt{\mu_1 q/K_1}, K_3, \delta_2, \mu_3 \sqrt{\nu_1 q/K_2} \right) \]

Where
\[ K_1 = \frac{4}{q} ||MTPD_1||^2 + D_1^T P D_2 + D_1^T P D_1; \]
\[ K_2 = \frac{4}{q} ||MTPD_2||^2 + D_2^T P D_2 + D_1^T P D_2; \]
\[ K_3 = |f'||E_0||E_1|; \]
\[ K_4 = \|Ex^*\| + \|E_0\|; \]

\[ K_5 = |g'| \|E_0\| \|E_2\|; \]

\[ K_6 = \|E_0\|; \]

and

\[ \varepsilon < \min \left( \frac{\nu_2}{K_4\|E_1\|} \sqrt{\frac{\mu_1q}{K_1}}, \frac{\nu_3}{K_6\|E_2\|} \sqrt{\frac{\nu_1q}{K_2}} \right). \]

- For the coexistence equilibrium the Lyapunov function exists under the following condition:

\[ \delta = \min \left( \delta_1, \mu_2 \sqrt{\mu_1q/K_1/K_3}, \delta_2, \mu_3 \sqrt{\nu_1q/K_2/K_5} \right) \]

Where

\[ \mu_1, \mu_2, \mu_3, \nu_1, \nu_2, \nu_3 > 0, \]

\[ K_1 = \frac{4}{q} \|MTPD_1\|^2 + |D_1^T PD_2| + |D_1^T PD_1|; \]

\[ K_2 = \frac{4}{q} \|MTPD_2\|^2 + |D_2^T PD_2| + |D_2^T PD_2|; \]

\[ K_3 = |f'| \|E_0\| \|E_1\|; \]
\[ K_4 = ||Ex'|| + ||E_0||; \]

\[ K_5 = |g'| ||E_0|| ||E_2||; \]

\[ K_6 = ||Ez'|| + ||\tilde{E}_0||; \]

and

\[ \varepsilon < \min \left( \frac{\nu_2}{K_4||E_1||} \sqrt{\frac{\mu_1 q}{K_1}}, \frac{\nu_3}{K_6||E_2||} \sqrt{\frac{\nu_1 q}{K_2}} \right). \]
Bibliography


