THE DYNAMICS OF PLANT-HERBIVORE INTERACTIONS AND THEIR IMPLICATIONS FOR SPATIAL EXPANSION

by

Yun Kang

A Dissertation Presented in Partial Fulfillment of the Requirements for the Degree
Doctor of Philosophy

ARIZONA STATE UNIVERSITY

August 2008
THE DYNAMICS OF PLANT-HERBIVORE INTERACTIONS AND THEIR
IMPLICATIONS FOR SPATIAL EXPANSION

by

Yun Kang

has been approved

May 2008

Graduate Supervisory Committee:

Dieter Armbruster, Co-Chair
Yang Kuang, Co-Chair
Steven Baer
Hal Smith
Horst Thieme

ACCEPTED BY THE GRADUATE COLLEGE
ABSTRACT

This dissertation investigates the population dynamics and spread of the gypsy moth population, which is a forest pest that was accidentally released near Boston in 1869, and now occupies more than 1,000,000 square kilometers of the northeastern United States.

A model of plant-herbivore interactions based on the nutrient recycling of the forest and the biological properties of the herbivore is constructed using a host-parasite model with density dependence acting before the parasite attack. The dynamical behavior of the host and parasite populations as a function of the growth rate of the plant and the damage done by the parasite is studied. Bistability and a crisis of a strange attractor suggest two control strategies: Reducing the population of herbivores under some threshold (this suggests control procedures to reduce the herbivore population by actions such as spraying pesticides) or increasing the growth rate of the plant leaves (this could occur naturally under highly favorable growing conditions but could also be supported by fertilizing the plants).

A second part of this dissertation investigates the impact of monotone plant growth models in general plant-herbivore models on the dynamics of the plant-herbivore interaction. It is shown that all monotone growth models generate a unique interior equilibrium. Monotone growth models with a single nonzero equilibrium of the plant population lead to noise sensitive bursting which is identified as a dynamical mechanism for almost periodic outbreaks of the herbivore infestation. Monotone and non-monotone plant growth models are contrasted with respect to bistability and crises of chaotic attractors.

A dynamical model generating bistability is used to study the behavior of the plant and herbivore populations in two identical coupled patches where one patch is infected with the herbivore and the other one is not. The influence of the bistable dynamics on the spread of the
infestation is considered. It is shown that an appropriate barrier (migration) between these two patches can regulate the population of herbivores in both patches under the bistability threshold, leading to an eventual extinction of the herbivore in both patches.
To my husband Nicolas and the rest of my family
Though the following dissertation is an individual work, I could never have reached the heights or explored the depths without the help, support, guidance and efforts of a lot of people. Firstly, I would like to thank my two advisors, Dr. Dieter Armbruster and Dr. Yang Kuang, for their patience, encouragement and guidance. Their mentorship were paramount in providing a well rounded experience consistent with my long-term career goals. I am really thankful to them for reading my reports, commenting on my views and helping me to understand and enrich my ideas. Especially, I would like to thank Dieter for his continually stimulating my analytical thinking and greatly assisting me with scientific writing.

I would like to thank a very special person-Dr. Mac Hyman for inspiring and encouraging me to pursue a career in mathematical biology. I first met Mac when I was a graduate student at the University of Arizona. Since then, he has been assisting and guiding me in writing and presenting. I probably could not get my graduate career started on the right foot without his help.

I also would like to thank the Department of Mathematics and Statistics at Arizona State University, especially the members of my doctoral committee for their input, valuable discussions and accessibility. In particular, I would like to thank Dr. Smith for helping revising Chapter Three of my dissertation and Dr. Thieme for helping revising the reference.

Finally, and most importantly, I would like to thank my husband and best friend, Nicolas for his support, encouragement, quiet patience and unwavering love. His tolerance of my occasional vulgar moods is a testament in itself of his unyielding devotion and love. I am extremely grateful to him spending hours reading the draft of my dissertation and giving me useful feedback.
This research was partially support by NSF grants DMS-0604986, DMS-0436341 and DMS/NIGMS-0342388.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIST OF TABLES</td>
<td></td>
<td>xii</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td></td>
<td>xiii</td>
</tr>
<tr>
<td>CHAPTER 1</td>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>1.</td>
<td>Plant-herbivore interactions</td>
<td>1</td>
</tr>
<tr>
<td>1.1.</td>
<td>Population dynamics of plants</td>
<td>3</td>
</tr>
<tr>
<td>1.2.</td>
<td>Population dynamics of herbivores</td>
<td>4</td>
</tr>
<tr>
<td>2.</td>
<td>Motivation and research focus</td>
<td>5</td>
</tr>
<tr>
<td>3.</td>
<td>Overview of chapters</td>
<td>7</td>
</tr>
<tr>
<td>CHAPTER 2</td>
<td>Dynamics of a plant-herbivore model</td>
<td>10</td>
</tr>
<tr>
<td>1.</td>
<td>Introduction</td>
<td>10</td>
</tr>
<tr>
<td>2.</td>
<td>A general plant-herbivore model and its boundary dynamics</td>
<td>12</td>
</tr>
<tr>
<td>3.</td>
<td>Interior equilibria</td>
<td>17</td>
</tr>
<tr>
<td>3.1.</td>
<td>Codimension one: Neimark-Sacker bifurcation</td>
<td>19</td>
</tr>
<tr>
<td>3.2.</td>
<td>Bifurcation diagram in the ((r, a))-parameter space</td>
<td>21</td>
</tr>
<tr>
<td>4.</td>
<td>Bistability and chaos</td>
<td>24</td>
</tr>
<tr>
<td>4.1.</td>
<td>Bistability</td>
<td>24</td>
</tr>
<tr>
<td>4.2.</td>
<td>Strange attractor and its collapse</td>
<td>26</td>
</tr>
<tr>
<td>5.</td>
<td>Discussion</td>
<td>27</td>
</tr>
<tr>
<td>CHAPTER 5</td>
<td>Conclusion and future work</td>
<td>77</td>
</tr>
<tr>
<td>-----------</td>
<td>----------------------------</td>
<td>----</td>
</tr>
<tr>
<td>1.</td>
<td>Summary</td>
<td>77</td>
</tr>
<tr>
<td>2.</td>
<td>Future directions</td>
<td>79</td>
</tr>
<tr>
<td>2.1.</td>
<td>Integrodifference models</td>
<td>79</td>
</tr>
<tr>
<td>2.2.</td>
<td>Modeling multi-tropical interactions</td>
<td>81</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>CHAPTER A</th>
<th>Appendix</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Derive normal form</td>
<td>1</td>
</tr>
<tr>
<td>1.1.</td>
<td>At the boundary equilibrium point (1, 0)</td>
<td>1</td>
</tr>
<tr>
<td>2.</td>
<td>Normal form analysis</td>
<td>6</td>
</tr>
<tr>
<td>3.</td>
<td>Model analysis</td>
<td>8</td>
</tr>
<tr>
<td>3.1.</td>
<td>Positive invariant and bounded</td>
<td>8</td>
</tr>
<tr>
<td>3.2.</td>
<td>Boundary equilibria</td>
<td>9</td>
</tr>
<tr>
<td>3.3.</td>
<td>Codimension two bifurcation at the boundary equilibrium point</td>
<td>13</td>
</tr>
<tr>
<td>4.</td>
<td>Interior equilibria</td>
<td>15</td>
</tr>
<tr>
<td>4.1.</td>
<td>Stability of the interior equilibria</td>
<td>18</td>
</tr>
<tr>
<td>4.2.</td>
<td>No codimension two bifurcation at the interior equilibria</td>
<td>19</td>
</tr>
<tr>
<td>4.3.</td>
<td>Codimension one: Neimark-Sacker bifurcation</td>
<td>22</td>
</tr>
<tr>
<td>4.4.</td>
<td>Codimension one: period doubling bifurcation</td>
<td>24</td>
</tr>
<tr>
<td>4.5.</td>
<td>Codimension one: saddle-node bifurcation</td>
<td>25</td>
</tr>
<tr>
<td>5.</td>
<td>Global stability of the boundary equilibrium</td>
<td>27</td>
</tr>
</tbody>
</table>
LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Bistability table</td>
<td>27</td>
</tr>
<tr>
<td>2. Growth models of plant population density</td>
<td>31</td>
</tr>
<tr>
<td>3. Average period of the herbivore dynamics when $a = 3.95, r = 4.55$</td>
<td>48</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>3.1</td>
<td>Interior equilibria</td>
</tr>
<tr>
<td>3.2</td>
<td>Bifurcation diagram of parameters $r$ and $a$</td>
</tr>
<tr>
<td>3.3</td>
<td>Periodic solution with period 9 for $r = 2.7, a = 2.1$</td>
</tr>
<tr>
<td>3.4</td>
<td>Dense orbit in phase space for $r = 2.45, a = 1.5</td>
</tr>
<tr>
<td>4.5</td>
<td>Bistability in region 3</td>
</tr>
<tr>
<td>4.6</td>
<td>Bistability in regions 6 and 7</td>
</tr>
<tr>
<td>4.7</td>
<td>How interior attractor collapses as $r$ increases</td>
</tr>
<tr>
<td>2.8</td>
<td>Possible configurations of the staircase diagrams</td>
</tr>
<tr>
<td>5.9</td>
<td>Schematic of the heteroclinic bifurcation of Holling-Type III model happens at $a = 0.71, r = 3.5$</td>
</tr>
<tr>
<td>5.10</td>
<td>The periodic orbit for the Beverton-Holt model when $a = 2, r = 2.5, 2.7, 2.8, 3$</td>
</tr>
<tr>
<td>5.11</td>
<td>Neimark-Sacker bifurcation and heteroclinic bifurcations</td>
</tr>
<tr>
<td>5.12</td>
<td>Time series of the herbivore population for the Beverton-Holt model. The parameters are $a = 3.95, r = 4.55$ and a noise level of $w = 0.01$</td>
</tr>
<tr>
<td>5.13</td>
<td>The resident time ratio as a function of the noise amplitude when $a = 3.95, r = 4.55$ with a threshold of 0.01</td>
</tr>
<tr>
<td>6.14</td>
<td>The interior strange attractor and the stable manifold of the boundary attractor</td>
</tr>
<tr>
<td>4.15</td>
<td>Time series of plant-herbivore population: $a = .98, r = 2.45$</td>
</tr>
<tr>
<td>Figure</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
</tr>
<tr>
<td>4.16. Phase portrait of plant-herbivore population in the case three and four</td>
<td>72</td>
</tr>
<tr>
<td>4.17. Basin of attraction for the interior equilibrium when ( a = 0.98, r = 2.45, l = 0 )</td>
<td>73</td>
</tr>
<tr>
<td>4.18. The ratio of initial conditions in the patch one that make the herbivore established when ( a = 0.98, r = 2.45 )</td>
<td>73</td>
</tr>
<tr>
<td>4.19. Basin of attraction for the interior attractor when ( a = 0.98, r = 2.45, l = 0.1 ). Notice that all initial conditions decay to zero.</td>
<td>74</td>
</tr>
<tr>
<td>4.20. Compare basin boundary for ( l = 0 ) and ( l = 0.2 )</td>
<td>75</td>
</tr>
<tr>
<td>4.21. Compare basin boundary for ( l = 0 ) and ( l = 0.4 )</td>
<td>76</td>
</tr>
<tr>
<td>4.22. Case one: ( \lambda_1 = 1, \lambda_2 = -1 )</td>
<td>21</td>
</tr>
<tr>
<td>4.23. Case two: ( \lambda_1 = \lambda_2 = 1 )</td>
<td>21</td>
</tr>
<tr>
<td>5.24. Three cases for different values of ( r ) and ( a )</td>
<td>29</td>
</tr>
</tbody>
</table>
CHAPTER 1 - Introduction

This dissertation is motivated by the persistence of invading forest insects populations in the United States. Forest pests cause the defoliation of millions of acres forests every year and are among the most significant threats to the stability of natural and agricultural ecosystems. I use mathematical modeling to build a theoretical framework of the interactions between forests and pests. The objective is to help forest managers design better biological control strategies to regulate the population of forest pests and eventually stop the invasions.

The interactions between forests and pests are only one example of a larger category of plant-herbivore interactions. In the following, I will introduce some basic properties of plant-herbivore interactions and discuss previous works in the following sections.

1. Plant-herbivore interactions

The understanding of the relationships between insects and plants is extremely important for land management, especially in forests. The remarkable variety of dynamical behaviors exhibited by plant and herbivore species plants has stimulated great interest in the development of dynamical system models of populations or ecosystems. There are several theoretical outcomes for mutual dependence between plant and herbivore populations. Classical approaches to model plant-herbivore systems have some analogies with prey-predator systems (Imanuel, 1975). There is no typical pattern resulting from plant-herbivore dynamics. Instead, the evolution strongly depend upon the demographic parameters of the plant and herbivore populations and also the timing, kind and degree of density dependence that they exhibit (Crawley, 1983).

There are many well established plant-herbivore models in the literature. The model of Gutierrez et al. (1985), which is based on the McKendrick von Foerster equation, is a system
of partial differential equations where the effect of herbivores on individual plant parts is considered. The model by Edelstein-Keshet (1986) is a system of partial differential equations describing a plant-herbivore system which depends on plant quality and herbivore density. The structural models analyzed by Edelstein-Keshet, (1986) and Gutierrez, et al., (1985) are at the individual level, whereas our model is at the population level. Pakes and Mailer (1990) develop and analyze a system of difference equations for an annual plant population with a seed bank. Allen (1993) developed a simple difference equation model to formulate and analyze a plant-herbivore system based on two control strategies: cane removal and pesticide application. Powell, et al. (1996,1997) developed mechanistic models that range from strategic population models of beetle outbreaks to tactical behavior models describing how beetles select host trees. These models identify the importance of beetle dynamics and host susceptibility as factors of beetle outbreak. Powell, et al. (2000) combine three different mathematical approaches to develop a spatial framework in which risk of mountain pine beetle (MPB) attack on individual hosts may be assessed. A density-based partial differential equation model describes the dispersal and focusing behavior of MPB. These models showed spatial risk structures which may also shed light on the role of climatic variables in population outbreaks. Powell, et al. (2001,2005) explore the quantitative modeling and analysis of direct temperature control and how these models shed light on adaptive seasonality to oviposition dates for subsequent generations. The uncontrolled plant-herbivore interaction models in van der Koppel, et al. (1996), supported by empirical evidence, predict a possible coexistence of dense vegetation and low herbivore numbers, in the absence of any predator. Belinda Barnes et al. (2005) continued the study of van der Koppel which describes briefly how van der Koppel, et al. (1996) derive their uncontrolled plant-herbivore interaction models.
1.1. Population dynamics of plants. Plants exist in different habitats like trees in forests, shrubs in deserts, annuals in early successional communities, herbaceous perennial in grasslands all of which are modular in construction. Hence, it is more meaningful to model the plant population in terms of biomass density rather than to count the number of individuals. Many plants are influenced by cyclical weather (e.g., deciduous trees grow leaves in spring and lose them in winter) and seasonal herbivores (e.g., forest pests, which eggs hatch in spring and adults die in winter), which makes it more realistic to model the plant population in a discrete time fashion. Let \( P_n \) be the biomass density of the plant at season \( n \), \( r \) be the maximum growth rate per season and \( f(r, P_n) \) be the net growth rate of the plant which is a nonlinear function in \( P_n \) describing the intra-specific competition. The biomass density of the plant \( P_{n+1} \) in the next season \( n + 1 \), can be modeled by

\[
P_{n+1} = P_n f(r, P_n).
\]

(1.1)

Different plants have different population dynamics, i.e., \( f(r, P_n) \) can be varied. Plant population dynamics are relatively tame compared to animal dynamics (Crawley, 1990). A paper by Crawley and May in 1987 states that more realistic plant models tend to exhibit much more stable dynamics than the plant dynamics that exhibit “interesting dynamics” like cycles or chaos (Pacala & Silander, 1985). However, there do have some documented examples of cyclical plant populations like certain annuals (Symonides, 1984, describes how the tiny annual crucifer \( Erophila verna \) undergoes a two-point cycle in inland dunes in Poland), vines (Mueller-Dombois, 1981), some shrubs (e.g., the so-called stand cycle of \( Calluna vulgaris \), Watt, 1964) and trees exhibiting “wave dynamics” (Sprugel, 1976).

The main purpose of my work is to investigate the interactions between plants and herbivores. There is strong ecological evidence showing that plant population dynamics
have more important effects on plant-herbivore interactions than herbivore population does. Hence, it is really necessary for us to consider the following two plant population dynamics: a population with (i) "interesting dynamics" like periodic cycles or chaos and (ii) stable dynamics, characterized by:

(i) Plant models that show an over-compensation for density dependence, i.e. for \( F(r, P) = Pf(r, P) \), \( F \) increases to a maximum and then decreases with respect to \( P \). Hence there exists \( P_m > 0 \) such that

\[
\frac{dF(r, P)}{dP} \bigg|_{P<P_m} > 0, \quad \frac{dF(r, P)}{dP} \bigg|_{P=P_m} = 0 \quad \text{and} \quad \frac{dF(r, P)}{dP} \bigg|_{P>P_m} < 0
\]

(ii) Plant models that shown an under-compensation for density dependence. In this case \( F(r, P) \) is non-decreasing and reflects an increasing utilization of available resources: i.e., \( \frac{dF(r, P)}{dP} \geq 0 \).

In this dissertation, I focus on both "over-compensating" plant models (such as Ricker type models) which can generate complicated dynamics such as cycles and chaos and "under-compensating" plant population models (such as Beverton-Holt type models) with stable dynamics.

1.2. Population dynamics of herbivores. Herbivores are animals that only feed on plants, hence their biomass is generated from whatever they eat. Therefore, their population dynamics are determined by the plants they feed on under the assumption that there are no other food resources. Let \( H_n \) be the biomass density of herbivores in season \( n \) and assume that \( a \) is a parameter that measures the herbivore’s food searching efficiency. Then the herbivore biomass density \( H_{n+1} \) in season \( n + 1 \) can be modeled as:

\[
H_{n+1} = P_nf(r, P_n)[1 - g(a, H_n)]. \quad (1.2)
\]
where \( g(a, H_n) \) is the fraction of reduction in the plant biomass density due to the feeding herbivores, and \( 1 - g(a, H_n) \) is the fraction of plants eaten by herbivores.

2. Motivation and research focus

Most plant-pest population models fall into one of the following categories:

(i) The simplest models are derived from regression analysis of data to obtain predictions of the population in the next year based on estimates from previous years (Campbell & Sloan, 1978 (a,b); Biging, et al., 1980). These models do not involve any explicit dependence on the pest’s biology. While useful as indicators, such models have very restricted ranges of applicability.

(ii) A slightly more complicated class of models includes those designed to examine within-generation behavior of one or several characteristics of the pest. These models are based on specific, known biological characteristics of the herbivores, and are in the form of difference equations or differential equations (Valentine & Talerico, 1980; Valentine, et al., 1980; Valentine, 1983; Gray, et al., 1991).

(iii) The most complicated ones are large models which allow prediction from one year to the next year utilizing numerous detailed submodels based on the pest’s biology and which require large quantities of data (on the pest’s terrain and the weather) in order to make predictions (McNamee, et al., 1983; Sheehan, 1989).

(iv) Simple spatial models have been used to study the spread of forest pests (Mason & McMannus, 1981; Liebhold, et al., 1991). Logan & Powell (1998) develop a spatially dynamic model on the MPB and forest interaction that includes chemical ecology, spatial redistribution of the beetle’s attack, and resulting host mortality. Their model
is a system of 6 coupled, partial differential equations with 7 state variables and 20 parameters.

Each of these four basic types of models is important and useful when applied appropriately. The type of model that one needs is based on what one is interested in studying or predicting. One of the most important questions when considering forest pests is predicting when the next outbreak will occur as well as how to manage it. Models described as type (i) can be used to make gross one year predictions, but successive uses to extend that prediction for a moderate time is inappropriate. In addition, they cannot effectively be used to predict the effects of various management strategies on the population since they do not include biological considerations. Type (ii) models are only based on looking at within year dynamics, and so are not applicable to long-term predictions. The size of type (iii) models, as well as their dependence on detailed information about the forest stand and the weather during the time being simulated, makes their usefulness very limited. Even a somewhat smaller model which has been developed recently (Sharov & Colbert, 1996) is extremely complex (involving five life stages of the pest, three classes of trees, four guilds of parasites, two guilds of predators and a virus) with a very large number of parameters, most of them being unknown. In addition, such models have shown at best a rough qualitative similarity with field data on timing of outbreaks (e.g., outbreaks having an average period of between 8 and 12 years) and have not been able to make quantitative predictions about future outbreaks (Sharov & Colbert, 1996). As a result, these models are of questionable use in risk assessment or pest management studies. Type (iv) models are concerned only with the dispersal of small larvae based on diffusion-like models, ignoring predictions about future population dynamics (Mason, et al., 1981), or are based on geostatistical methods of interpolating populations at any
given location given measurements at specific sites (Liebhold, et al., 1991). Some Type (iv) models are so complicated that it is mathematically untractable (Powell, et al., 1998,2000).

In this work, I am concerned with developing a model as small as possible which not only contains the essential features of the pest’s biology, but which can be used for predicting and controlling studies. Unlike other models designed recently to examine the time evolution of the population (Wilder, et al., 1994; Sharov & Colbert, 1996), the goal here is not to derive a model which has only qualitatively similar characteristics to field data (such as outbreaks every 8-12 years, etc.), but to develop a model which successfully predicts outbreaks given a reasonable amount of data and control the population of forest pests with the best strategies.

In this dissertation, I want to model the interactions between plants and herbivores based on the nutrient recycling of the forest and the biological properties of herbivores with density dependence acting before parasitism. In addition, I explore how invasive forest pests spread into different areas. I focus on the following three main questions:

(i) What is the most likely population dynamics of forest pests (e.g., gypsy moths)? Which strategies are the best for forest managers to control their populations?

(ii) How do the different population dynamics of the plant affect the herbivores?

(iii) How does a barrier between patches affect the spreading of gypsy moths? Which biological control strategies can regulate the pest’s population and eventually stop the invasion?

3. Overview of chapters

The rest of this dissertation is organized as follows: Chapter 2 derives a model on the interactions between plants and herbivores based on the nutrient recycling of the forest and
the biological properties of herbivores by using a host-parasite model with density dependence acting before parasitism. The complete mathematical analysis of this discrete model has been performed. The parameter space consists of the growth rate of the plant population and a parameter describing the damage inflicted by herbivores. The study shows insightful bifurcation diagrams in that parameter space. Bistability and a crisis of a strange attractor suggest two control strategies: Reducing the population of the herbivore under some threshold or increasing the growth rate of the plant leaves. In addition, the persistence of the plant population and the global stability of the boundary equilibrium \((1, 0)\) in the case when \(0 < r \leq a < 1\) and \(0 < a^\frac{e^{\frac{r-1}{r}}}{r} < 1\) have been presented.

Chapter 3 investigates two general plant-herbivore models: The first model involves a single plant species that has an increasing population dynamics with a decreasing growth function (the Beverton-Holt model), while the second model has a Holling-Type III function as its plant's population dynamics. One key feature of these two models is that monotone boundary dynamics generates a unique interior equilibrium. The interior equilibrium goes through a Neimark-Sacker bifurcation, which generates invariant orbits and periodic or quasi-periodic behavior. The study shows that for the Beverton-Holt model the environmental fluctuations are important to generate almost periodic bursting behavior of the herbivore population. In contrast, the Holling-Type III model does not have such a property but instead shows a heteroclinic bifurcation, as a result of the existence of more than 2 boundary equilibria. The models, in which herbivores attack plants before or after the plants' uptake of nutrients from soil, have the similar dynamics. In addition, the comparison between the dynamics of monotone plant growth models and plant-herbivore models with unimodal (or multimodal) functions as plant growth models have been shown.
Chapter 4 investigates the influence of bistability on a two-patch plant-herbivore model by introducing a new parameter to measure the barrier between one infected patch and one uninfected patch. These two patches are identical, i.e., with the same growth rate of the plant and the same damage cost by the herbivore. One of the most interesting results shows that an appropriate barrier between these two patches can decrease the population of herbivores in both patches under some threshold, which suggests that a possible biology control strategy to stop the invasion is to adjust the barrier between the patches. In addition, the study indicates that a patchy environment can both stabilize and destabilize the dynamics.

The last chapter is a summary of the dissertation work and introduces possible future works.
CHAPTER 2  –  Dynamics of a plant-herbivore model

We formulate a simple host-parasite type model to study the interaction of certain plants and herbivores. Our two dimensional discrete time model utilizes leaf and herbivore biomass as state variables. The parameter space consists of the growth rate of the host population and a parameter describing the damage inflicted by herbivores. We present insightful bifurcation diagrams in that parameter space. Bistability and a crisis of a strange attractor suggest two control strategies: Reducing the population of the herbivore under some threshold or increasing the growth rate of the plant leaves.

1. Introduction

The usual framework for discrete-generation host-parasite models has the form

\begin{align}
    P_{n+1} &= \lambda P_n f(P_n, H_n), \\ 
    H_{n+1} &= c\lambda P_n [1 - f(P_n, H_n)],
\end{align}

where \( P \) and \( H \) are the population biomasses of the host (a plant) and the parasite (a herbivore) in successive generations \( n \) and \( n + 1 \) respectively, \( \lambda \) is the host's inherent rate of increase (\( \lambda = e^r \) where \( r \) is the intrinsic rate of increase) in the absence of the parasites, \( c \) is the biomass conversion constant, and \( f \) is the function defining the fractional survival of hosts from parasitism. Throughout the rest of this chapter, \( n \) takes nonnegative integer values.

The simplest version of this model is that of Nicholson (1933) and Nicholson and Bailey (1935) who explored in depth a model in which the proportion of hosts escaping parasitism is given by the zero term of the Poisson distribution namely,

\[ f(P_n, H_n) = e^{-aH_n}, \]
where \( a \) is the mean encounters per host. Thus, \( 1 - e^{-aH_n} \) is the probability of a host will be attacked. Substituting (2.3) into the equations (2.1) and (2.2) gives:

\[
P_{n+1} = \lambda P_n e^{-aH_n},
\]

(2.4)

\[
H_{n+1} = c\lambda P_n [1 - e^{-aH_n}].
\]

(2.5)

When \( \lambda > 1 \), the Nicholson-Bailey model has a positive equilibrium which is unstable (p57 in Edelstein-Keshet, 1988).

Beddington et al. (1975) considered the following modified Nicholson-Bailey model

\[
P_{n+1} = \lambda P_n e^{\left(\frac{rP_n}{P_{\text{max}}} - aH_n\right)}
\]

(2.6)

\[
H_{n+1} = c\lambda P_n (1 - e^{-aH_n}),
\]

(2.7)

where \( P_{\text{max}} \) is the so-called environment imposed "carrying capacity" for the host in the absence of the parasite. What was an unstable positive equilibrium when no density dependent is assumed for host population growth becomes locally stable for a large set of parameter values (Beddington et al. 1975). For other parameter values, the model can generate attractors of various complexity, ranging from a set of limit cycles of various periods to strange and chaotic ones.

Observe that the structure of equations (2.6) and (2.7) implies that the host density-dependence acts at a particular time in their life cycle in relation to the stage attacked by the parasites. The \( H_n \) herbivores search for \( P_n \) hosts \textit{before} the density dependent growth regulation takes effect. Hence the next generation of herbivores depends on \( P_n \), the initial
host population prior to parasitism. This leads to the following general form:

\[ P_{n+1} = \lambda P_n g(P_n) f(H_n), \quad (2.8) \]

\[ H_{n+1} = c\lambda P_n [1 - f(H_n)]. \quad (2.9) \]

where \( f(H_n) \) represents the fraction of hosts surviving parasitism, and the host density dependence takes the form \( g(P_n) = e^{(1 - \frac{rP_n}{P_{\text{max}}})}. \)

In many observable plant-herbivore (host-parasite) interactions, herbivores (parasites) are not attracted to and attack plants until their leaves form good canopies. Moreover, the feeding process continues throughout most periods of the growing season. This argues for plant-herbivore (host-parasite) models where the herbivore (parasitization) occurs after the density dependent growth regulation of the host takes place. The importance of the sequencing of events when constructing discrete time models is well known (Edelstein-Keshet, 1988; Caswell Hal, 2006). We propose the following discrete models for such plant-herbivore interactions:

\[ P_{n+1} = \lambda P_n g(P_n) f(H_n), \quad (2.10) \]

\[ H_{n+1} = c\lambda P_n g(P_n) [1 - f(H_n)]. \quad (2.11) \]

May, et al. 1981 introduced (2.10) and (2.11). Here we assume that the consumed plant biomass is fully converted to herbivore biomass, i.e. model (2.10)-(2.11) observes the conservation of biomass production. This basic conservation law is often ignored in existing population models without proper justification.

2. A general plant-herbivore model and its boundary dynamics

In the following, we apply the above model framework to the interaction between a plant species and a herbivore species. We are motivated by the gypsy moth, which
is a notorious forest pest in North Central United States whose outbreaks are almost periodic and cause significant damage to the infested forests. In our discrete-time model, we assume that herbivore population growth is a non-linear function of herbivore feeding rate, and that plant population growth decreases gradually with increasing herbivore. Also, in the absence of the herbivore, plant population density is regulated by intraspecific competition (Harper, 1977; Antonovics & Levin, 1980; Watkinson, 1980), so we allow for density dependence in the plant. We model the plant and herbivore dynamics through their biomass changes. We assume that the soil acts as an unlimited reservoir for biomass growth. A plant takes up the nutrient from the soil and stores the nutrient in its stem, bark, twig and leaves. During spring, leaves emerge in a deciduous forest. A herbivore in our model has a one year life cycle, like the insects. For example, the gypsy moth larvae hatch from the egg mass after bud-break and feed on new leaves. At the end of the season \( n \), adult gypsy moths lay eggs and die. We make the following assumptions:

A1: \( P_n \) represents the plant population's (nutritious) biomass after the attacks by the herbivore but before its defoliation. \( H_n \) represents the biomass of the herbivore before they die at the end of the season \( n \).

A2: Without the herbivore, the biomass of the plant population follows the dynamics of the Ricker model (Ricker 1954),

\[
P_{n+1} = P_n e^{r \left[1 - \frac{P_n}{P_{\text{max}}} \right]}
\]

(2.12)

with a constant growth rate \( r \) and plant carrying capacity \( P_{\text{max}} \). The Ricker dynamics determines the amount of new leaves available for consumption for the herbivore.
A3: We assume that the herbivores search for food randomly. The leaf area consumed is measured by the parameter \( a \), i.e., \( a \) is a constant that correlates the total amount of the biomass that an herbivore consumes. The herbivore has a one-year life cycle, the larger \( a \), the faster the feeding rate.

After attacks by herbivores, the biomass in the plant population is reduced to a fraction \( e^{-aH(n)} \) of that present in the absence of herbivores. Hence,

\[
P_{n+1} = P_n e^{r \left(1 - \frac{P_n}{P_{\text{max}}} \right)^{-aH_n}}. \tag{2.13}
\]

The amount of decreased biomass in the plants is converted to the biomass of the herbivore. Mathematically, the conversion parameter can be scaled away by a simple change of variable \( H_n/c \rightarrow H_n \). Hence, for convenience, we assume below that the biomass conversion parameter is 1. Therefore, at the end of the season \( n \), we have

\[
H_{n+1} = P_n e^{r \left(1 - \frac{P_n}{P_{\text{max}}} \right)} \left[1 - e^{-aH_n}\right]. \tag{2.14}
\]

In nature, densities of the host plants are usually high for long periods, during which insect densities are correspondingly low. Periods of high plant abundance are punctuated by sudden insect outbreaks, followed by a rapid crash and rapid recovery of the host plant (McNamee, et al., 1981; Crawley, 1983; Berryman, 1987). The system (2.13)-(2.14) captures these dynamics (Abbott, et al., 2007). There are three parameters in our system \( r, a \) and \( P_{\text{max}} \). We can scale \( P_{\text{max}} \) away by setting \( x_n = \frac{P_n}{P_{\text{max}}} \), \( y_n = \frac{H_n}{P_{\text{max}}} \), \( a \rightarrow aP_{\text{max}} \). This yields the following
non-dimensionalized system:

\[ x_{n+1} = x_ne^{r(1-x_n)-ay_n}, \quad (2.15) \]
\[ y_{n+1} = x_ne^{r(1-x_n)} \left[ 1 - e^{-ay_n} \right]. \quad (2.16) \]

It is easy to see that if \( x_0 = 0 \) \( (y_0 = 0) \), then \( x_n = 0 \) \( (y_n = 0) \) for \( n > 0 \). We assume that \( a > 0 \) and \( r > 0 \). Observe that \( x_{n+1} + y_{n+1} = x_ne^{r(1-x_n)} \leq e^{r-1}/r \). We thus have the following propositions.

**Proposition 2.1.** Assume that \( a > 0, r > 0, x_0 > 0 \) and \( y_0 > 0 \), then \( x_n > 0 \) and \( y_n > 0 \) for all \( n > 0 \). In addition we have \( \max_{n \in \mathbb{Z}^+} \{x_n, y_n\} \leq e^{r-1}/r \) for \( n > 0 \).

**Proof.** For the detailed proof please see the Appendix A Proposition 3.1.

The exponential nonlinearity in Ricker-type models is a prototype for an ecological model describing discrete-time populations with a one hump dynamics. One hump dynamics indicate an optimal population size that maximizes reproductive success - deviations from which lead to reduced populations in the next generation. This reflects limitations to population growth at high densities such as limited food, water or space (Abbott & Dwyer, 2007).

The system (2.15)-(2.16) has the two boundary equilibria \((0,0)\) and \((1,0)\) and possibly multiple interior equilibria depending on the parameter values of \( r \) and \( a \).

At the boundary equilibrium point \((0,0)\), the Jacobian matrix takes the form of

\[ J_{(0,0)} = \begin{bmatrix} e^r & 0 \\ 0 & 0 \end{bmatrix} \quad (2.17) \]

with eigenvalues \( \lambda_1 = e^r \geq 1 \) and \( \lambda_2 = 0 < 1 \). Hence, the origin is a saddle which is stable on the \( y \)-axis and unstable on the \( x \)-axis. This implies that plants can not die out.
At the boundary equilibrium point $(1,0)$, the Jacobian matrix is

\[
J_{(1,0)} = \begin{bmatrix}
1 - r & -a \\
0 & a
\end{bmatrix}
\]

with eigenvalues $\lambda_1 = 1-r$ and $\lambda_2 = a$. As a result, we have two codimension-one bifurcations from this equilibrium:

- Near $r = 2$ and $\alpha \neq 1$, the Taylor expansion of equations (2.15) on the invariant manifold $y = 0$ gives

\[
u_{n+1} = (-1 - \gamma)\nu_n + \frac{2\nu_n^3}{3}
\]

where $\gamma = r - 2$ and $\nu_n = x_n - 1$. Equation (2.19) satisfies the necessary and sufficient conditions for period doubling (Wiggins, 2003) consistent with the Ricker dynamics.

- Near $\alpha = 1$ and $r \neq 0,2$, we can perform a center manifold reduction and obtain the equation (if $r = 2$ then our system has a codimension-two bifurcation).

\[
v_{n+1} = (1 + \alpha)v_n - \frac{(\alpha + \gamma)v_n^2}{2} - \frac{v_n^3}{3}
\]

where $\gamma = r - 2$, $\alpha = a - 1$ and $v_n = y_n$. For $\gamma \neq 0$, Equation (2.20) satisfies the necessary and sufficient conditions for a transcritical bifurcation. For $\alpha = \gamma = 0$, we have a pitchfork bifurcation.

- We can unfold the transcritical bifurcation to obtain a saddle node bifurcations at

\[
\nu = \sqrt{-3\alpha}, \quad \gamma = -\frac{4}{3}\sqrt{-3\alpha} - \alpha, \quad (2.21)
\]

\[
\nu = -\sqrt{-3\alpha}, \quad \gamma = \frac{4}{3}\sqrt{-3\alpha} - \alpha. \quad (2.22)
\]

Notice that the equilibrium (2.22) lies in the second quadrant and hence is biologically uninteresting. Equilibrium (2.21) exists only when $\alpha < 0$. 
• When $r = 2$ and $a = 1$, we have the most degenerate case with eigenvalues $\lambda_1 = -1$ and $\lambda_2 = 1$.

For the detailed proof, please check the Appendix Section 3 and Section 4.

3. Interior equilibria

Let $E = (x^*, y^*)$ be an interior equilibrium of model (2.15)-(2.16). From (2.15) we obtain $x^* = 1 - \frac{ay^*}{r}$ and from (2.16) we obtain $x^* = y^*/(e^{ay^*} - 1)$ (since $ay^* = r(1 - x^*)$). Let

$$f_1(y) = 1 - \frac{ay}{r} \quad \text{and} \quad f_2(y) = \frac{y}{e^{ay} - 1}.$$ 

Then the interior equilibria are the intersection points of these two functions in the first quadrant $Q^+$.

Clearly, $f_1(y)$ is a decreasing linear function. It is easy to show that $f_2(y)$ is also decreasing. In addition, we have $\lim_{y \to 0} f_2(y) = 1/a$ and $\lim_{y \to 0} f_2'(y) = -1/2$. Observe that if $a = 1, r = 2, f_1(y)$ and $f_2(y)$ are tangent at the boundary equilibrium $(1,0)$ with a slope of $-1/2$. Straightforward computation shows that $f_2''(y) \geq 0$ and $f_2'(y) \in (-1/2, 0)$, for $y > 0$. Hence the intersection of $f_1(y)$ and $f_2(y)$ in the first quadrant $Q^+$ has 0 (Figure 3.1(a)), 1 (Figure 3.1(b)) or 2 (Figure 3.1(c)) interior equilibria.

Parameter $r$ measures growth rate of plants and $a$ measures average area of leaves consumed by a herbivore. If $r, a$ are relatively small, for instance, $a < 1$ and $r < 2$, then herbivores die out because of either not enough food for consumption or the herbivore consumption rate is not high enough. This is the essence of the following proposition.

**Proposition 3.1.** For $0 < r < 2, 0 < a < 1$, model (2.15)–(2.16) has no positive equilibrium (see Fig. 3.1(a)).
Nullclines

(a) No interior equilibrium: $r = 1.2, a = 0.8$

(b) One interior equilibrium: $r = 2.4, a = 1.2$

(c) Two interior equilibria: $r = 2.6, a = 0.98$

Figure 3.1: Interior equilibria

Proof. : We note that if $0 < a < 1, 0 < r < 2$ and $y \geq 0$, then

$$F(y) = f_2(y) - f_1(y) = \frac{y}{e^{ay} - 1} + \frac{ay}{r} - 1 = \frac{N(y)}{e^{ay} - 1},$$

where

$$N(y) = y + \frac{ay}{r} (e^{ay} - 1) - (e^{ay} - 1).$$

Since $0 < a < 1$, we see that $N(0) = 0, N'(0) = 1 - a > 0$. Since $0 < r < 2$, we see that $N''(y) = a^2 e^{ay} (ay/r + 2/r - 1) > 0$. Hence, $F(y) > 0, y \in R^+$. This shows that model (2.15) - (2.16) has no positive equilibrium points.
If herbivores consume the plant at a faster rate, e.g., \( a > 1 \), which amounts to saying that herbivores eat enough food during their growth season, then the following proposition suggests that herbivores may persist.

**Proposition 3.2.** For \( a > 1 \), model (2.15) — (2.16) has an unique positive equilibrium (see Figure 3.1(b)).

**Proof.** For \( a > 1 \), we see that \( f_2(0) < f_1(0) \). Moreover, \( f_2'(y) \in (-1/2, 0) \), \( f_3''(y) \geq 0 \), \( f_1'(y) = -a/r \) and \( f_2(r/a) > f_1(r/a) = 0 \).

By the Jury test (p57 in Edelstein-Keshet 2005), we see that the interior equilibrium is stable if

\[
2 > 1 + \det(J) = 1 + ax^*(1 - rx^*)e^{ay^*} > |\text{tr}(J)| = |1 + (a - r)x^*|. \quad (2.23)
\]

The biological implication of inequality (2.23) is simple: if it holds, then the plant herbivore interaction exhibit simple stable steady state dynamics. However, it is not clear what biologically mechanisms ensure that the inequalities in (2.23) holds, since the dynamical outcomes are very sensitive to the two parameters \( r \) and \( a \) (see Figure 3.2).

3.1. **Codimension one: Neimark-Sacker bifurcation.** The condition for a Neimark-Sacker bifurcation is that \( \lambda \bar{\lambda} = 1 \) and \( \lambda \) is not a real number. This translates into the three equations

\[
\begin{align*}
  r(1 - x) - ay &= 0 \quad (2.24) \\
  x(e^{ay} - 1) &= y \quad (2.25) \\
  a(1 - rx)(x + y) &= 1 \quad (2.26)
\end{align*}
\]

and the inequality

\[
|1 + (a - r)x| < 2. \quad (2.27)
\]
Equations 2.24 - 2.26 cannot be solved in closed form but it is easy to solve them numerically for $x$ and $y$ values in the first quadrant. It is easy to check that the Trace condition (2.23) is always satisfied for those values of $x$ and $y$. The curve drawn with small circles in Figure 3.2 that forms the boundary between region 6 and 7 depicts the numerical solutions for these equations and hence represents the codimension one parameter set for the Neimark-Sacker bifurcation.

Neimark-Sacker bifurcations generate dynamically invariant circles. As a result, we may find isolated periodic orbits as well as trajectories that cover the invariant circle densely. Figure 3.3 shows a period 9 orbit while Figure 3.4 illustrates a dense orbit resembling an invariant circle.

There exists no bifurcation with codimension higher than 1 in the interior of parameter space $(r, a)$ except the point $(2, 1)$. The most degenerated case occurs at the boundary equilibrium $(1, 0)$ which simultaneously undergoes a pitchfork and a period doubling bifurcation.
Plant-Herbivore model

Periodical solution with period 9
a=2.1, r=2.7

Figure 3.3: Periodic solution with period 9 for \( r = 2.7, a = 2.1 \)

at \((r,a) = (2,1)\).

3.2. Bifurcation diagram in the \((r,a)\)-parameter space. The codimension-one bifurcations discussed in Section 3.1 allow us to determine regions in parameter space \( r \) and \( a \) for which the dynamics of the system are topologically equivalent (Detailed proof also can be found in the Appendix Section 3 and Section 4). Figure 3.2 shows the relevant \((r,a)\) space.

Recall that the dynamics on the invariant manifold \( y = 0 \) is a unimodal map (the Ricker model) yielding a period doubling cascade to chaos as the parameter \( r \) is increased. In Figure 3.2, the parameter region for which the equilibrium in the Ricker model is stable \((r < 2)\) is to the left of shaded region. The parameter region exhibiting stable periodic orbits in the Ricker model defined by \( 2 \leq r < r_c \) is indicated by a a strong shaded region. For \( r > r_c \), the Ricker model generates progressively more complex dynamics including chaotic behavior (light shading). In addition, Figure 3.2 shows the following codimension-one curves.

(i) The transcritical bifurcation at \( a = 1 \) is shown as a dashed-dotted line.

(ii) The saddle node bifurcation emanating from the pitchfork bifurcation at \( a = 1, r = 2 \)
Figure 3.4: Dense orbit in phase space for $r = 2.45, a = 1.5$

is drawn dashed. Only the part that leads to a saddle node bifurcation in the first quadrant is shown.

(iii) The Neimark Sacker bifurcation generated numerically is shown as circles.

(iv) The black line connects simulations shown as small rectangles representing values of $r$ and $a$ when a strange attractor collapses. The line approximately indicates the collapse of a strange attractor through a crisis.

These bifurcation curves divide the parameters space $(r, a)$ into seven regions labeled one to seven in Figure 3.2.

Our simulation results suggest the following.

1). The boundary equilibrium $(1, 0)$ is a globally stable attractor for $0 < r < 2, 0 < a < 1$. In this parameter region, herbivores can not coexist with plants. The biological interpretation for this is that both values of $r, a$ are relatively small which implies that either the plant can not produce enough food for the herbivores because of the small
growth rate \( r \), or the herbivores' feeding rate \( a \) is too small to provide enough food for its persistence.

2). The system has no interior equilibrium and the Ricker dynamics is globally attracting to either periodic orbits or to chaotic orbits on the \( x \)-axis. While the value of \( r \) producing such dynamics is larger than the values producing the simple global dynamics described in 1), it can not compensate the small value of \( a \), leading to the demise of the herbivores.

3). Further increasing the plant growth rate enables the system to gain two interior equilibria. The one with the larger \( y \)-value is stable. The boundary equilibrium is still stable with respect to perturbations into the \( y \)-direction. In this case, the value of \( r \) is large enough to compensate for the low herbivore feeding rate.

4). The stable interior equilibrium loses stability through a Neimark Sacker bifurcation. We numerically find stable periodic orbits (isolated and dense) for some moderate values of \( r \) and \( a \), and strange attractors for larger values of \( r \) and \( a \).

5). The transition between region 4 and the region 5 is the numerically generated curve where the strange attractor collapses in a crisis bifurcation. Inside region 5, there is no attractor in the interior of the phase space. All interior points are attracted to \( x \)-axis which exhibits mostly chaotic dynamics.

6). The system has only one interior equilibrium which is unstable. There is an invariant loop around the unstable interior equilibrium. As the values of \( r \) and \( a \) increase, that invariant loop becomes unstable and forms a strange attractor. The transition between the region 6 and the region 7 is again through a Neimark-Sacker bifurcation.
7). The system has a stable interior equilibrium which appears to be the global attractor. Herbivores can consume enough food to coexist with plant. The transition between the regions 5, 6, 7 and the regions 1, 2, 3, 4 is a transcritical bifurcation.

4. Bistability and chaos

In the following two subsections we focus on the frequently observed dynamics: bistability and chaos.

4.1. Bistability. Theorem 4.1 below implies that when model (2.15) - (2.16) has an attractor in the interior of the phase space, and \( a < 1 \), it produces bistability between the attractor in the interior and the attractor on the \( x \)-axis. This is true for regions 3 and 4 where we have stable interior attractors (equilibria, periodic orbits and strange attractors) and stable attractors in the \( x \)-boundary Ricker dynamics (periodic orbits and strange attractors).

The eigenvalue governing the local transverse stability of an otherwise attracting periodic orbit of model (2.15) - (2.16) on the invariant manifold \( y = 0 \) is given by \( \Pi_{n=1}^{n=N} a x_n e^{r(1-x_n)} \) where the set \( \{x_n\} \) denotes all iterations of a periodic orbit and \( N \) denotes its period. If this eigenvalue is less than \( 1 \), then we say that the periodic orbit on the invariant manifold is transversally stable.

**Theorem 4.1.** If \( a < 1 \), then all periodic orbits on the invariant manifold \( y = 0 \) are transversally stable.

*Proof.* Since \( x_n e^{r(1-x_n)} = x_{n+1} \), we see that the transverse eigenvalue for a periodic orbit of period \( N \) is \( \Pi_{n=1}^{n=N} a x_n \). At the equilibrium \( x = 1 \) the eigenvalue becomes \( a \) and hence the equilibrium is attractive in the \( y \)-direction for \( a \leq 1 \). It is known that for the Ricker map, the time average of cycles is identical to the positive fixed point (Ryusuke, 2006).
Figure 4.5: Bistability in region 3

application of the inequality between arithmetic and geometric means yields

\[ (\prod_{n=1}^{N} ax_n)^{\frac{1}{N}} \cdot \frac{1}{N} \sum_{n=1}^{N} ax_n = a, \]

implying that if \( a < 1 \), then all the period orbits on the invariant manifold \( y = 0 \) are transversally stable.

Numerically we find that, for \( a < 1 \) any set that is an attractor on the invariant manifold is transversally stable and hence a local attractor.
Figure 4.6: Bistability in regions 6 and 7

Figure 4.5 a) – d) shows an example of bistability between a period two orbit on the x-axis and a stable interior equilibrium. The Table 1 illustrates the different cases of bistable phenomena in regions 6 and 7 with $a = 1.5$ and $r$ varying from $r < 2$ up to $r = 3.6$. Figure 4.6 shows the associated phase space dynamics.

4.2. Strange attractor and its collapse. Simulations in regions 4 and 6 show strange attractors. The small rectangles in Figure 3.2 are the result of a manual search for the stability boundary of the interior strange attractor. These points represent the values of
interior attractor vs. boundary attractor | Value of $r$ | Value of $a$
--- | --- | ---
Case 1. an invariant loop versus period two | 2.6265 | 1.5
Case 2. an invariant loop versus period four | 2.65 | 1.5
Case 3. period 21 versus chaotic on $x$-axis | 2.81 | 1.5
Case 4. period 6 versus chaotic on $x$-axis | 2.98 | 1.5

*Table 1: Bistability table*

$a$ and $r$ where the strange attractor collapses. The black curve connects these points. If the values of $r$ or $a$ are in region 5 in Figure 3.2, the strange attractor disappears and the population of $y_n$ goes to zero.

Figure 4.7 (a) – (c) gives an indication of how the strange attractor collapses. For $a = 0.95, r = 3.8$ we have bistability between two strange attractors, an interior one and a boundary one, i.e. the $\Omega$-limit sets of some solutions with initial conditions in the interior are on the $x$-axis. The shaded set of Figure 4.7 (a) is the interior strange attractor while the streaks of iteration points outside lie on the stable manifold of the strange attractor on the $x$-axis. It is highly likely that in the empty space between these two sets of trajectories there is a periodic orbit of saddle type with high period. As the interior strange attractor becomes larger (see Figure 4.7 (b)), it will collide with that unstable periodic orbit, leading to a “leakage” of the strange attractor towards the $x$-axis in Figure 4.7 (c).

5. Discussion

This chapter considers a general plant-herbivore model, partly motivated by the dynamics of a gypsy moth infestation through biomass transfer from plants to the gypsy moth. Our discrete 2 D model is controlled by the two parameters $r$, the nutrient uptake rate of the plant, and $a$ the amount of leaves eaten by the herbivore. Mathematical analysis and simulations of this model provides us with biological insights that may be used to devise control strategies
to regulate the population of the herbivore. Our results suggest the following two strategies.

(i) **Exploiting bistability.** In region 3, 4, 6 and 7 of Figure 3.2, the system shows bistability between attractors with nonzero population sizes for the herbivore corresponding to coexistence between plant and herbivore, and attractors on the x-axis corresponding to the extinction of the herbivores. Hence, if the population of the herbivores initially is small, it may eventually die out. This suggests control procedures to reduce the herbivore population by actions such as spraying of pesticides. Bistable dynamics is often generated in models through an explicit introduction of a threshold level below which the herbivore will die out regardless of the plant population levels. The bistability dynamics in our model (2.15) – (2.16) resulted from the intricate and plausible interaction of the plant and herbivore species. Namely, complex dynamics in a plant-herbivore model can lead to a multiple attractor case.

(ii) **Exploiting the crisis of the strange attractor.** For all values of $a$, as the parameter $r$ becomes large enough, the interior dynamics becomes unstable and all trajectories starting in the interior eventually approach the x axis, corresponding again to the extinction of the herbivore population. As $r$ represents the growth rate of the plant species an increase could correspond to a natural occurrence of highly favorable growing conditions but also could be supported by fertilizing the plants. This seems to agree with the observation that herbivores such as gypsy moths produce outbreaks often in the year following some draught period and when plants suffer a period of sustained slow growth. Indeed, draught is regarded as the main culprit the severe gypsy moth outbreak in Maryland in summer 2007, US (USDA, 2007).
(a) The interior strange attractor and the stable manifold of the boundary attractor $a = 0.95, r = 3.8$

(b) The interior strange attractor and the stable manifold of the boundary attractor $a = 0.95, r = 3.8$

(c) The interior strange attractor collapses to the boundary attractor $a = 0.95, r = 3.84$

*Figure 4.7: How interior attractor collapses as $r$ increases*
CHAPTER 3 - Monotone functional responses

In this chapter, we investigate two general plant-herbivore models: The 1st model involves a single plant species that has an increasing population dynamics with a decreasing growth function, while the 2nd model has a Holling-Type III function as its plant's population dynamics. One key feature of these two models is that the boundary dynamics generate a unique interior equilibrium. The interior equilibrium goes through the Neimak-Sacker bifurcation, which generates limit cycles and periodic orbits. Our study shows that the environmental fluctuations is an important factor to promote the burst population of herbivore for the 1st model. However, the 2nd model does not have such property, instead, it has heteroclinic bifurcation, which is caused by the fact that it has more than 2 boundary equilibria. We also notice that these two models with herbivore attacks plant before or after plant taking up nutrient from soil have similar dynamics. In addition, we compare the dynamics of our models to plant-herbivore models with unimodal (or multimodal) functions as plant's dynamics.

1. Introduction

Interactions between plants and herbivores have been studied by ecologists for many decades. One focus of research is the effects of herbivores on plant dynamics (Crawley, 1983, 1989). In contrast, there is strong ecological evidence indicating that the population dynamics of plants has an important effect on the plant-herbivore interactions. In this chapter, we investigate how plants with different population dynamics contribute to the interactions. Models for plant growth vary strongly (Crawley, 1990): Table 1 lists eight discrete-time models of plant population growth. The first seven models are introduced in the paper by Law and Watkinson (1987) without inter-specific competition. All models are
seasonal models of the form \( P_{t+1} = P_t f(P_t) \), where \( P_t \) is the density of a plant in season \( t \) and \( f(\cdot) \) the per capita growth rate. In the absence of intra-specific competition the latter is given by \( f(0) \), i.e. \( 1 + q \) in models 1-3 and \( w \) in models 4-8. The equilibrium density of the plant is given by \( K \). The parameter \( c \) is the space per plant at which interference with neighbors becomes appreciable (Watkinson, 1980). The interpretation of the power parameters, \( b \), depends on the model. Generally, these models fall into two classes, depending on whether \( P f(P) \) is a monotone function of \( P \) or not. Models 1-3 are unimodal, i.e., they have a single hump. They lead to complicated dynamics including period doubling, period windows and chaos (Guckenheimer, 1979). Models 4-8 are monotone, leading to much simpler dynamics. Model 8 has a growth function of Holling-Type III (Real, 1977).

<table>
<thead>
<tr>
<th>Model</th>
<th>( f(P) )</th>
<th>Number of par.</th>
<th>( f(0) )</th>
<th>equilibrium</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( 1 + q - \frac{qP}{K} )</td>
<td>2</td>
<td>( 1 + q )</td>
<td>( K )</td>
</tr>
<tr>
<td>2</td>
<td>( e^{\ln(1+q)[1-\frac{K}{P}]} )</td>
<td>2</td>
<td>( 1 + q )</td>
<td>( K )</td>
</tr>
<tr>
<td>3</td>
<td>( e^{\ln(1+q)[1-\ln(1+P)]} )</td>
<td>2</td>
<td>( 1 + q )</td>
<td>( K )</td>
</tr>
<tr>
<td>4</td>
<td>( \frac{w}{1+cP} )</td>
<td>2</td>
<td>( w )</td>
<td>( \frac{w-1}{c} )</td>
</tr>
<tr>
<td>5</td>
<td>( \frac{w}{1+P^b} )</td>
<td>2</td>
<td>( w )</td>
<td>( (w - 1)^{\frac{1}{b}} )</td>
</tr>
<tr>
<td>6</td>
<td>( \frac{w}{1+P^c} )</td>
<td>2</td>
<td>( w )</td>
<td>( w^{\frac{1}{c}} - 1 )</td>
</tr>
<tr>
<td>7</td>
<td>( \frac{w}{1+cP^b} )</td>
<td>3</td>
<td>( w )</td>
<td>( \frac{w^{b-1}}{c} )</td>
</tr>
<tr>
<td>8</td>
<td>( \frac{w}{1+cP^b} )</td>
<td>2</td>
<td>0</td>
<td>positive roots of ( w_{x}^{b-1} = 1 + P_{b}^{b} )</td>
</tr>
</tbody>
</table>

Table 2: Growth models of plant population density

Notice that Model #2 is the well known Ricker model (Ricker, 1954) which is unimodal and usually written as

\[
P_{t+1} = P_te^{r(1-\frac{P_t}{K})}
\]  (3.1)

while Model #4 is the Beverton-Holt model (Beverton & Holt, 1957) usually written as

\[
P_{t+1} = \frac{KP_t}{e^{-r}K + P_t(1-e^{-r})}
\]  (3.2)
The dynamics of the Ricker model (3.1) has been well studied. It shows period-doubling, chaos and period windows. Ricker dynamics in a plant-herbivore model has been studied in (Kang, Armbruster, & Kuang, 2008) and (Abbott & Dwyer, 2007) showing many forms of complex dynamics.

In this chapter, we investigate the impact of general monotone plant growth models on the dynamics of the plant-herbivore interaction. The chapter is organized as follows. In Section 2 we define two classes of monotone dynamics of single plant species. In Section 3 we formulate general plant-herbivore models for the plant dynamics introduced in Section 2. In Section 4 we analyze the dynamic behavior of these two general models. In Section 5 we illustrate the results for a Beverton-Holt model and a Holling-Type III model. Our study shows that noise is an important factor for outbreak of herbivore. Finally, we compare monotone plant growth models to unimodal and multimodal plant growth models regarding their influence of the plant herbivore dynamics.

2. Monotone growth dynamics for a single plant species

Consider

\[ P_{t+1} = P_t f(r, P_t) = F(r, P_t), \quad t \geq 0. \]  

(3.3)

where \( P_t \) is the density of biomass in plant at generation \( t \) and \( f(r, P_t) \) is the per capita growth rate of the biomass density. Without intra-specific competition, we have \( f(r, 0) = r \), i.e. \( r \) is the maximal per capita growth rate of the plant. This simple formulation (3.3) can give rise to a great diversity of dynamical behavior, depending on the expression used for the growth function \( f(r, \cdot) \) and the values given to the parameters of that function. Several different functions have been considered. See (Cohen, 1995) for a partial list of models with
per capita growth rates that decline with increasing population density:

\[
\frac{\partial f(r, P_t)}{\partial P_t} \leq 0, \quad P_t \geq 0. \quad (3.4)
\]

In biological terms, this means that the per capita growth rate \( f(r, P_t) \) decreases due to negative density dependent mechanism such as intra-specific competition between individuals within a population. The well known prototypes of the model (3.3) under this biological assumption are the Beverton-Holt and Ricker models. We focus on the Beverton-Holt prototype, i.e., the dynamics of the plant is monotonically increasing,

\[
\frac{\partial F(r, P_t)}{\partial P_t} \geq 0, \quad P_t \geq 0. \quad (3.5)
\]

We can characterize the growth models of a single plant with two assumptions \( \textbf{H1} \) and \( \textbf{H2} \):

\[\textbf{H1}: \quad F(r, 0) = 0, \quad F(r, P_t)|_{P_t > 0} > 0, \quad \frac{\partial F(r, P_t)}{\partial P_t} > 0, \quad \text{and} \lim_{P_t \to +\infty} F(r, P_t) = C > 0.\]

\[\textbf{H2}: \quad f(r, P_t)|_{P_t \geq 0} \geq 0, \quad \frac{\partial f(r, P_t)}{\partial P_t} < 0, \quad \text{and} \lim_{P_t \to +\infty} f(r, P_t) = 0.\]

In the biological sense, \( \textbf{H1} \) implies that the population density of a plant is an increasing function of its density and its per capita growth function may be increasing or decreasing or both. \( \textbf{H2} \) implies that the per capita growth function of the plant is a decreasing function due to intra-specific competition and the population density of a plant can be an increasing or decreasing function or both with respect to its density. In this chapter, we study the population dynamics associated with plants that satisfy either \( \textbf{H1} \) or both \( \textbf{H1} \) and \( \textbf{H2} \).

**Proposition 2.1.** Let \( F(r, P) \) satisfy \( \textbf{H1} \) and assume there are \( n + 1 \) consecutive, distinct and non-degenerate solutions \( P_i, i = 0, 1, \ldots, n \) of \( P = F(r, P) \) with \( \bar{P}_0 = 0 \). If \( \bar{P}_0 \) is stable
(unstable) then the even $P_i$ are stable (unstable) while the odd $P_i$ are unstable (stable). In particular, $P_n$ is always stable.

**Proof.** Possible configurations of the staircase diagrams of Figure 2.8 shows the alternating stable and unstable equilibria. Since $\lim_{P \to +\infty} F(r, P_t) = C > 0$, $\frac{\partial F(r, P_t)}{\partial P_t}|_{P_n}$ has to be positive and less than one.

![Figure 2.8: Possible configurations of the staircase diagrams](image)

**Proposition 2.2.** Let $F(r, P)$ satisfy H1 and assume there are $n + 1$ consecutive, distinct and non-degenerate solutions $P_i, i = 0, 1, \ldots, n$ of $P = F(r, P)$ with $P_0 = 0$. Define the map $P_{t+1} = F(r, P_t)$, then for any $\epsilon > 0$, there exists $N$ large enough, such that for all $t > N$, we have $P_{t+1} = F(r, P_t) \leq P_n + \epsilon$.

**Proof.** Assume $P_i$ is a stable equilibrium for the map $P_{t+1} = F(r, P_t)$. If an initial condition $P_0$ satisfies $P_0 \leq P_n$ then H1 implies $P_1 = F(r, P_0) \leq F(r, P_n) = P_n$ and by induction, $P_i \leq P_n$ for all $i$. In the case that the initial condition is larger than $P_n$, i.e., $P_0 > P_n$, then the sequence $\{P_i\}$ is decreasing and converges to $P_n$ as $t \to \infty$, i.e., for any $\epsilon > 0$, there
exists \( N \) large enough, such that for all \( t > N \), we have \( P_{t+1} = F(r, P_t) \leq \bar{P}_n + \epsilon \). In other cases, we have \( P_{t+1} = F(r, P_t) < \bar{P}_n \) for all \( t > 0 \). Therefore, the statement holds.

**Proposition 2.3.** Let \( f(r, \cdot) \) satisfy the assumptions of \( H2 \), then \( P = Pf(r, P) \) has at most two roots, i.e., \( P = 0 \) and \( 1 = f(r, P) \).

**Proof.** Since \( f(r, P) \) is a differentiable and strictly decreasing function of \( P \), \( 1 = f(r, P) \) has at most one solution.

3. **Plant-herbivore models**

Insect and plant survival rates often appear to be non-linear functions of plant and insect density, respectively (Harper, 1977; Crawley, 1983). In our discrete-time models, we therefore assume that herbivore population growth is a non-linear function of herbivore and plant density, and that plant population growth decreases gradually with increasing herbivore. Similarly, we assume that the density of herbivore population depends on plant density rather than herbivore density (Crawley, 1983). A final key feature of many plant-herbivore interactions is that, in the absence of the herbivore, we have a monotone growth dynamics as discussed in the previous section.

Let \( P_t \) represent the density of edible plant biomass in generation \( t \) and \( H_t \) represent the population density of the herbivore. The effect of the herbivore on the plant population growth rate is described by the function \( g(a, H_t) \) with \( g(a, 0) = 1 \). Here the parameter \( a \) measures the damage caused by herbivore, e.g., feeding rate. We assume that herbivore population density is proportional to a function of plant density \( h(P_t) \) and a non-linear function of herbivore density \( l(H_t) \). Therefore, the structure of our models is:
Many consumer-resource models assume a non-linear relationship between resource population size and attack rate (Beddington, 1975; Tang & Chen, 2002). For plants and insect herbivores, we similarly expect a non-linear functional relationship, due to herbivore foraging time and satiation. The relationship is expressed in terms of plant biomass units rather than population size, because herbivores are unlikely to kill entire plants (Harper, 1977; Crawley, 1983).

Our model has the following features: Without the herbivore, we assume a monotone growth rate, i.e. assumption H1. The growth $F(r, P_t)$ determines the amount of new leaves available for consumption for the herbivore. We assume that the herbivores search for plants randomly. The area consumed is measured by the parameter $a$, i.e., $a$ is a constant that correlates to the total amount of the biomass that an herbivore consumes. The herbivore has a one year life cycle, the larger $a$, the faster the feeding rate. After attacks by herbivores, the biomass in the plant population is reduced to a fraction $e^{-aH_t}$ of that present in the absence of herbivores, i.e.,

$$g(a, H_t) = e^{-aH_t}$$

(3.8)

Hence,

$$P_{t+1} = P_t f(r, P_t) e^{-aH_t}.$$  

(3.9)

The term $h(P_t)$ describes how the biomass in the plants is converted to the biomass of the herbivore. It differs depending on the relative timing of herbivore feeding and growth. If
the herbivore attacks the plant before the plant grows, then we have \( h(P_t) = P_t \), otherwise, \( h(P_t) = P_t f(r, P_t) \). Since the biomass of herbivore comes from whatever they eat, \( h(P_t) \) is the available biomass of a plant that can be converted into the herbivore’s biomass. The term \( l(H_t) \) describes the fraction of \( h(P_t) \) that can be used by the herbivore, i.e., \( l(H_t) = 1 - e^{-aH_t} \).

Therefore, the evolution of the plant-herbivore system is either described by **Model I** :

\[
\begin{align*}
  P_{t+1} &= F(r, P_t) e^{-aH_t} \\
  H_{t+1} &= P_t \left[ 1 - e^{-aH_t} \right]
\end{align*}
\]  

(3.10) (3.11)

describing the dynamics of a system where the plant is attacked before it has a chance to grow while **Model II** :

\[
\begin{align*}
  P_{t+1} &= F(r, P_t) e^{-aH_t} \\
  H_{t+1} &= F(r, P_t) \left[ 1 - e^{-aH_t} \right]
\end{align*}
\]  

(3.12) (3.13)

describes the dynamics when the plant grows first before being attacked.

4. **Mathematical analysis**

Both Model I and II are positively invariant.

**Proposition 4.1.** If **H1** holds, then \( \limsup_{t \to \infty} P_t \leq \tilde{P}_n \) and \( \limsup_{t \to \infty} H_t \leq \tilde{P}_n \) for both Model I and II.

**Proof.** : For Model I,

\[
H_{t+1} = P_t \left[ 1 - e^{-aH_t} \right] \leq P_t
\]

For Model II,

\[
H_{t+1} = P_t f(r, P_t) \left[ 1 - e^{-aH_t} \right] \leq F(r, P_t)
\]
Since $F(r, P_t) \in H1$, then from Proposition (2.2), we can conclude that for any $\epsilon > 0$, there exists $N$ large enough, such that for all $t > N$, the following holds

$$P_{t+1} = F(r, P_t)e^{-aH_t} \leq F(r, P_t) \leq \bar{P}_n + \epsilon.$$ 

Therefore, we have $\limsup_{t \to \infty} P_t \leq \bar{P}_n$ and $\limsup_{t \to \infty} H_t \leq \bar{P}_n$ for both Model I and II. 

4.1. **Equilibria and their stability.** If, in the absence of the herbivore there exist $n + 1$ equilibria of the plant dynamics, then both Model I and II have $n + 1$ boundary equilibria of the form

$$E_{00} = (0, 0) \text{ and } E_{i0} = (\bar{P}_i, 0), i = 1, 2, .., n.$$ 

Their local stability can be determined by the eigenvalues of their Jacobian matrices.

(i) Model I:

$$J_1 = \begin{bmatrix}
\frac{\partial F}{\partial r} e^{-aH} & -aP \\
1 - e^{-aH} & aP
\end{bmatrix} \quad (3.14)$$

(ii) Model II:

$$J_2 = \begin{bmatrix}
\frac{\partial F}{\partial r} e^{-aH} & -aP \\
\frac{\partial F}{\partial P} [1 - e^{-aH}] & aP
\end{bmatrix} \quad (3.15)$$

It is easy to check that at the boundary equilibria the two Jacobian matrices are identical with eigenvalues $\frac{\partial F}{\partial r}(r, 0)$ and 0 at $(0,0)$ and $\frac{\partial F}{\partial r}(r, \bar{P}_i)$ and $a\bar{P}_i$ at $(\bar{P}_i, 0)$.

The following theorems summarize the global dynamics:
Theorem 4.1. If \( \frac{\partial F}{\partial P}(r,0) < 1 \) and there is no other boundary equilibrium \((\bar{P}_0,0)\), then Model I and II are globally stable at \((\bar{P}_0,0) = (0,0)\). More generally, if \( a\bar{P}_n < 1 \), then
\[
\lim_{t \to \infty} H_t = 0.
\]

Proof. :

From Proposition (4.1), we know that for any \( \epsilon > 0 \), there exists \( N \) large enough, such that for all \( t > N \), we have
\[
P_{t+1} = F(r, P_t)e^{-aH_t} \leq F(r, P_t) \leq \bar{P}_n + \epsilon
\] (3.16)

Since \( a\bar{P}_n < 1 \), then for \( \epsilon \) small enough, we have \( aP_t \leq a(\bar{P}_n + \epsilon) < 1 \) and \( aF(r, P_t) \leq a(\bar{P}_n + \epsilon) < 1 \). Therefore, for Model I,
\[
H_{t+1} = P_t \left[1 - e^{-aH_t}\right] = H_t P_t \frac{1 - e^{-aH_t}}{H_t} \leq aH_t P_t \leq a(\bar{P}_n + \epsilon)H_t
\] (3.17)

and for Model II,
\[
H_{t+1} = F(r, P_t)H_t \frac{1 - e^{-aH_t}}{H_t} \leq aH_t F(r, P_t) \leq aH_t P_t \leq a(\bar{P}_n + \epsilon)H_t
\] (3.18)

Therefore, \( H_t \leq [a(\bar{P}_n + \epsilon)]^{t-N} H_N \), for all \( t > N \) and \( \lim_{t \to \infty} H_t = 0 \) in both Model I and II. This implies that both Model I and II are globally attracted to the boundary dynamics. ■

Remark: In the case \( n = 1 \), then from Proposition (2.1), we have the following:

(i) If \( \frac{\partial F}{\partial P}(r,0) < 1 \), then \( \bar{P}_1 \) is a source;

(ii) If \( \frac{\partial F}{\partial P}(r,0) > 1 \), then \( \bar{P}_1 \) is a sink.

Hence, if \( \frac{\partial F}{\partial P}(r,0) > 1 \) and \( n = 1 \), then \((\bar{P}_1,0)\) attracts all nontrivial solutions.
4.2. *Unique interior equilibrium.* Interior equilibria are determined by the intersections of the nullclines. Notice that if \( H1 \) holds, then \( y = F(r, P) \) is a differentiable and monotone function of \( P \) and mapping \( R^+ \) to \([0, C)\). Its inverse exists and can be written as \( P = F^{-1}(r, y) \) which is mapping \([0, C)\) to \( R^+ \). Similarly, if \( H2 \) holds, then \( y = f(r, P) \) is a differentiable and monotone function of \( P \) and mapping \( R^+ \) to \([0, M)\). Its inverse exists and can be written as \( P = f^{-1}(r, y) \) which is mapping \([0, M)\) to \( R^+ \). Here \( C = F(r, \infty) \) and \( M = f(r, \infty) \) are some positive constants. If \((\bar{P}, \bar{H})\) is an interior equilibrium, then it is the solution of the two equations

(i) For Model I:

\[
P = f^{-1}(r, e^{aH})
\]

\( H_1 - e^{-aH} \) \hspace{1cm} (3.19)

(ii) For Model II:

\[
P = \frac{H}{e^{aH} - 1}
\]

\( P = F^{-1}(r, \frac{H}{1 - e^{-aH}}) \) \hspace{1cm} (3.22)

If \( F(r, P) \) is monotonically increasing, then \( F^{-1}(r, \frac{H}{1 - e^{-aH}}) \) is an increasing function of \( H \). Similarly, since if \( f(r, P) \) is monotonically decreasing, then \( f^{-1}(r, e^{aH}) \) is a decreasing function of \( H \).

**Proposition 4.2.** a) If \( F(r, P) \) satisfies the assumptions in \( H1 \) and \( f(r, P) \) the assumptions of \( H2 \), then Model I has at most one interior equilibrium. The interior equilibrium emerges generically through a transcritical bifurcation from the largest boundary equilibrium \( P_n \) when \( P_n = \frac{1}{a} \), where \( n \geq 1 \).
b) If $F(r, P) \in H1$, then Model II has at most one interior equilibrium. The interior equilibrium emerges generically through a transcritical bifurcation from the largest boundary equilibrium $\bar{P}_n$ when $\bar{P}_n = \frac{1}{a}$, where $n \geq 1$.

**Proof.** The proofs for a) and b) are similar. We show case b): The interior equilibria of Model II are determined by the intersections of the nullclines (3.21) and (3.22). Since (3.21) is a decreasing function and (3.22) is an increasing function, they have only one interior intersection if $F^{-1}(r, \frac{1}{a}) < \frac{1}{a}$. $F^{-1}(r, P) = P$ has the same equilibrium solutions as $P = F(r, P)$. Recall that the Jacobian matrix of Model II is

$$
J_2 = \begin{bmatrix}
\frac{\partial F}{\partial P} e^{-aH} & -aP \\
\frac{\partial F}{\partial P} [1 - e^{-aH}] & aP
\end{bmatrix}
$$

with eigenvalues

$$
\lambda_1 = \frac{aP + \frac{\partial F}{\partial P} e^{-aH} + \sqrt{(aP + \frac{\partial F}{\partial P} e^{-aH})^2 - 4aP \frac{\partial F}{\partial P}}}{2}
$$

and

$$
\lambda_2 = \frac{aP + \frac{\partial F}{\partial P} e^{-aH} - \sqrt{(aP + \frac{\partial F}{\partial P} e^{-aH})^2 - 4aP \frac{\partial F}{\partial P}}}{2}
$$

At the boundary equilibrium $(\bar{P}_n, 0)$, the eigenvalues satisfy

(i) $\lambda_1(\bar{P}_n, 0) = a\bar{P}_n$ and $\lambda_2(\bar{P}_n, 0) = \frac{\partial F}{\partial P}|_{P=\bar{P}_n} < 1$;

(ii) $\frac{\partial \lambda_1}{\partial a}(\bar{P}_n, 0) = \bar{P}_n$ and $\frac{\partial \lambda_2}{\partial a}(\bar{P}_n, 0) = 0$

In the case $\bar{P}_n = \frac{1}{a}$, we have $\lambda_2 < \lambda_1 = 1$ and $\frac{\partial \lambda_2}{\partial a}(\bar{P}_n, 0) = \bar{P}_n = \frac{1}{a} > 0$. The Jacobian matrix of Model II evaluated at $(\bar{P}_n, 0)$ is

$$
J_2|_{(\bar{P}_n, 0)} = \begin{bmatrix}
\frac{\partial F}{\partial P}|_{P=\bar{P}_n} & -a\bar{P}_n \\
0 & a\bar{P}_n
\end{bmatrix}
$$
The eigenvector associated with the eigenvalue $\lambda_1 = aP_n$ is

$$V|_{\lambda_1 = aP_n} = \begin{bmatrix} -\frac{aP_n - \frac{\partial F}{\partial P} |_{P = P_n}}{aP_n} x_2 \\ x_2 \end{bmatrix} \quad (3.23)$$

If $aP_n = 1$, then the two components of (3.23) have the opposite sign. This implies that by choosing $x_2 > 0$, the unstable manifold of $E_{n0}$ points toward the interior of $X_{11}$. Therefore, apply Theorem 13.5 in the book by Smoller (P173, Smoller, 1994), the unique interior equilibrium of Model II emerges generically through a transcritical bifurcation from the largest boundary equilibrium $P_n$ when $P_n = \frac{1}{a}$, where $n \geq 1$.

5. Application and simulations

5.1. The Beverton-Holt and Holling-Type III models. In this section, we focus on two typical models for the plant dynamics and apply our results:

(i)

$$P_{t+1} = F(r, P_t) = \frac{rP_t}{1 + P_t} \quad (3.24)$$

is the Beverton-Holt model where $F(r, P_t)$ satisfies the assumptions of $H1$ and $f(r, P_t)$ those of $H2$. The two equilibria are $P_0 = 0$ and $P_1 = r - 1$. From Proposition 2.1, we know that $P_0$ is a sink if $r < 1$; $P_0$ is a source if $r > 1$. In addition, $P_1$, if it exists, is always a sink.

(ii) A Holling type III model is given by

$$P_{t+1} = F(r, P_t) = \frac{rP_t^2}{1 + P_t^2} \quad (3.25)$$
where \( F(r, P_t) \) satisfies H1. The equilibria are \( P_0 = 0, P_1 = \frac{r - \sqrt{r^2 - 4}}{2} \) and \( P_2 = \frac{r + \sqrt{r^2 - 4}}{2} \).

If \( r < 2 \) then \( P_0 \) is the only equilibrium and it is globally stable. If \( r > 2 \); \( P_0 \) is a sink, \( P_1 \) is a source and \( P_2 \) is a sink.

The plant-herbivore models with (3.24) and (3.25) as plant dynamics become:

Model I:

(i)

\[
P_{t+1} = \frac{r P_t}{1 + P_t} e^{-a H_t} \quad (3.26)
\]

\[
H_{t+1} = P_t \left[1 - e^{-a H_t}\right] \quad (3.27)
\]

(ii)

\[
P_{t+1} = \frac{r P_t^2}{1 + P_t^2} e^{-a H_t} \quad (3.28)
\]

\[
H_{t+1} = P_t \left[1 - e^{-a H_t}\right] \quad (3.29)
\]

Model II:

(i)

\[
P_{t+1} = \frac{r P_t}{1 + P_t} e^{-a H_t} \quad (3.30)
\]

\[
H_{t+1} = \frac{r P_t}{1 + P_t} \left[1 - e^{-a H_t}\right] \quad (3.31)
\]

(ii)

\[
P_{t+1} = \frac{r P_t^2}{1 + P_t^2} e^{-a H_t} \quad (3.32)
\]

\[
H_{t+1} = \frac{r P_t^2}{1 + P_t^2} \left[1 - e^{-a H_t}\right] \quad (3.33)
\]
Applying the results of the previous section, we can summarize

**Corollary 5.1.** The three models (3.26)-(3.27), (3.30)-(3.31) and (3.32)-(3.33) have at most one interior equilibrium. The interior equilibria of Model I (3.26)-(3.27) and Model II (3.30)-(3.31) emerge through a transcritical bifurcations from the boundary equilibrium $(\tilde{P}_1, 0) = (r - 1, 0)$ when $a(r - 1) = 1$ and $r > 1$; The interior equilibrium of Model II (3.32)-(3.33) emerges through a transcritical bifurcations from the boundary equilibrium $(\tilde{P}_2, 0) = \left(\frac{r + \sqrt{r^2 - 4}}{2}, 0\right)$ when $a = \frac{r + \sqrt{r^2 - 4}}{2} = 1$ and $r > 2$.

5.2. **Periodic orbits and heteroclinic bifurcations.** The stability of the single interior equilibrium of models (3.26) to (3.33) depends on the values of the parameters $r$ and $a$. As the values of $r$ or $a$ increase, the interior equilibrium goes through a Neimark-Sacker bifurcation generating an invariant cycle.

Since Model I and Model II have similar dynamics, we only focus on Model II and discuss the Beverton-Holt model (3.24) and the Holling-Type III model (3.25), respectively. The main difference between the Beverton-Holt model and the Holling-Type III model is that the Holling-Type III model can show a heteroclinic bifurcation where a periodic orbit grows until it becomes a heteroclinic connection between boundary equilibria whereas the Beverton-Holt model does not show such a bifurcation. Figure 5.9 shows the heteroclinic bifurcation schematically: When $a = 0.71$ and $r = 2.5$, the system has a stable interior equilibrium (the dark dot that is in the middle of the figure, which is generated by the Matlab); When we increase $r$ to 3.5 and keep $a = 0.71$, the system has an invariant orbit (the grey orbit in the figure, which is generated by the Matlab); However, if we continue to increase the values of $a$ or $r$, the invariant orbit disappears and the system converges to the boundary equilibrium $(0, 0)$. This suggests that a heteroclinic bifurcation occurs (The dark line with arrows in the
figure, which is generated schematically).

Since the Beverton-Holt model only has the origin as a saddle and one other boundary equilibrium and since the stable manifold of the origin is the $H$-axis which is an invariant manifold, the periodic orbit in the interior cannot become heteroclinic. However, it can become very large and pass the origin arbitrarily close to the coordinate axes as shown in Figure 5.10. Figure 5.10 is the numerical simulations generated by the Matlab for 2000 generations when $a = 2$ and $r = 2.5, 2.7, 2.8, 3$. When $a = 2$ and $r = 2.5$, the system has a stable interior equilibrium as shown in the figure (small dark dot); when $r = 2, 7, 2.8, 3$, the system has an invariant orbit. Numerical simulations of this case hint at an interesting phenomenon: A standard numerical simulation shows the periodic orbit disappearing and
Figure 5.10: The periodic orbit for the Beverton-Holt model when $a = 2, r = 2.5, 2.7, 2.8, 3$ the trajectory approaching the nontrivial boundary equilibrium as time increases. However, that boundary equilibrium is a saddle and the trajectory should leave into the interior but it does not do so over any simulation time that we checked. The resolution of the puzzle comes from the considerations of the accuracy of the simulations: As the limit cycle gets closer to the origin the herbivore values become so small that they are approximated as zero. Hence the dynamics is reduced to the dynamics of the plant which has a stable equilibrium on the invariant manifold determined by $H = 0$ and hence the trajectory never leaves.

Figure 5.11(a) shows a “bifurcation diagram” for the Beverton-Holt model, which describes the Neimark-Sacker bifurcation curve (dashed line) and the “collapse curve” (solid line). The later represents an interpolation of numerical simulations with $a$ and $r$ values for which a standard matlab numerical precision simulation does not detect a population of the herbivore. Figure 5.11(b) is a bifurcation diagram for a Holling-Type III model showing interpolations of the Neimark-Sacker bifurcation curve (dashed line) and the heteroclinic
bifurcation (solid line), respectively.

Figure 5.11: Neimark-Sacker bifurcation and heteroclinic bifurcations

5.3. Noise-generated outbreaks. The extreme sensitivity of the periodic orbit in the Beverton-Holt model suggests that noise may play a much bigger role than previously discussed in the outbreaks of herbivore infestations. Once the periodic orbit disappears due to accuracy issues, we can make it re-appear by adding small amount of noise to the simulation:

(i) Noise: we use positive white noise to make sure the positivity of the system, i.e., we discard the negative white noise in the simulations;

(ii) Population of herbivores: for each generation, we add the noise to the herbivore, i.e.,

\[ H_{t+1} = \frac{rP_t e^{-aH_t}}{1 + P_t} + \omega R_n \]  

(3.34)

where \( R_n \) is a positive standard white noise and \( \omega \) is the amplitude of the noise. See Figure (5.12) for example, in this case, the amplitude of the positive standard white
noise is $\omega = 0.01$.

At that time the trajectories look like a randomly occurring bursting phenomenon that nevertheless has a well defined average periodicity (see Figure 5.12). Given by the exact nature of the model there will be a threshold at which the population of the herbivore cannot be detected in nature. We define the resident time as the time interval for which the population of the herbivore stays below some threshold, e.g., 0.01 and the resident time ratio as the ratio of the residence time to the period of the bursting. Table (5.3) shows the period as a function of the mean square amplitude of the noise level. Figure 5.13 shows the resident time ratio as a function of the noise amplitudes. The figure is generated by calculating the resident time ratio for each noise amplitude for 50 trajectory with 1000 generations. The Figure shows that over many orders of magnitude the residence ratio stays around 80% indicating that the herbivore is dormant for most of the time and only appears for about 20% of its periodic cycle. The Table indicates that by choosing a particular noise level, we can control the apparent periodicity of the bursts.
Figure 5.13: The resident time ratio as a function of the noise amplitude when $a = 3.95, r = 4.55$ with a threshold of 0.01.

<table>
<thead>
<tr>
<th>Amplitude of Noise $w$</th>
<th>0.01</th>
<th>0.001</th>
<th>0.0001</th>
<th>0.00001</th>
<th>0.000001</th>
<th>0.0000001</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period $t$</td>
<td>8</td>
<td>10</td>
<td>12</td>
<td>14</td>
<td>17</td>
<td>19</td>
</tr>
</tbody>
</table>

Table 3: Average period of the herbivore dynamics when $a = 3.95, r = 4.55$.

In particular time intervals of the herbivore outbreaks around 8 – 12 years can be generated which fits the ecological data for gypsy moth out-breaks (Liebhold, 1996). Also, for larger noise levels, the distribution of the periods is rather broad which also seems to be happening for real data (Kendall, 1999; Sergio, 2001).

5.4. **Uniformly persistence of the Beverton-Holt model.** The numerical simulations in the previous subsections suggest that the Beverton-Holt model is uniformly persistent. In this subsection, we apply the persistence theory to the Beverton-Holt model.
Define

\[ X = \{(P,H) : P \geq 0, H \geq 0\} \]

\[ X_{11} = \{(P,H) \in X, P > 0 \text{ or } H > 0\} \]

\[ \partial X_{11} = X \setminus X_{11} \]

**Lemma 5.1.** \( X_{11} \) and \( \partial X_{11} \) are positively invariant for (3.30)-(3.31).

**Proposition 5.1.** If \( a(r-1) > 1 \), then (3.30)-(3.31) is uniformly persistent with respect to \((X_{11}, \partial X_{11})\), i.e., there exists some \( \epsilon > 0 \) such that \( \liminf_{t \to \infty} P_t \geq \epsilon \) and \( \liminf_{t \to \infty} H_t \geq \epsilon \).

**Proof.** Since \( a(r-1) > 1 \), from Corollary (5.1), we have the unstable boundary equilibria \( E_{00} = (0,0) \) and \( E_{10} = (r-1,0) \), in addition, the interior equilibrium \( E_{11} \) emerges from \( E_{10} \) through a transcritical bifurcation. From the Jacobian matrix evaluated at \( E_{10} \),

\[ J|_{E_{10}} = \begin{bmatrix} \frac{1}{r} & -a(r-1) \\ 0 & a(r-1) \end{bmatrix} \] (3.35)

we can calculate the eigenvector associated with the eigenvalue \( a(r-1) \) is

\[ V|_{a(r-1)} = \begin{bmatrix} -\frac{a(r-1)-1}{a(r-1)} x_2 \\ x_2 \end{bmatrix} \] (3.36)

Since the two components of (3.36) has the opposite sign, this implies that the unstable manifold of \( E_{10} \) points toward the interior of \( X_{11} \).

From Lemma (5.1) and Proposition (4.1), we obtain that the system (3.30)-(3.31) is point dissipative. In order to show that \( X_{11} \) has a global attractor, we need to show that the map
\(G(P_t, H_t)\) is asymptotically smooth and eventually bounded on every bounded set (Theorem 2.48, p25, Smith&Thieme, 2005), where
\[
G(P_t, H_t) = \begin{bmatrix} F(r, P_t)e^{-aH_t} \\ F(r, P_t)[1 - e^{-aH_t}] \end{bmatrix}
\] (3.37)

Since \(F(r, P_t) = \frac{rP_t}{1 + P_t} < r\), then after the first generation, \(G(R^+, R^+) \subset ((0, r), (0, r))\). This implies that \(G\) is eventually bounded for every set in \(X_{11}\). Let \(A\) be any forward invariant bounded closed set of \(X_{11}\), then \(G(A) \subset ((0, r), (0, r))\). For any positive integer sequences \((t_j), t_j \to \infty\) as \(j \to \infty\) and \((P_j, H_j) \in A\), \((G(P_{t_j+j}, H_{t_j+j}))\) is bounded by \(((0, r), (0, r))\), hence it has a convergent subsequence. Therefore, \(X_{11}\) has a global attractor by Theorem 2.48 (Smith & Thieme, Fall 2005).

Let
\[
M_\partial = \{(P_0, H_0) : (P_t, H_t) \text{ satisfies (3.30) and (3.31) and } (P_t, H_t) \in \partial X_{11}, \forall n \geq 0\}
\]

It is easy to check that
\[
M_\partial = \partial X_{11}
\] (3.38)

Let \(S\) be the maximal invariant set of the system (3.30)-(3.31) in \(\partial X_{11}\), then \(S = \{E_{00}, E_{10}\}\) since \(E_{00} = (0, 0)\) and \(E_{10} = (P_1, 0)\) are the only equilibria in \(M_\partial\). Note that every orbit with \(P_0 = 0\) in \(M_\partial\) tends to \(E_{00}\) and every orbit with \(P_0 > 0\) in \(M_\partial\) tends to \(E_{10}\) as \(n \to \infty\). This shows that both \(E_{00}\) and \(E_{10}\) are isolated invariant sets in \(X\) and are acyclic in \(M_\partial\).

Let \(W^{s}(E_{00})\) and \(W^{s}(E_{10})\) be the stable set for \(E_{00}\) and \(E_{10}\) respectively. In order to apply Theorem 4.1 in (Hofbauer & So, 1989) to show that the system (3.30)-(3.31) is uniformly persistent, we should prove that \(W^{s}(S) \subset \partial X_{11}\), which is equivalent to show the following
\[
W^{s}(E_{00}) \cap X_{11} = \emptyset
\] (3.39)
\[ W^c(E_{10}) \cap X_{11} = \emptyset \]  
(3.40)

Suppose that (3.39) is not true. Then there exists a solution \( (P_t, H_t) \) of the system with \( P_0 > 0 \) such that

\[ (P_t, H_t) \rightarrow (0, 0) \text{ as } t \rightarrow \infty \]

Then, for any \( \epsilon > 0 \), there exists \( T > 0 \) such that \( H_t < \epsilon \) for any \( t > T \). Choose \( \epsilon > 0 \) such that \( r e^{-\alpha \epsilon} > 1 \) (this holds since \( a(r - 1) > 1 \)). This implies that

\[ P_{t+1} = \frac{r P_t e^{-aH_t}}{1 + P_t} \geq \frac{r e^{-\alpha \epsilon} P_t}{1 + P_t}, \text{ for all } t > T \]

Note that the sequence \( \{ \frac{r e^{-\alpha \epsilon} P_t}{1 + P_t} \} \) is monotonically increasing and the condition \( r e^{-\alpha \epsilon} > 1 \) makes sure that it converges to a positive point \( r e^{-\alpha \epsilon} - 1 \). This implies that

\[ \liminf_{t \rightarrow \infty} P_t \geq r e^{-\alpha \epsilon} - 1 > 0. \]

Hence, we have a contradiction.

Similarly, if (3.40) is not true. Then there exists a solution \( (P_t, H_t) \) of the system with \( H_0 > 0 \) such that

\[ (P_t, H_t) \rightarrow (\bar{P}_1, 0) \text{ as } t \rightarrow \infty \]

Then, for any \( \epsilon > 0 \), there exists \( T > 0 \) such that \( P_t < \bar{P}_1 - \epsilon = r - 1 - \epsilon \) for any \( t > T \).

Choose \( \epsilon > 0 \) such that \( a(r - 1 - \epsilon) > 1 \) (this holds since \( a(r - 1) > 1 \)). This implies that

\[ H_{t+1} = \frac{r P_t [1 - e^{-aH_t}]}{1 + P_t} \geq \frac{r [1 - e^{-aH_t}] (r - 1 - \epsilon)}{1 + (r - 1 - \epsilon)}, \text{ for all } t > T \]

The condition \( a(r - 1 - \epsilon) > 1 \) makes sure that the sequence \( \{ \frac{r [1 - e^{-aH_t}] (r - 1 - \epsilon)}{1 + (r - 1 - \epsilon)} \} \) is monotonically increasing and converges to some positive point \( \bar{P}(\epsilon) \). This implies that
\[ \liminf_{t \to \infty} H_t \geq \dot{P}(\epsilon) > 0 \]

which is a contradiction. Therefore,

\[ W^s(E_{00}) \cap X_{11} = \emptyset \text{ and } W^s(E_{10}) \cap X_{11} = \emptyset \]

and the statement holds.

6. Conclusions and additional features

For most plant species it is conceivable that there is density dependent regulation of its growth. However, very few plants show periodic or strongly chaotic variation of the plant density from generation to generation. Hence it is important to determine the influence of models of monotone growth dynamics on the plant-herbivore interaction model. We proved three key features of such interactions that are important for model building:

- All monotone growth models generate a unique interior equilibrium.

- Monotone growth models with just one sustainable equilibrium for the plant population (e.g. the Beverton-Holt model) lead to noise sensitive bursting. This certainly happens for many plant-herbivore systems and the dynamical mechanism discussed here has not been noticed before in plant-herbivore systems (however, see Sergio, 2001).

- The Beverton-Holt model does not have more complicated dynamics than a periodic orbit in the interior of the phase space. Although we cannot prove this, we conjecture that this is true for all models that satisfy the assumptions of H1 and H2, i.e. have just one equilibrium for the pure plant dynamics.
Without any claim to a complete analysis of all types of model we note a few additional features associated with monotone and non-monotone plant growth models.

**Bistability:** The paper (Kang, *et al.*, 2008) study plant-herbivore systems of Model II type with a Ricker model for the pure plant dynamics, also known as the modified Nicholson-Bailey model. It is shown that for a large set of parameters the system exhibits bistability between complicated (possibly chaotic) dynamics in the interior of the phase space and equally complicated dynamics on the boundary (Figure 6.14(a)). Ryusuke (Ryusuke, 2006) discusses a similar bistability phenomenon for Model I. Since unimodal maps are all topologically equivalent (Guckenheimer, 1979), we expect bistability to be a defining feature for plant-herbivore models with unimodal plant growth models.

In contrast, models that satisfy the assumptions of H1 and H2, e.g. the Beverton-Holt model cannot show bistability since the global attractor either is a fixed point on the boundary or some set in the interior of the phase space. However, it is conceivable that models that do not satisfy H2, e.g. Holling-Type III models, show bistability between an interior attractor and a boundary equilibrium that is not the largest equilibrium for the pure plant population.

**Crisis of Interior Attractors:** All models seem to show some sort of global attraction to the boundary dynamics, i.e. extinction of the parasite for large growth rates $r$:

- Unimodal models show a crisis type of bifurcation whereas the chaotic dynamics in the interior collapses and the system becomes globally attracted to the boundary dynamics (Kang, *et al.*, 2008). For instance the interior strange attractor in Figure 6.14 that exists for a growth parameter of $r = 3.8$ will grow and hit the stable manifold of the boundary attractor for $r = 3.85$. 

Figure 6.14: The interior strange attractor and the stable manifold of the boundary attractor $a = 0.95, r = 3.8$.

- Holling-Type III models shows a heteroclinic orbit which breaks and leads to global attraction to a boundary fixed point.

- Conjecture: The Beverton-Holt model does not lead to complete extinction (from Proposition (5.1)) but the limit cycle come arbitrarily close to the axis $H = 0$ and hence for practical purposes might be called extinct.
CHAPTER 4 - Spatio-temporal modeling: two-patch model

There are three stages for an alien species to invade a new area: the arrival, the establishment of the population and the expansion. In general, we do not know the precise circumstance of an alien species' arrival, therefore the population dynamics and the expansion of alien species become the two main themes which have been extensively studied by ecologists for decades. In previous chapters, we have studied the dynamics of the interactions between plants and herbivores by adapting a host-parasite model with density-dependence acting before parasitism. Our study shows that plants' growth dynamics have a strong influence on the complicated plant-herbivore interactions.

In this chapter we develop spatio-temporal models to study how invasive species expand to new areas. Mathematical models can be either discrete or continuous in space and time depending on the species' life span and life cycle and the methods of dispersal (e.g., its own mobility or by other carriers, such as predator or human behavior). Our study is motivated by gypsy moths which are invasive forest pests with a strong seasonal life cycle, hence we model the dynamics in a discrete time fashion. Here we focus on a two compartment model with different initial conditions.

1. **Introduction**

In nature, different subpopulations of a metapopulation have various behaviors and habitats with non-identical quality and connectivity. These so called spatial heterogeneities play an important role in the stability and persistence of the population dynamics. In 1935, Nicholson and Bailey (Nicholson & Bailey, 1935) introduced a classical model to study the growth of the interacting host \( (H) \) and parasite \( (P) \) populations which are unstable and extinction-prone. May (May, 1978) and Reeve (Reeve, 1988) studied the statistical aspect
of the stability of the $H - P$ dynamics by considering the effect of environmental variability on persistence of a "population" of subpopulations of these $H - P$ models (Singh, Rao, Ramaswamy, & Sinha, 2004). Hassell (Hassell, et al., 1981,1988) and Comins (Comins, Hassell, & May, 1992) used the spatially extended models of the $H - P$ system and showed that the ensemble of populations could survive when individuals are allowed to disperse to neighboring patches.

One aim of studying spatio-temporal models is to investigate biological invasions. In particular, biological invasions of pest species are among the most significant threats to the stability of natural and agricultural ecosystems (Liebhold, Macdonald, Bergdahl, & Mastro, 1995). Their cascading direct and indirect effects are well studied (Parker, et al., 1999; Mack, et al., 2000; Pimentel, et al., 2000; Mooney & Cleland, 2001). Understanding the population dynamics with dispersal is crucial for ecologists to apply biological control strategies to regulate pests' populations and eventually stop their spreading. Models that deal with dispersals can be characterized into three categories: "islands" (or "metapopulations"), "stepping-stones" and a continuum (Kareiva, Mullen, & Southwood, 1990).

The two-patch model is the simplest way to study how pests disperse from an infected area to an uninfected one. Gyllenberg (Gyllenberg, Söderbacka, & Ericsson, 1993) studied a discrete time model for a metapopulation consisting of two local populations connected by migration. The study paid particular attention to the sense in which migration has a stabilizing and synchronizing effect on local dynamics. Weisser (Weisser & Hassell, 1996) investigated the effects of dispersal on the stability of host-parasitoid systems. Dispersal in their paper means the absence of individuals from breeding sites. The studies by Maynard Smith (1974), Allen (1975) and Reeve (1988) show that the unstable equilibrium of a
single-patch predator-prey model cannot be stabilized by diffusive coupling with identical patches, since coupled system behave identically to the single-patch system if the patches are synchronized. Thus maintenance of asynchrony among populations large enough to avoid extinction determines the persistence of coupled locally unstable systems (Alder, 1993). Taylor (Taylor, 1988) proposed that heterogeneity among patches, low but nonzero migration rates and large numbers of patches are three mechanisms that maintain this asynchrony. Heterogeneity among patches can take many forms such as variability in the host's growth rates, parasite's different attacking rates and non-identical dispersal rates. However, less attention has been paid to the heterogeneity such as identical coupled systems with different initial conditions. Adler (1993) showed that this mechanism can maintain bounded oscillations of two deterministic Nicholson-Bailey models coupled by migration.

Our study has extended the Nicholson-Bailey models to plant-herbivore models that show bistability (Kang, et al., 2008). The goal of this chapter is to study how bistability of a plant-herbivore model affects the spreading of the herbivore population from an infected patch to an otherwise identical uninfected patch. We study the behavior of this system as a function of the coupling between the two patches, i.e the barrier for dispersal. The most important result is that for a certain set of coupling parameters the population of herbivores in both patches drops under the threshold and hence the herbivore dies out in both patches. This suggests a possible biology control strategy to stop the invasion of an herbivore by controlling the migration between patches. In addition, our study indicates that a patchy environment can destabilize the dynamics and that heterogeneity in the initial conditions can cause asynchrony of both patches. In the following sections, we focus on the model formulation, mathematical analysis and the implications of numerical simulations.
2. Model formulation

The plant-herbivore models studied by Kang, et al. (2008) model the plant and the herbivore dynamics through their biomass changes by assuming that the herbivore population growth is a non-linear function of herbivore feeding rate, and that the plant population growth decreases gradually with increasing herbivores. In the absence of the herbivore, they allow for a density dependence growth rate in the plant since the plant population density is regulated by intraspecific competition. Let $P_n$ represent the plant population (nutritious) biomass after the attacks by the herbivore but before its defoliation. Let $H_n$ represent the biomass of the herbivore before it dies at the end of season $n$. There are two parameters in the model. Namely, $r$ is a constant, describing the maximum growth rate and $a$ is a constant that correlates with the total amount of the biomass that an herbivore consumes:

$$P_{n+1} = P_n e^{r(1-P_n) - aH_n} \quad (4.1)$$
$$H_{n+1} = P_n e^{r(1-P_n)} \left[ 1 - e^{-aH_n} \right] \quad (4.2)$$

Kang et al. (2008) show that the dynamics of model (4.1) and (4.2) are complicated and include quasi-periodicity, period-doubling, chaos, intermittency etc. In particular, the system shows bistability, i.e., initial population densities determine whether two species coexist for a specific set of parameter values. For the two-patch model we have the following definitions and assumptions:

- $P_n^I$ and $H_n^I$ represent the density of edible plant biomass and the population density of herbivores respectively in patch I at generation $n$. Similarly, $P_n^{II}$ and $H_n^{II}$ represent the density of plants and herbivores respectively in patch II at generation $n$. 
• The herbivore is established in patch I and extinct in patch II. Since model (4.1) and (4.2) has bistability between the boundary attractor and the interior attractors, the initial condition of the herbivore population is above the threshold $\theta$ in patch I ($H_0^I > \theta$) and zero in patch II ($H_0^{II} = 0$).

• Patch I and patch II have identical values of the parameters $r$ and $a$.

• Assume that the herbivore is the only species that disperses, and its dispersal occurs at the beginning of its life cycle before the density-dependence acts on the plant and herbivore, i.e., the dispersal of herbivores and the interactions between plants and herbivores are separated in time.

• Let $l \in [0,1)$ be the fixed fraction of migrating herbivores leaving its patch. The net effect on a patch is density-dependent since the patch above the mean density always loses herbivores, whereas those below it receive them, i.e., there are $lH_n^I$ herbivores leaving patch I during generation $n$ and $lH_n^{II}$ herbivores entering patch I at the same time. Therefore the net change of the herbivore population in patch I is given as $H_n^I - lH_n^I + lH_n^{II} = (1 - l)H_n^I + lH_n^{II}$. $l$ can be interpreted as a parameter measuring the barrier between two patches. The smaller $l$, the more difficult for herbivores to disperse (or the longer the distance between the two patches).

Let $H_{n+d}^I, H_{n+d}^{II}$ be the population of herbivores in patches I and II respectively after the dispersal during generation $n$, i.e.,

$$H_{n+d}^I = (1 - l)H_n^I + lH_n^{II} \quad (4.3)$$

$$H_{n+d}^{II} = (1 - l)H_n^{II} + lH_n^I \quad (4.4)$$
Then the population of plants and herbivores at generation \( n+1 \) can be modeled by

\[
P_{n+1}^I = P_n^I e^{r(1-P_n^I)-aH_{n+1}^I}
\]

\[
H_{n+1}^I = P_n^I e^{r(1-P_n^I)} \left[ 1 - e^{-aH_{n+1}^I} \right]
\]

\[
P_{n+1}^{II} = P_n^{II} e^{r(1-P_n^{II})-aH_{n+1}^{II}}
\]

\[
H_{n+1}^{II} = P_n^{II} e^{r(1-P_n^{II})} \left[ 1 - e^{-aH_{n+1}^{II}} \right]
\]

where \( H_0^I > \theta \) and \( H_0^{II} = 0 \).

3. Steady states

It is easier to study the steady state of model (4.5)-(4.8) by changing variables to

\[
U_n^I = (1-l)H_n^I + lH_n^{II}, \text{ and}
\]

\[
U_n^{II} = (1-l)H_n^{II} + lH_n^I.
\]

Then we have the new system

\[
P_{n+1}^I = P_n^I e^{r(1-P_n^I)-aU_n^I}
\]

\[
U_{n+1}^I = (1-l)P_n^I e^{r(1-P_n^I)} \left[ 1 - e^{-aU_n^I} \right] + lP_n^{II} e^{r(1-P_n^{II})} \left[ 1 - e^{-aU_n^{II}} \right]
\]

\[
P_{n+1}^{II} = P_n^{II} e^{r(1-P_n^{II})-aU_n^{II}}
\]

\[
U_{n+1}^{II} = (1-l)P_n^{II} e^{r(1-P_n^{II})} \left[ 1 - e^{-aU_n^{II}} \right] + lP_n^I e^{r(1-P_n^I)} \left[ 1 - e^{-aU_n^I} \right]
\]

Since the system (4.5)-(4.8) is equivalent to the system (4.9)-(4.12), we can conclude that as long as the herbivore dispersal and the interactions between plants and herbivores occur at distinct stages, the order in which the two steps occur is irrelevant.
Let \((P^I, U^I, P^{II}, U^{II})\) be a steady state of the system (4.9)-(4.12), then

\[
0 = r(1 - P^I) - aU^I
\]  
\[U^I = (1 - l)P^I \left[ e^{aU^I} - 1 \right] + lP^{II} \left[ e^{aU^{II}} - 1 \right]
\]  
\[
0 = r(1 - P^{II}) - aU^{II}
\]  
\[U^{II} = (1 - l)P^{II} \left[ e^{aU^{II}} - 1 \right] + lP^I \left[ e^{aU^I} - 1 \right].
\]

After simplification, we obtain

\[
U^I = (1 - l)(1 - \frac{aU^I}{r}) \left[ e^{aU^I} - 1 \right] + l(1 - \frac{aU^I}{r}) \left[ e^{aU^{II}} - 1 \right]
\]  
\[U^{II} = (1 - l)(1 - \frac{aU^{II}}{r}) \left[ e^{aU^{II}} - 1 \right] + l(1 - \frac{aU^I}{r}) \left[ e^{aU^I} - 1 \right].
\]

Define the function \(f(U) = \left(1 - \frac{aU}{r}\right) [e^{aU} - 1]\). Then (4.17) and (4.18) can be rewritten as

\[
U^I = (1 - l)f(U^I) + lf(U^{II})
\]  
\[U^{II} = (1 - l)f(U^{II}) + lf(U^I)
\]

From which it follows that

\[
U^I = \frac{(1 - l)U^{II}}{l} + \frac{(2l - 1)f(U^{II})}{l}
\]  
\[U^{II} = \frac{(1 - l)U^I}{l} + \frac{(2l - 1)f(U^I)}{l}.
\]

Define \(F(U) = \left(1 - \frac{aU}{r}\right) + \frac{(2l - 1)f(U)}{l}\). Then

\[
U^I = F(F(U^I))
\]  
\[U^{II} = F(F(U^{II})).
\]
Hence we have the following:

**Theorem 3.1.** If the model (4.1) and (4.2) has no positive interior steady state and 
\( l \neq \frac{1}{2} \), then the coupled system (4.5)-(4.8) has no interior positive steady state either.

**Proof.** Since the model (4.1) and (4.2) has no positive interior steady state, then

\[
\frac{U}{e^{aU} - 1} - \left( 1 - \frac{aU}{r} \right) > 0
\]

which implies \( U > f(U) \). Hence

\[
F(U) = \left( \frac{1-l}{l} \right) U + \left( \frac{2l-1}{l} \right) f(U) > U \text{ if } l < \frac{1}{2}
\]

and

\[
F(U) = \left( \frac{1-l}{l} \right) U + \left( \frac{2l-1}{l} \right) f(U) < U \text{ if } l > \frac{1}{2}
\]

Therefore, either \( F(F(U)) > F(U) > U \) or \( F(F(U)) < F(U) < U \).

**Proposition 3.1.** If \((P,U)\) is an interior steady state of the system (4.1) and (4.2), then 
\((P,U,P,U)\) is an interior steady state of the system (4.9)-(4.12). In particular, we have 
\( U = F(F(U)) \).

**Proof.** Since \((P,U)\) is an interior steady state of the system (4.1) and (4.2), then \((P,U)\) is the intersection of the functions 
\( P = 1 - \frac{aU}{r} \) and \( U = P(e^{aU} - 1) \), i.e., \( U \) is the solution of

\[
U = \left( 1 - \frac{aU}{r} \right)(e^{aU} - 1) = f(U)
\]

Hence,

\[
F(U) = \left( \frac{1-l}{l} \right) U + \left( \frac{2l-1}{l} \right) f(U) = U
\]

Therefore, \( U = F(F(U)) \).
Theorem 3.2. If \( U = F(F(U)) \) has only one positive root, then the system has only one interior steady state \((P, U, P, U)\) and \((P, U)\) is an interior steady state of the system (4.1) and (4.2). In particular, if the system (4.9)-(4.12) has a steady state \((P^I, U^I, P^{II}, U^{II})\) with \( U^I \neq U^{II} \), then \( U = F(F(U)) \) must have more than two positive distinct roots.

Proof. If the system (4.1) and (4.2) has no interior steady state, then by Theorem (3.1), the system (4.9)-(4.12) has no interior steady state either. Therefore \( U = F(F(U)) \) has no positive root, which is a contradiction to the condition. Hence, according to Proposition (3.1) the system (4.1) and (4.2) also has only one interior steady state \((P, U)\) where \((P, U, P, U)\) is the only interior steady state for the system (4.9)-(4.12) and \( P = 1 - \frac{ak}{r} \). All these arguments imply that if the system (4.9)-(4.12) has a steady state \((P^I, U^I, P^{II}, U^{II})\) with \( U^I \neq U^{II} \), then \( U = F(F(U)) \) must have more than two positive distinct roots.

Theorem 3.3. There exists a barrier parameter \( l = l^* \) such that for \( l > l^* \), \((P^I, U^I, P^{II}, U^{II})\) is a steady state of the system (4.9)-(4.12) with \( U^I = F(U^{II}) \) and \( U^{II} = F(U^I) \) and \( P^I \neq P^{II}, U^I \neq U^{II} \). At \( l = l^*, U^I = U^{II} = U^* \) and \( 2f_{U^I U^I}(U) + 3^{2l-1}(f_{U^I U^I}(U))_U^U \neq 0 \) the map \( F(U) \) undergoes a period doubling bifurcation, where \( U^* = f(U^*) \).

Proof. Please see the detailed proof in Appendix 6.2.

4. Analysis and simulations

Proposition 4.1. If the model (4.1) and (4.2) has a stable steady state at \((P, H)\) and \( l \) is small enough, then the synchronized steady state \((P, H, P, H)\) of the coupled system (4.5)-(4.8) is stable.
Proof. For \( l = 0 \), the system (4.5)-(4.8) becomes a decoupled system with the stable steady state \((P, H, P, H)\). Since eigenvalues of the Jacobian matrix of this coupled system evaluated at the synchronized steady state \((P, H, P, H)\) depend continuously on the parameter \( l \), there exists an open interval of \( l \) such that the synchronized steady state is stable for all \( l \) in this interval.

One of the most interesting findings of the model (4.1) and (4.2) by Kang, et al. (2008) is the bistability between the boundary attractor \((H = 0)\) and the interior attractor. We can expect the same behavior for the coupled system. Using a similar argument as in Theorem 4.1 of Kang, et al. (2008) we have, after a Taylor expansion for small \( l \):

**Theorem 4.1.** For \( a < 1 \) and \( l \) small enough, all the periodic orbits on the invariant manifold \( H^I = H^{II} = 0 \) are transversally stable.

Periodic orbits on the invariant manifold \( H^I = H^{II} = 0 \) occur when \( r > 2 \). In the case \( r < 2 \) and \( a < 1 \), according to Theorem (3.1), the system has no interior steady state and only a stable synchronized boundary steady state \((1, 0, 1, 0)\) with the eigenvalues \( \lambda_1 = 1 - r, \lambda_2 = a, \lambda_3 = 1 - r \) and \( \lambda_4 = a - 2al \). Hence, we can expect that the coupled system has global stability at \((1, 0, 1, 0)\) when \( r < 2 \) and \( a < 1 \).

**Theorem 4.2.** For \( r < 2 \) and \( a > 1 \), the coupled system (4.5)-(4.8) has no boundary attractor, hence, there is no bistability between the boundary attractor and the interior attractors.

The main purpose of this section is to study how bistability between the boundary attractor and the interior attractors affects the expansion of herbivores from infected patches to
uninfected patches. We therefore focus on the parameter region that can generate bistability, i.e., \( r > 2 \).

In order to focus on the relationship between the expansion of the herbivore and the barrier parameter \( l \) from an infected patch I to an uninfected patch II we set the initial conditions in patch II to \( P_0^{II} = 0.5 \) and \( H_0^{II} = 0 \). We set \( r = 2.45 \) at which value the pure plant dynamics have a period two boundary attractor. Then we vary the values of \( a \) and study 5 cases:

(i) Case 1: Set \( a = 0.98 \) and \( r = 2.45 \). The single patch model has two steady states in the interior attractor: one is stable and the other is unstable (Figure 4.15).

(ii) Case 2: Set \( a = 1.2 \) and \( r = 2.45 \). The single patch model has only one stable steady state in the interior attractor. There is a period two boundary attractor.

(iii) Case 3: Set \( a = 1.8 \) and \( r = 2.45 \). The single patch model has a period-17 solution in the interior attractor; the plant has a period two orbit in the boundary attractor (see Figure 4.16-(a)).

(iv) Case 4: Set \( a = 5.8 \) and \( r = 2.45 \). The single patch model has a strange attractor; the plant has a period two orbit in the boundary attractor (see Figure 4.16-(b)).

(v) Case 5: Set \( a = 6.8 \) and \( r = 2.45 \). The single patch model has a crisis of the strange attractor; the plant has a period two orbit in the boundary attractor.

4.1. The basin of attractor of the interior equilibrium. We focus on the spread of the herbivores from the infected patch into the uninfected one and consider the following questions:
(i) For which values of the barrier parameter $l$ can herbivores establish themselves in the uninfected patch?

(ii) How does the barrier $l$ affect the size and location of the basin of attraction of the interior equilibrium?

Figure (4.15) illustrates the dynamics of the coupled system when $l = 0$ for case 1: Patch I has a stable steady state (Figure (4.15-(a))) and patch II has a period two orbit for the boundary dynamics of the plant (Figure (4.15-(b))). In the case $l = 0$, both patch I and II become uncoupled and behave independently. Figure (4.17) represents the basin of attraction of the interior attractor when $l = 0$. Shown is the $(P, H)$ phase-plane of initial conditions in patch I with a color coding for the steady state value of a long time simulation for patch I (left) and patch II (right). Recall that the initial condition for patch II is zero for the herbivores. Since the two systems are independent, the herbivore does not get established in patch II for all the initial conditions of patch I. The dark brown area determines the set of initial conditions for which the system in patch I converges to a stable steady state (see Figure (4.15-(a))). The dark blue area is the set of initial conditions for which the system in patch I decays to the boundary dynamics of a period two orbit for the plant evolution. When $l = 0.1$, both patches converge to their boundary dynamics for all initial conditions in patch I. This can be seen in Figure 4.19 since the population of the herbivore stays below the magnitude $10^{-10}$. This is an unexpected response to the first question posed above: The herbivore not only does not expand but dies out even in patch I where the population of herbivores was well established. The mechanisms behind this phenomenon comes from the bistability: Originally, the population of plants and herbivores in patch I lies in the dark brown area of basin boundary (4.17). However, dispersal of the herbivore into patch II
makes the population of herbivores in both patches lie below the threshold of the bistability and hence converges to the boundary dynamics in both cases. This suggests that the right values of $l$ can shrink the area of the interior attractor or even kill the interior attractor completely.

To investigate the relationship between $l$ and the area of the interior attractor, we define

**Definition 4.1 (Total Area).** is the area of the rectangle in phase space for which the model is valid. It is defined as the product of the maximum population of plants $P_{\text{max}} = 1$ and herbivores $H_{\text{max}} = \frac{r}{a}$.

**Definition 4.2 (Basin area).** is defined as the area of the initial population of plants and herbivores in patch I for which solutions approach the interior attractor for long simulations. For example, the dark brown area in Figure (4.17) is the basin area for $a = 0.98$ and $r = 2.45$.

**Definition 4.3 (Area Ratio).** is defined as the ratio of area of the basin area to the total area.

Figure (4.18) shows the Area Ratio for patch I (red dots) and the patch II (blue dots) as a function of the barrier $l$. We find:

(i) At $l = 0$, patches are uncoupled: the Area ratio of patch I (the red dot) is about 0.32 and the Area ratio of patch II (the blue dot) is 0.

(ii) For $0.02 < l < 0.18$, the Area Ratio of both patches is 0: there is no initial conditions of patch I that can lead to an endemic equilibrium of the herbivore.
(iii) For $0.18 < l < 0.38$, the barrier $l$ shrinks the basin area, i.e., the area ratio is smaller than in the case $l = 0$ for patch I. By comparing Figures (4.20)(a) and (b), we can see that the basin area of $l = 0.2$ is contained in the basin area of $l = 0$.

(iv) For $0.38 < l < 0.45$, the barrier $l$ expands the basin area, i.e., the area ratio is greater than in the case $l = 0$ for patch I. When $l = 0.4$, the coupled systems are synchronized: both two patches have the same stable steady state when the initial conditions of patch I are taken in the dark brown area and have the same boundary dynamics ($H^I = H^{II} = 0$) when the initial conditions of patch I are taken in the dark blue area. By comparing Figures (4.21) (a) and (b), we see that the minimal initial population of the herbivore that leads to infestation in the case $l = 0.4$ is significantly higher than the minimal initial population in the case $l = 0$.

(v) For $l > 0.45$ is not biologically interesting.

5. Conclusion

This chapter has been focused on the dynamics of the coupled systems (4.5)-(4.8) and how bistability affects the spreading from the infected patch to the uninfected patch depending on the barrier $l$. We conclude the findings as follows:

(i) If the dynamics of the single patch have no positive interior equilibrium, then the coupled system has no such equilibrium either.

(ii) If the dynamics of the single patch have bistability between the boundary attractor and the interior attractor, then for the appropriate values of $l$ the coupled systems also have such bistability.

(iii) The barrier $l$ can both stabilize and destabilize the system.
(iv) Success of the expansion of an equilibrium population of herbivores into a virgin patch depends on the barrier parameter $l$. For a very small $l$ the two systems are essentially uncoupled and the expansion does not succeed. For intermediate values, the dispersal of herbivores will reduce the possibility of the infestation in both patches. This may even lead to extinction of the herbivore in both patches. For a larger $l$ the set of initial conditions that lead to the establishment of the herbivore in both patches increases until almost all initial conditions lead to the synchronized equilibrium. This dispersal phenomenon that leads to extinction may have a useful application to control the spread of the herbivore. Reducing the barrier through the spraying of the right amount of insecticides in the boundary region may not only prevent spreading but may also weaken the population in the infected region enough to lead to a collapse of the population. This phenomenon also provides a possible explanation for the fact that in some years the boundary of the gypsy moths from the Northeast of the US to the Southwest retreated.
Figure 4.15: Time series of plant-herbivore population: $a = .98, r = 2.45$
(a) Phase portrait of plant-herbivore population in the infected patch when $a = 1.8, r = 2.45$.

(b) Phase portrait of plant-herbivore population in the infected patch when $a = 5.8, r = 2.45$.

*Figure 4.16*: Phase portrait of plant-herbivore population in the case three and four
Figure 4.17: Basin of attraction for the interior equilibrium when \( a = 0.98, r = 2.45, \lambda = 0 \).

Figure 4.18: The ratio of initial conditions in the patch one that make the herbivore established when \( a = 0.98, r = 2.45 \).
Figure 4.19: Basin of attraction for the interior attractor when $a = 0.98, r = 2.45, l = 0.1$. Notice that all initial conditions decay to zero.
Figure 4.20: Compare basin boundary for \( l = 0 \) and \( l = 0.2 \)
(a) The basin boundary of patches when $l = 0$.

(b) The basin boundary of patches when $l = 0.4$.

*Figure 4.21:* Compare basin boundary for $l = 0$ and $l = 0.4
CHAPTER 5 - Conclusion and future work

In this chapter, I summarize my dissertation work and discusses possible future works. The future research direction will be motivated by practical issues of plant-gypsy moths interactions. We plan to:

(i) model the spatio-temporal model on plant-herbivore interactions by using integrodifference equations with two-scale dispersals (Sharov Alex, et al., 1998) and exploring its traveling wave solutions of such models;

(ii) use the ecological data to validate our models (USDA, 2008) and incorporating multi-tropical interactions to our models such as predator-rodents in the system which is known as intraguild predation in ecology.

We will detail these two plans after the summary.

1. Summary

The main purpose of my dissertation is to build a theoretical framework of the interactions between plants and herbivores to help forest managers design better biological control strategies to regulate the population of forest pests and eventually stop their invasion. I try to answer the following questions:

(i) What are the most likely population dynamics of forest pests (e.g., gypsy moths)? Which strategies are the best for forest managers to control their populations?

(ii) How do the different population dynamics of the plant affect the herbivores?

(iii) How does a barrier between patches affect the spreading of gypsy moths? Which biological control strategies can regulate the pest’s population and eventually stop their invasion?
The answer to the first question can be found in Chapter 2. I formulate a model on the interactions between plants and herbivores based on the nutrient recycling of the forest and the biological properties of the herbivores by using a host-parasite model with density dependence acting before parasitism. Bifurcation curves have been derived in the parameter space which consists of the growth rate of the plant population $r$ and parameter $a$ describing the damage inflicted by herbivores. Bistability and a crisis of a strange attractor suggest two control strategies: Reducing the population of the herbivores under some threshold or increasing the growth rate of the plant.

The answer to the second question can be found in Chapter 3. I investigate two general plant-herbivore models: The first model involves a single plant species that has an increasing population dynamics with a decreasing growth function (called Beverton-Holt model), while the second model has a Holling-Type III function as its plant's population dynamics (called Holling-Type III model). One key feature of these two models is that the boundary dynamics generate a unique interior equilibrium. This equilibrium goes through the Neimak-Sacker bifurcation, which generates periodic or quasi-periodic dynamics on invariant cycles. Our study shows that noise, i.e. environmental fluctuations, constitute an important factor to generate the bursting behavior of the populations of herbivores for the Beverton-Holt model. In contrast, the Holling-Type III model shows a heteroclinic bifurcation connecting two boundary equilibria. By comparing the dynamics of our models to plant-herbivore models with unimodal (or multimodal) functions as a plant’s dynamics, we can see that the plant’s population dynamics determine the outcomes of the plant-herbivore interaction. The over-compensation in plant’s dynamics is responsible for the complicated dynamical behavior, while the under-compensation in a plant’s dynamics can generate more stable dynamics.
The last question is partly answered in Chapter 4. I study the influence of bistability on a two-patch plant-herbivore model by introducing a new parameter to measure the barrier between one infected patch and one uninfected patch. These two patches are identical, i.e., with the same growth rate of the plant and the same damage cost by the herbivore. One of the most interesting results shows that the right barrier between these two patches can drive the population of the herbivore in both patches under the bistability threshold. This suggests that a possible biology control strategy to stop the invasion is to adjust the right barrier between the patches. In addition, the study indicates the patchy environment can destabilize or stabilize the dynamics depending on the values of the barrier.

2. Future directions

We modeled the general plant-herbivore interactions. In the future, we will focus on the following two topics:

2.1. Integrodifference models. Biological invasion of pest species are among the most significant threats to the stability of natural and agricultural ecosystems. The gypsy moth in North America represents an excellent example of the population biology of invasions. Studying its dynamics and invasion can help us to understand other alien invasive species.

Ecologists start to apply mathematical models to study spatio-temporal population dynamics of gypsy moths. The models by Wilder (1993) considered the interaction among the gypsy moth biomass density, the foliage biomass density and the natural enemy biomass density with traditional diffusion-local dispersal. Their models show a constant-shape, constant-velocity traveling waves; however, the predicted speed of traveling waves is lower than the one found from the ecological data. We believe that the reason is that their model assumes a single, continuous form of dispersal which implicates that the range expansion is a smooth,
continuous process. However, gypsy moths are able to disperse in two ways: local dispersal and long-distance dispersal. The existence of two forms of dispersal is referred to as 'stratified dispersal'; in those situations, range expansion will proceed through the formation of multiple discrete, isolate colonies established ahead of the infested front. These colonies in turn will expand their range and ultimately coalesce. The result of this phenomenon is that range expansion could occur much faster than it would do under a simpler diffusion model. The paper by Sharov Alex, et al. (1998) considered these two forms of dispersal, but they ignore all the factors that effect the population dynamics such as the interaction between plants and gypsy moths. All the previous models do not realistically take into account the dispersal or interaction mechanisms of the species. It will be nice to build an integrodifference model with two-scale dispersals for the herbivore based on our previous model, which is discrete in time and continuous in space for the spatial interactions between plants and herbivores.

In nature, herbivores have different dispersals during their lifetime, e.g., the short-distance dispersal, which is caused by the larvae moving from one place to another; and the long-distance dispersal, which can be caused by human transportation. It is worth exploring the traveling wave solutions of such models, and to study how long-distance dispersals affect the speed of invasion if it has any. Habitat structure has broad impacts on many biological systems. In particular, habitat fragmentation can increase the probability of species extinction but also lead to population outbreaks in response to a decline of natural enemies. An extreme consequence of fragmentation is the isolation of small regions of suitable habitat surrounded by a large region of hostile matrix. This scenario can be interpreted as a critical patch-size problem, well studied in a continuous-time framework, but relatively
new in discrete-time models. The future study intends to gain understanding of how insect outbreaks are influenced by both habitat size and dispersal kernels. In particular, we can examine the interaction among the pest emergence time, dispersal and patch size in ensuring plant-herbivore persistence.

The herbivore population is affected by the plant quality (see (Schultz & Baldwin, 1982)). The quality of leaves has a great effect on the survival and reproduction rate of the pest. If larvae feed on bad leaves, they more likely die before reaching the adult stage, and dead bodies are recycled back to the soil. Studying how leaf quality effect the out-break of the pest would be very exciting.

2.2. Modeling multi-tropical interactions. Oaks (Quercus spp.) are deciduous hardwood, which produce acorns, the main diet of white-footed mouse. Oaks are “masting” trees, meaning that in some years they produce prodigious amounts of acorn and in others, they produce virtually none (Roberson, 2007). The abundant years are called “mast” years, or “good mast” years. Mast seeding, the intermittent production of large seed crops, can generate large fluctuations in abundance of granivores, and can have indirect effects that extend to a surprising array of species and ecological processes (Ostfeld, Jones, & Wolff, 1996) and (Elkinton, Liebhold, & Muzika, 2004). Acorn masting has been hypothesized to indirectly control the initiation of gypsy moths outbreaks mediated by the direct effect of acorns on the abundance of white-footed mice which are a major predator of gypsy moths (Selâs, 2003) and (Elkinton et al., 1996). The relationship among oaks, gypsy moths and white-footed mice is called the intraguild predation in ecology. Motivated by this example, it is possible to develop a general mathematical model on the intraguild predation by introducing predators into our previous models. We can use this new model to help us understand how predators
regulate the dynamics of forest pests and how the production of seeds indirectly affects the outbreak of pest.

Finally, the USDA has huge data sets on the population of gypsy moths and its spreading (USDA, 2008). It would be helpful for us to validate our models by using these data and eventually improve our models.
1. Derive normal form

We have the following two-dimensional discrete model:

\[ N_{n+1} = N_n e^{r(1 - \frac{N_n}{N_{\text{max}}}) - aH_n} \]
\[ H_{n+1} = \frac{N_n}{\theta} e^{r(1 - \frac{N_n}{N_{\text{max}}}) (1 - e^{-aH_n})} \]

This model has two boundary equilibrium points, \((0,0)\) and \((N_{\text{max}},0)\), and an interior equilibrium point \((N^*,H^*)\). Let, \(s_n = \frac{N_n}{N_{\text{max}}}, t_n = H_nN_{\text{max}}, a_m = N_{\text{max}}a\), then the original system can be rewritten as:

\[ s_{n+1} = s_n e^{r(1-s_n) - a_m t_n} = f(s_n, t_n) \]
\[ t_{n+1} = s_n e^{r(1-s_n) (1 - e^{-a_m t_n})} = g(s_n, t_n) \]

The three equilibria become: \((0,0)\), \((1,0)\), and \((x_0,y_0)\). The Jacobian matrix of the model is the following:

\[ J := \begin{bmatrix} \frac{f(s,t)}{s} - r f(s,t) & -a_m f(s,t) \\ \frac{g(s,t)}{s} - r g(s,t) & a_m f(s,t) \end{bmatrix} \]

1.1. At the boundary equilibrium point \((1,0)\). At the boundary equilibrium point \((1,0)\) the Jacobian matrix is

\[ J|_{(1,0)} := \begin{bmatrix} 1 - r & -a_m \\ 0 & a_m \end{bmatrix} \]

with eigenvalues \(\lambda_1 = 1 - r\) and \(\lambda_2 = a_m\). When \(r = 2\) and \(a_m = 1\), we have the most degenerate case in which the eigenvalues \(\lambda_1 = -1\) and \(\lambda_2 = 1\). To study the unfolding at this degenerate point, we need to get the normal form for our dynamical system. Let
\[ s_n = u_n + 1, v_n = t_n, r = \gamma + 2, \text{ and } a_m = a + 1. \] Then the original dynamical system becomes

\[ u_{n+1} + 1 = (u_n + 1)e^{(\gamma+2)(1-(u_n+1))-(a+1)v_n}, \]
\[ v_{n+1} = (u_n + 1)e^{(\gamma+2)(1-(u_n+1))-(a+1)v_n} \left( 1 - e^{-(a+1)v_n} \right) \]

Simplifying the system, we get the following:

\[
\begin{align*}
    u_{n+1} &= 2/3 u_n^3 - 1/6 \gamma^3 u_n^3 - 1/2 \gamma^2 u_n^3 - \gamma u_n^2 v_n \\
    &- 1/2 \gamma^2 u_n^2 v_n - \alpha \gamma u_n^2 v_n + 1/2 \gamma^2 u_n^2 + \gamma u_n^2 \\
    &- 1/2 \alpha \gamma u_n^2 v_n - u_n - 1/2 \gamma u_n v_n^2 + \alpha \gamma u_n v_n + u_n v_n \\
    &- 1/2 u_n v_n^2 - 1/2 \alpha^2 u_n v_n^2 + \gamma u_n v_n - \gamma u_n - \alpha \gamma u_n v_n^2 \\
    &- 1/2 \alpha^2 \gamma u_n v_n^2 + \alpha u_n v_n - \alpha u_n v_n^2 - v_n + 1/2 \alpha^2 v_n^2 \\
    &- 1/2 \alpha^2 v_n^3 - 1/2 \alpha v_n^3 - \alpha v_n + \alpha v_n^2 + 1/2 v_n^2 - 1/6 v_n^3 \\
    &- 1/6 \alpha^3 v_n^3 \\
    v_{n+1} &= 1/6 \alpha^3 v_n^3 + 1/2 \alpha^2 v_n^3 + 1/2 \alpha v_n^3 + 1/6 v_n^3 \\
    &+ 1/2 \alpha^2 \gamma u_n v_n^2 + \alpha \gamma u_n v_n^2 - 1/2 \alpha^2 v_n^2 \\
    &- \alpha v_n^2 - 1/2 v_n^2 + 1/2 u_n v_n^2 + 1/2 \gamma u_n v_n^2 + 1/2 \alpha^2 u_n v_n^2 \\
    &+ \alpha u_n v_n^2 + 1/2 \gamma^2 u_n^2 v_n + v_n + \alpha \gamma u_n^2 v_n + \gamma u_n^2 v_n \\
    &+ \alpha v_n - u_n v_n - \alpha \gamma u_n v_n - \gamma u_n v_n - \alpha u_n v_n + 1/2 \alpha \gamma^2 u_n^2 v_n
\end{align*}
\]

We have the Jacobian matrix as the follows:

\[
J|_{(1,0)} := \begin{bmatrix}
-\gamma - 1 & -\alpha - 1 \\
0 & \alpha + 1
\end{bmatrix}
\]
(i) First step. Do the linear transformation so that we can have standard form. The eigenvalues are \( \lambda_1 = -1 - \gamma \) and \( \lambda_2 = 1 + \alpha \), and the associate eigenvectors are

\[
V_1|_{\lambda_1} := \begin{bmatrix} 1 \\ 0 \end{bmatrix}
\]

and

\[
V_2|_{\lambda_2} := \begin{bmatrix} 1 \\ \frac{-\gamma+2+\alpha}{\alpha+1} \end{bmatrix}
\]

Let

\[
T := \begin{bmatrix} 1 & 1 \\ 0 & \frac{-\gamma+2+\alpha}{\alpha+1} \end{bmatrix}
\]

Then

\[
T^{-1} := \begin{bmatrix} 1 & \frac{\alpha+1}{\gamma+2+\alpha} \\ 0 & \frac{-\alpha+1}{\gamma+2+\alpha} \end{bmatrix}
\]

Set

\[
\begin{bmatrix} u_n \\ v_n \end{bmatrix} := T \begin{bmatrix} x_n \\ y_n \end{bmatrix}
\]

Then we have

\[
\begin{bmatrix} x_n \\ y_n \end{bmatrix} := T^{-1}J_{(1,0)} T \begin{bmatrix} x_n \\ y_n \end{bmatrix} + \begin{bmatrix} N_1(u_n, v_n) \\ N_2(u_n, v_n) \end{bmatrix}
\]

where
\[ N_1(u,v) = -1/6(-6\alpha uv + 3\nu^2\gamma^3\alpha + 6\nu^2\gamma^2\alpha \\
+ 3\nu^2w\gamma^2\alpha^2 - 4\nu^3\alpha - 6\nu - 3\alpha^2\gamma v^2 - 3\alpha^2u^2 \\
- 6\alpha\gamma u^2 - 6\alpha\gamma v^2 + 3uw^2 + 3\alpha^2uv^2 + 6\alpha uv^2 - 8u^3 \\
+ \nu^3 - 6\nu^2uv - 3\gamma v^2 - 3\nu^2 - 4\nu^3\gamma + \nu^3\gamma \\
+ \gamma^4u^3 - 3\alpha^2v^2 - 6\alpha v^2 + \alpha^3\nu^3 + 3\alpha^2\nu^3 \\
+ 3\alpha v^3 - 12\gamma u^2 + 5\gamma^3 u^3 + 6\gamma^2 u^3 - 12\gamma^2 u^2 \\
+ 9\gamma^2 u^2 v + 6\gamma^2 v^2 + 6\gamma uv^2 + 6\alpha\gamma u^2 v \\
+ 6\alpha^2\gamma uv^2 - 12\alpha\gamma uv + 9\alpha^2u^2v - 3\gamma^3 u^2 \\
+ 3uv^2\gamma^3 + 3\gamma^2 u^3 \alpha + \alpha^3\nu^3 \gamma + 3\alpha^2\nu^3 \gamma \\
+ 3\alpha v^3 \gamma + \gamma^3 u^3 \alpha + 3uv^2u\gamma^2 - 6\alpha\gamma^2 uv \\
- 12\gamma uv + 12\alpha\gamma uv^2)/(\alpha + 2 + \gamma) \]

and

\[ N_2(u,v) = -1/6(\alpha + 1)v(-6\alpha\gamma u + 3\alpha^2u^2 + 6\alpha\gamma uv \\
+ 3\alpha^2\gamma uv + 6\alpha\gamma u^2 - 6\gamma u + 3\gamma uv + 6\gamma u^2 \\
- 6\alpha u - 6u + 3uv + 3\alpha^2uv + 6\alpha uv + v^2 - 3v + 3\gamma^2 u^2 - 3\alpha^2 v \\
- 6\alpha v + \alpha^3 \nu^2 + 3\alpha^2 \nu^2 + 3\alpha \nu^2)/(\alpha + 2 + \gamma) \]

Let \( u_n = x_n + y_n \) and \( v_n = -\frac{(\gamma + 2 + \alpha)y_n}{\alpha + 1} \). Then we have the following standard form:

\[
\begin{bmatrix}
x_{n+1} \\
y_{n+1}
\end{bmatrix}
:=
\begin{bmatrix}
(1 - \gamma)x_n \\
(1 + \alpha)y_n
\end{bmatrix}
+ \begin{bmatrix}
N_1(x_n + y_n, -\frac{(\gamma + 2 + \alpha)y_n}{\alpha + 1}) \\
N_2(x_n + y_n, -\frac{(\gamma + 2 + \alpha)y_n}{\alpha + 1})
\end{bmatrix}
\]
Denote

\[ N_1(x, y) = g_{11}xy + \frac{g_{02}x^2}{2} + \frac{g_{20}y^2}{2} + \frac{g_{12}xy^2}{2} + \frac{g_{21}y^2x}{2} + \frac{g_{03}y^3}{6} + \frac{g_{30}x^3}{6} \]

\[ N_2(x, y) = h_{11}xy + \frac{h_{02}x^2}{2} + \frac{h_{20}y^2}{2} + \frac{h_{12}xy^2}{2} + \frac{h_{21}y^2x}{2} + \frac{h_{03}y^3}{6} + \frac{h_{30}x^3}{6} \]

(ii) Second step. Do a nonlinear transformation by setting

\[ \xi = x + G_{11}xy + \frac{G_{20}x^2}{2} + \frac{G_{02}y^2}{2} + \frac{G_{12}xy^2}{2} + \frac{G_{21}y^2x}{2} + \frac{G_{03}y^3}{6} + \frac{G_{30}x^3}{6} \]

\[ \eta = y + H_{11}xy + \frac{H_{20}x^2}{2} + \frac{H_{02}y^2}{2} + \frac{H_{12}xy^2}{2} + \frac{H_{21}y^2x}{2} + \frac{H_{03}y^3}{6} + \frac{H_{30}x^3}{6} \]

Let

\[ H_{11} = -\frac{h_{11}}{2}, G_{02} = \frac{g_{02}}{2}, G_{20} = \frac{g_{20}}{2} \]

(iii) Third step. To eliminate as many terms as possible, choose

\[ H_{20} = \frac{4}{3}, G_{11} = 0, H_{02} = 2, H_{03} = \frac{7}{4}, G_{30} = 0, H_{21} = -\frac{7}{6} \]

Then we eventually get the following unfolding up to degree three:

\[ \xi_{n+1} = (-1 - \gamma)\xi_n - \xi_n\eta_n \]

\[ \eta_{n+1} = (1 + \alpha)\eta_n + (\gamma + 3\alpha)\xi_n\eta_n^2 - \frac{\xi_n^2\eta_n}{2} - \frac{(\alpha + \gamma)\eta_n^2}{2} + \frac{2(\alpha - 2\gamma)\xi_n^2\eta_n}{3} - \frac{\eta_n^3}{3} \]

Let \( \alpha = 0, \gamma = 0 \). Then we have:

\[
\begin{bmatrix}
    x_{n+1} \\
    y_{n+1}
\end{bmatrix} :=
\begin{bmatrix}
    -\xi_n - \xi_n\eta_n \\
    \eta_n - \frac{\xi_n^2\eta_n}{2} - \frac{\eta_n^3}{3}
\end{bmatrix}
\]
To keep the property that $y = 0$ is an invariant manifold, we do the nonlinear transformation by setting:

$$
\begin{align*}
\xi &= x + G_{11}xy + \frac{G_{20}x^2}{2} + \frac{G_{02}y^2}{2} + \frac{G_{12}xy^2}{2} + \frac{G_{21}x^2y}{2} + \frac{G_{30}x^3}{6} + \frac{G_{03}y^3}{6} \\
\eta &= y + H_{11}xy + \frac{H_{02}y^2}{2} + \frac{H_{12}xy^2}{2} + \frac{H_{21}x^2y}{2} + \frac{H_{03}y^3}{6}
\end{align*}
$$

Let

$$H_{11} = -h_{11}/2, G_{02} = g_{02}/2, G_{20} = g_{20}/2, H_{20} = 4/3$$

and

$$G_{11} = 0, H_{02} = 2, H_{03} = 0, G_{30} = 0, H_{21} = -1/2$$

Then we eventually get the following unfolding up to degree three:

$$
\begin{align*}
\xi_{n+1} &= (-1 - \gamma)\xi_n - \xi_n\eta_n + \frac{2\xi_n^3}{3} \\
\eta_{n+1} &= (1 + \alpha)\eta_n + (\gamma + 3\alpha)\xi_n\eta_n^2 - \frac{\xi_n^2\eta_n}{2} - \frac{(\alpha + \gamma)\eta_n^2}{2} - \frac{\eta_n^3}{3}
\end{align*}
$$

2. Normal form analysis

Recall that our normal form for the model is:

$$
\begin{align*}
\bar{u}_{n+1} &= (-1 - \gamma)u_n - u_nv_n \\
\bar{v}_{n+1} &= (1 + \alpha)v_n + (\gamma + 3\alpha)u_nv_n^2 - \frac{u_n^2v_n}{2} - \frac{(\alpha + \gamma)v_n^2}{2} + \frac{2(\alpha - 2\gamma)u_n^2}{3} - \frac{v_n^3}{3}
\end{align*}
$$

We consider the following two scenario:
(i) If $\gamma = 0$, then our normal form becomes:

\[
\begin{align*}
    u_{n+1} &= -u_{n} - u_{n} v_{n} \\
v_{n+1} &= (1 + \alpha) v_{n} + 3\alpha u_{n} v_{n}^{2} - \frac{u_{n}^{2} v_{n}}{2} - \frac{\alpha v_{n}^{2}}{2} + \frac{2\alpha u_{n}^{2}}{3} - \frac{v_{n}^{3}}{3}
\end{align*}
\]

If $\alpha \neq 0$, then we have the following Jacobian matrix:

\[
J|_{(1,\rho)} := \begin{bmatrix}
-1 & -\alpha - 1 \\
0 & \alpha + 1
\end{bmatrix}
\]

Then we can apply the center manifold theorem of maps. Setting:

\[
v_{n} = h(u_{n}) = a_{2} u_{n}^{2} + a_{3} u_{n}^{3},
\]

We need to figure out the value of $a_{2}$ and $a_{3}$. Since we have

\[
\begin{align*}
v_{n+1} &= (1 + \alpha) v_{n} + 3\alpha u_{n} v_{n}^{2} - \frac{u_{n}^{2} v_{n}}{2} - \frac{\alpha v_{n}^{2}}{2} + \frac{2\alpha u_{n}^{2}}{3} - \frac{v_{n}^{3}}{3} \\
&= (1 + \alpha) h(u_{n}) + 3\alpha u_{n} h(u_{n})^{2} - \frac{u_{n}^{2} h(u_{n})}{2} - \frac{\alpha h(u_{n})^{2}}{2} + \frac{2\alpha u_{n}^{2}}{3} - \frac{h(u_{n})^{3}}{3}
\end{align*}
\]

and

\[
\begin{align*}
v_{n+1} &= h(u_{n+1}) \\
&= h(-u_{n} - u_{n} v_{n}) \\
&= h(-u_{n} - u_{n} h(u_{n}))
\end{align*}
\]

we have the equality:

\[
\begin{align*}
v_{n+1} &= (1 + \alpha) h(u_{n}) + 3\alpha u_{n} h(u_{n})^{2} - \frac{u_{n}^{2} h(u_{n})}{2} - \frac{\alpha h(u_{n})^{2}}{2} + \frac{2\alpha u_{n}^{2}}{3} - \frac{h(u_{n})^{3}}{3} \\
&= h(-u_{n} - u_{n} h(u_{n}))
\end{align*}
\]

Therefore we can solve for the values $a_{2}$ and $a_{3}$

\[
a_{2} := -\frac{2}{3}, a_{3} := 0
\]
Hence, the center manifold is

\[ v_n = h(u_n) = -\frac{2u_n^2}{3} \]

The dynamics on the center manifold which describes a period doubling bifurcation is given by

\[ u_{n+1} = (-1 - \gamma)u_n + \frac{2u_n^3}{3} \]

(ii) If \( \alpha = 0 \), then the normal form of our dynamical system is:

\[
\begin{align*}
    u_{n+1} &= (-1 - \gamma)u_n - u_n v_n \\
    v_{n+1} &= v_n + \gamma u_n v_n - \frac{v_n^2}{2} - \frac{\gamma v_n^2}{2} + \frac{4\gamma v_n^3}{3} - \frac{v_n^3}{3}
\end{align*}
\]

If \( \gamma \neq 0 \), then we have the following Jacobian matrix:

\[
J|_{(1,0)} := \begin{bmatrix}
    -\gamma - 1 & -1 \\
    0 & +1
\end{bmatrix}
\]

Since \( u_n = 0 \) is an invariant manifold. It becomes the center manifold and the dynamics on it reduces to

\[ v_{n+1} = (1 + \alpha)v_n - \frac{(\alpha + \gamma)v_n^2}{2} - \frac{v_n^3}{3} \]

3. Model analysis

In this section, we focus on the mathematical analysis of the model derived in Chapter two.

3.1. Positive invariant and bounded.

**Proposition 3.1.** For \( a > 0 \) and initial conditions in the first quadrant \( Q^+ \), i.e. \( x_0 > 0 \) and \( y_0 > 0 \), we have: \( x_n > 0 \) and \( y_n > 0 \) for all \( n \in \mathbb{Z}^+ \). In addition we can find some positive number \( M \), such that \( \max_{n \in \mathbb{Z}^+} \{x_n, y_n\} \leq M \).
Proof. Show by induction.

Since $x_0 > 0$ and $e^{r(1-x_0) - ay_0} > 0$, hence

$$x_1 = x_0 e^{r(1-x_0) - ay_0} > 0.$$  

Assume that for $n \leq k$, we have $x_k > 0$. Then for $n = k + 1$ we have

$$x_{k+1} = x_k e^{r(1-x_k) - ay_k} > 0.$$  

since for any value $y_k$, we have $e^{r(1-x_k) - ay_k} > 0$. Therefore $x_n > 0$ for any $n \in \mathbb{Z}^+$. Similarly, we can show that $y_n > 0$ for any $n \in \mathbb{Z}^+$.

Adding the equation (2.15) and the equation (2.16), we get

$$x_{n+1} + y_{n+1} = x_n e^{r(1-x_n)} \leq \max_{x \in \mathbb{R}^+} \{ xe^{r(1-x)} \}$$  

Define $f(x) = xe^{r(1-x)}$, then $f'(x) = (1-rx)e^{r(1-x)}$ and $f(x)$ has critical points at $x = \frac{1}{r}$. Since $f'(x) > 0$ if $x < \frac{1}{r}$ and $f'(x) < 0$ if $x > \frac{1}{r}$, then $x = \frac{1}{r}$ is the maximal point of $f(x)$, i.e., $\max_{x \in \mathbb{R}^+} \{ f(x) \} = f(\frac{1}{r})$. Hence,

$$x_{n+1} + y_{n+1} = x_n e^{r(1-x_n)} \leq \max_{x \in \mathbb{R}^+} \{ xe^{r(1-x)} \} = f(\frac{1}{r}).$$  

Choose $M > f(\frac{1}{r}) = \frac{e^{r-1}}{r}$.

3.2. Boundary equilibria. For equations (2.15) and (2.16), we find two boundary equilibria;

$$(x, y) = (0, 0) \text{ and } (1, 0).$$
The Jacobian matrix of (2.15) and (2.16) is
\[
J := \begin{bmatrix}
\frac{f(x,y)}{x} - rf(x,y) & -af(x,y) \\
\frac{g(x,y)}{x} - rg(x,y) & af(x,y)
\end{bmatrix}
\]
where
\[
f(x,y) = xe^{r(1-x)-ay}, \quad g(x,y) = xe^{r(1-x)} [1 - e^{-ay}].
\]

(i) At the boundary equilibrium point (0, 0), Jacobian becomes
\[
J|_{(0,0)} = \begin{bmatrix}
e^r & 0 \\
0 & 0
\end{bmatrix}
\]
with eigenvalues \(\lambda_1 = e^r \geq 1\) and \(\lambda_2 = 0 < 1\). Hence if \(r > 0\), the boundary equilibrium point \((0,0)\) is a saddle which is stable on the y-axis and unstable on the x-axis.

If \(r = 0\), then we have \(\lambda_1 = 1\). The system reduces to
\[
x_{n+1} = x_ne^{-ay_n} = g_1(x_n, y_n, 0, a) \quad (1.2)
\]
\[
y_{n+1} = x_n[1 - e^{-ay_n}] = g_2(x_n, y_n, 0, a) \quad (1.3)
\]

**Lemma 3.1.** For equations (1.2) and (1.3) with initial conditions in the first quadrant \(Q^+\), the \(\Omega\)-limit set of all trajectories is \((x^*, 0)\) where \(x^* \geq 0\).

**Proof.** If \(x_0 > 0, y_0 > 0\), then from the positivity of the dynamical system, we know that \(0 < x_{n+1} < x_n\) for any \(n\). In addition \(0 < y_{n+1} < x_n\) for any \(n\). Since \(\{x_n\}\) is a bounded decreasing sequence, it has a limit \(x^*\) as \(n \to \infty\). By adding (1.2) and (1.3), we get
\[
x_{n+1} + y_{n+1} = x_n
\]
Therefore, \( \{y_n\} \) also has a limit \( y^* = 0 \). So eventually we have \( x_n \to x^*, y_n \to 0 \) as \( n \to \infty \). Biologically \( r = 0 \) implies that host’s reproduction rate is zero, and is attacked by a parasite. If the parasite is a specialist on the host, then it has to die in some time in the future since there is no enough food for it to survive.

From the equations (2.15) and (2.16), we have the Taylor expansion near \((x,y) = (0,0)\) as

\[
x_{n+1} = (1 + r)x_n [1 - rx_n - ay_n]
\]

(1.4)

\[
y_{n+1} = a(1 + r)y_n x_n [1 - rx_n]
\]

(1.5)

For \( r = 0 \), this becomes

\[
x_{n+1} = x_n [1 - ay_n]
\]

(1.6)

\[
y_{n+1} = ay_n x_n.
\]

(1.7)

Hence the whole line \( y = 0 \) becomes equilibria, i.e., without reproduction, the parasite dies and the host stays a constant eventually. ■

(ii) At the boundary equilibrium point \((1,0)\), the Jacobian matrix becomes

\[
J\big|_{(1,0)} = \begin{bmatrix}
1 - r & -a \\
0 & a
\end{bmatrix}
\]

(1.8)

with eigenvalues \( \lambda_1 = 1 - r \) and \( \lambda_2 = a \).

Again, \( y = 0 \) is an invariant manifold.

- If \( r = 2 \) and \( a \neq 1 \), the Taylor expansion of equations (2.15) and (2.16) gives
\[ u_{n+1} = (-1 - \gamma)u_n + \frac{2u_n^3}{3} = g(u_n, \gamma) \quad (1.9) \]

where \( \gamma = r - 2 \) and \( u_n = x_n - 1 \). Hence

\[
g(0, 0) = 0 \quad (1.10)
\]
\[
\frac{\partial g(u, \gamma)}{\partial u}\bigg|_{(0,0)} = -1 \quad (1.11)
\]
\[
\frac{\partial g^2(u, \gamma)}{\partial \gamma}\bigg|_{(0,0)} = 0 \quad (1.12)
\]
\[
\frac{\partial^2 g^2(u, \gamma)}{\partial u^2}\bigg|_{(0,0)} = 0 \quad (1.13)
\]
\[
\frac{\partial^2 g^2(u, \gamma)}{\partial u \partial \gamma}\bigg|_{(0,0)} \neq 0 \quad (1.14)
\]
\[
\frac{\partial^3 g^2(u, \gamma)}{\partial u^3}\bigg|_{(0,0)} \neq 0 \quad (1.15)
\]

Therefore, from the theorem by Wiggins (Wiggins, 2003), we have a period doubling bifurcation.

- If \( a = 1 \) and \( r \neq 0, 2 \), one dimension center manifold is given by

\[ v_{n+1} = (1 + \alpha)v_n - \frac{(\alpha + \gamma)v_n^2}{2} - \frac{v_n^3}{3} = g(v, \alpha) \quad (1.16) \]

where \( \gamma = r - 2, \alpha = a - 1 \) and \( v_n = y_n \). Hence

\[
g(0, 0) = 0 \quad (1.17)
\]
\[
\frac{\partial g(v, \alpha)}{\partial v}\bigg|_{(0,0)} = 1 \quad (1.18)
\]
\[
\frac{\partial g(v, \alpha)}{\partial \alpha}\bigg|_{(0,0)} = 0 \quad (1.19)
\]
\[
\frac{\partial^2 g(v, \alpha)}{\partial v^2}\bigg|_{(0,0)} = -\gamma \neq 0 \quad (1.20)
\]
\[
\frac{\partial^2 g(v, \alpha)}{\partial v \partial \alpha}\bigg|_{(0,0)} = 1 \quad (1.21)
\]
\[
\frac{\partial^3 g(v, \alpha)}{\partial v^3}\bigg|_{(0,0)} \neq 0 \quad (1.22)
\]
Therefore, from the theorem by Wiggins (Wiggins, 2003), we have a transcritical bifurcation.

- When \( r = 2 \) and \( a = 1 \), then we have the most degenerate case with the eigenvalues \( \lambda_1 = -1 \) and \( \lambda_2 = 1 \). And we will discuss this special case in the next section.

### 3.3. Codimension two bifurcation at the boundary equilibrium point.

At \( r = 2, a = 1 \), the eigenvalues of the boundary equilibrium \( (x, y) = (1, 0) \) become

\[
\lambda_1 = 1, \quad \lambda_2 = -1.
\]

The resulting bifurcation is a codimension two bifurcation.

**Proposition 3.2.** The system (2.15) and (2.16) near the boundary equilibrium \((1, 0)\) and in a neighborhood of the parameters \( r = 2, a = 1 \), can be transformed from original system up to third order into

\[
\begin{align*}
    u_{n+1} &= (-1 - \gamma)u_n - u_nv_n \\
    v_{n+1} &= (1 + \alpha)v_n - \frac{u_n^2 v_n}{2} - \frac{(\alpha + \gamma)v_n^2}{2} + \frac{2(\alpha - 2\gamma)u_n^3}{3} - \frac{v_n^3}{3}
\end{align*}
\]

(1.23)

(1.24)

where \( \alpha = a - 1, \gamma = r - 2, u_n = x_n - 1, v_n = y_n \).

**Proof.** See appendix Section 1 and 2 and reference (Kuznetsov, Meijer, & Van, 2004).

**Corollary 3.1.** When \( \alpha = 0, \gamma = 0 \), we have:

\[
\begin{bmatrix}
    u_{n+1} \\
    v_{n+1}
\end{bmatrix} :=
\begin{bmatrix}
    -u_n - u_nv_n \\
    v_n - \frac{v_n^3}{3} - \frac{u_n^2 v_n}{2}
\end{bmatrix}
\]

**Proposition 3.3.** Center manifold reduction for the system of (1.23) and (1.24):
(i) If $\gamma = 0, \alpha \neq 0$, then dynamics of the center manifold can be parameterized up to degree 3 as (1.9)

$$u_{n+1} = (-1 - \gamma)u_n + \frac{2u^3_n}{3} = g(u_n, \gamma)$$  \hspace{1cm} (1.25)

giving a period doubling bifurcation of equations (2.15) and (2.16).

(ii) If $\alpha = 0, \gamma \neq 0$, then the center manifold can be parameterized up to degree 3 as (1.16)

$$v_{n+1} = (1 + \alpha)v_n - \frac{(\alpha + \gamma)v^2_n}{2} - \frac{v^3_n}{3} = g(v_n, \alpha, \gamma)$$  \hspace{1cm} (1.26)

giving a transcritical bifurcation of equations (2.15) and (2.16).

In the equation (2.16), we see that $y = 0$ is an invariant manifold. But in the normal form by using the method in (Kuznetsov et al., 2004), $y = 0$ is not invariant. Since it is biologically meaningful to keep $y = 0$ invariant, we have to seek another normal form. Hence, by choosing another nonlinear transformations, we get:

**Proposition 3.4.** The system (2.15) and (2.16) near the boundary equilibrium $(1,0)$ and in a neighborhood of the parameters $r = 2, \alpha = 1$, can be transformed from original system up to third order into

$$u_{n+1} = (-1 - \gamma)u_n - u_nv_n + \frac{2u^3_n}{3}$$  \hspace{1cm} (1.27)

$$v_{n+1} = (1 + \alpha)v_n - \frac{u^2_nv_n}{2} - \frac{(\alpha + \gamma)v^2_n}{2} - \frac{v^3_n}{3}.$$  \hspace{1cm} (1.28)

where $\alpha = a - 1, \gamma = r - 2, u_n = x_n - 1, v_n = y_n$.

**Corollary 3.2.** When $\alpha = 0, \gamma = 0$, we have:

$$\begin{bmatrix} u_{n+1} \\ v_{n+1} \end{bmatrix} := \begin{bmatrix} -u_n - u_nv_n + \frac{2u^3_n}{3} \\ v_n - \frac{u^2_nv_n}{2} - \frac{v^3_n}{3} \end{bmatrix}$$
And from the equations (1.27) and (1.28), we see that the center manifold for the both cases \( \gamma = 0 \) or \( \alpha = 0 \) are trivial, i.e., they simply are \( v = 0 \) or \( u = 0 \). This implies that period doubling bifurcation (1.25) happens when \( \gamma = 0 \) and pitchfork bifurcation happens when \( \alpha = 0 \) are independent. Therefore codimension two bifurcation at the boundary equilibrium \((1,0)\) of our system is very simple, and there is no complicated heteroclinic structure as we should expect from (Kuznetsov et al., 2004). If we change the property that \( y = 0 \) is invariant to be not invariant by adding some positive constant \( c \) to (2.16), as

\[
\begin{align*}
    x_{n+1} &= x_n e^{r(1-x_n)-ay_n} \\
    y_{n+1} &= x_n e^{r(1-x_n)} \left[1 - e^{-(ay_n)}\right] + c.
\end{align*}
\]

Then from the mathematical analysis of (Kuznetsov et al., 2004), the system should have more complicated dynamics than our current model has.

All mathematical proofs of this section can be found in Appendix A Section 1 and Section 2.

4. Interior equilibria

Define \( f_1(y) = 1 - \frac{ay}{r} \) and \( f_2(y) = \frac{y}{e^{ay} - 1} \). Then the interior equilibrium points are exactly the intersection points of these two functions in the first quadrant \( Q^+ \). We can easily see that \( f_1(y) \) is a decreasing linear function since its slope is \( -\frac{a}{r} < 0 \). Now we are going to show that \( f_2(y) \) is also decreasing.

**Lemma 4.1.** \( f_2(y) = \frac{y}{e^{ay} - 1} \) is decreasing, and \( \lim_{y \to 0} f_2(y) = \frac{1}{a} \). In addition, \( \lim_{y \to \infty} f_2(y)' = -\frac{1}{2a} \).
Proof. Using the Taylor expansion on \( e^{ay} \), we have

\[
e^{ay} = \sum_{i=0}^{\infty} \frac{(ay)^i}{i!} = 1 + \sum_{i=1}^{\infty} \frac{(ay)^i}{i!}
\]

Therefore,

\[
f_2(y) = \frac{y}{e^{ay} - 1} = \frac{y}{\sum_{i=1}^{\infty} \frac{(ay)^i}{i!}} = \frac{1}{a + a \sum_{i=2}^{\infty} \frac{(ay)^{i-1}}{i!}}
\]

Since \( \frac{1}{a + a \sum_{i=2}^{\infty} \frac{(ay)^{i-1}}{i!}} \) is a decreasing function, then so is \( f_2(y) \), and \( \lim_{y \to 0} f(y) = \frac{1}{a} \).

We have,

\[
f_2(y)' = \frac{e^{ay} - 1 - ay e^{ay}}{(e^{ay} - 1)^2} \leq 0
\]

which implies that \( e^{ay} - 1 - ay e^{ay} \leq 0 \).

Since

\[
e^{ay} - 1 - ay e^{ay} = \sum_{i=1}^{\infty} \frac{(ay)^i}{i!} - ay \sum_{i=0}^{\infty} \frac{(ay)^i}{i!} = -\frac{ay^2}{2} + \sum_{i=3}^{\infty} \frac{(ay)^i}{i!} - \frac{(ay)^i}{(i-1)!}
\]

and

\[
(e^{ay} - 1)^2 = ay^2(1 + \sum_{i=2}^{\infty} \frac{(ay)^{i-1}}{i!})^2
\]

Therefore,

\[
f_2(y)' = \frac{e^{ay} - 1 - ay e^{ay}}{(e^{ay} - 1)^2} = \frac{-\frac{ay^2}{2} + \sum_{i=3}^{\infty} \frac{(ay)^{i-2}}{i!} - \frac{(ay)^{i-2}}{(i-1)!}}{a(1 + \sum_{i=2}^{\infty} \frac{(ay)^{i-1}}{i!})^2}
\]

Hence, \( \lim_{y \to 0} f_2(y)' = -\frac{1}{2a} \).


Proposition 4.1. If \( a = 1, r = 2, f_1(y) \) and \( f_2(y) \) are tangent at the boundary equilibrium \((1,0)\).
Proof. For \( a = 1 \) and \( r = 2 \), we have:

\[
f_1(y) = 1 - \frac{y}{2}, \quad f_2(y) = \frac{y}{e^y - 1}.
\]

Both \( f_1 \) and \( f_2 \) pass through the point \((1, 0)\). From Lemma 4.1, we can see that they have the same slope \(-\frac{1}{2}\) at the boundary equilibrium \((1, 0)\).

Lemma 4.2.

\[
f''_2(y) \geq 0, \quad f'_2(y) \in (-\frac{1}{2a}, 0), \quad \forall y > 0
\]

Proof. From the equation (1.31), we have

\[
f''_2(y) = \frac{ae^{ay}(-2e^{ay} + 2 + ay + e^{ay} + ay)}{(e^{ay} - 1)^3}
\]  \hspace{1cm} (1.32)

By using Taylor expansion, we can see that

\[f''_2(y) \geq 0.\]

Since,

\[
\lim_{y \to \infty} f'_2(y) = 0.
\]

Therefore,

\[f'(y) \in (-\frac{1}{2a}, 0).\]

Hence the intersection of \( f_1(y) \) and \( f_2(y) \) in the first quadrant \( Q^+ \) has 0, 1 or two interior equilibria:

(i) No interior equilibrium point. From Lemma 4.1 and 4.2, we can see that \( f_2(y) \) is concave down. And \( f_1(y) \) is a line with negative slope, hence there is no intersection if \( f_2(y) \) is above \( f_1(y) \). See Figure 3.1 (a).
(ii) Only one interior equilibrium point in $Q^+$

There are two situations:

- $a < 1$, when $f_1(y)$ is tangent to $f_2(y)$, there is one interior equilibrium.

- $a > 1$, See Figure 3.1 (b).

**Lemma 4.3.** For $a > 1$, there is only one intersection between $f_1$ and $f_2$ in $Q^+$.

**Proof:**

Since $a > 1$, then $f_2(0) < f_1(0)$. And also $f_2'(y) \in (-\frac{1}{2a}, 0), f_2''(y) \geq 0$ and $f_1'(y) = -\frac{a}{r}$, therefore there is only one intersection between $f_1$ and $f_2$ in $Q^+$.

(iii) Two interior equilibria. See Figure 3.1 (c).

If $(x_0, y_0)$ is an interior equilibrium point, then it should be on the line $f_1(y)$ and $f_2(y)$.

Hence, $0 < x_0 < \min\{1, \frac{1}{a}\}$ and $0 < y_0 < \frac{r}{a}$.

**4.1. Stability of the interior equilibria.** The Jacobian Matrix at the interior equilibrium point $E_i = (x_0, y_0)$ becomes

$$J_i = \begin{bmatrix}
1 - r x_0 & -a x_0 \\
(1 - r x_0)(e^{a y_0} - 1) & a x_0
\end{bmatrix} \quad (1.33)$$

Therefore the determinant and trace of the Jacobian matrix $J_i$ are:

$$\det(J_i) = a x_0 e^{a y_0} (1 - r x_0) \quad (1.34)$$

$$\text{trace}(J_i) = 1 - r x_0 + a x_0 \quad (1.35)$$
In addition, for \((x_0, y_0)\) to be an interior equilibrium point, it has to satisfy the two equations:

\[
r(1-x_0) = ay_0 \quad (1.36)
\]

\[
y_0 = x_0 (e^{ay_0} - 1) \quad (1.37)
\]

In order to study the stability of equilibria, we introduce the following standard Lemma (see p57 of Edelstein-Keshet, 1988).

Lemma 4.4. (Jury Test) Let \(A\) be a \(2 \times 2\) constant matrix. Both characteristic roots of \(A\) have magnitude less than 1 if and only if

\[
2 > 1 + \det(A) > |\text{trace}(A)|. \quad (1.38)
\]

Hence applying the Jury test we know that the interior equilibrium is stable if and only if:

\[
2 > 1 + \det(J) = 1 + ax_0 (1 - rx_0) (e^{ay_0} - 1) = 1 + a(1 - rx_0)y_0 > |\text{trace}(J)| = |1 - rx_0 + ax_0|.
\]

4.2. No codimension two bifurcation at the interior equilibria. We have at most three codimension two cases:

- \(\lambda_1 = 1\) and \(\lambda_2 = -1\);
- \(\lambda_1 = \lambda_2 = 1\);
- \(\lambda_1 = \lambda_2 = -1\)
(i) \( \lambda_1 = 1 \) and \( \lambda_2 = -1 \). Then we have the following four equations:

\[
det(J_i) = ax_0 e^{a y_0} (1 - r x_0) = -1 \tag{1.39}
\]

\[
trace(J_i) = 1 - r x_0 + a x_0 = 0 \Rightarrow x_0 = \frac{1}{r - a} \Rightarrow r > a \tag{1.40}
\]

\[
r(1 - x_0) = a y_0 \Rightarrow y_0 = \frac{r(1 - x_0)}{a} \Rightarrow y_0 = \frac{r(r - a - 1)}{a(r - a)} \Rightarrow r > a + 1 \tag{1.41}
\]

\[
y_0 = x_0 [e^{a y_0} - 1] \Rightarrow e^{a y_0} = \frac{y_0 + x_0}{x_0} \tag{1.42}
\]

By eliminating \( x_0, y_0 \) and \( a \), we get an equation in \( r \) with \( r > 2 \):

\[
\frac{r(r - 2)}{e^{r - 1}} = (r - 1)^2 \tag{1.43}
\]

Let \( f(r) = e^{r - 1} = e^{(r - 1)} = e^{r - 1} = e^{-1} \frac{1}{\xi} = g(r) = (r - 1)^2 = \xi^2 \). Then since \( r > 2 \), we have \( \xi > 1 \), and \( \xi - \frac{1}{\xi} > 0 \). Therefore

\[
F(r) = F(\xi + 1) = f(\xi + 1) - g(\xi + 1) \tag{1.44}
\]

Hence

\[
F(\xi)' = (1 + \frac{1}{\xi^2}) e^{\frac{\xi - 1}{\xi}} - 2 \xi \geq (1 + \frac{1}{\xi^2}) (1 + \xi - \frac{1}{\xi}) - 2 \xi = 1 - \xi + \frac{1}{\xi^2} - \frac{1}{\xi^3} \geq 0 \tag{1.46}
\]

In addition, the equality holds exactly when \( \xi = 1 \), i.e., \( r = 2 \). Hence when \( r > 2 \), we have \( F(r) > 0 \). Therefore, there is no fixed point satisfying all the conditions, i.e., there doesn't exist an interior equilibrium point with eigenvalues \( \lambda_1 = 1 \) and \( \lambda_2 = -1 \).
(ii) $\lambda_1 = 1$ and $\lambda_2 = 1$. Then we have the following four equations:

\[
\begin{align*}
\text{det}(J_1) &= ax_0e^{a y_0}(1-rx_0) = 1 \\
\text{trace}(J_1) &= 1 - rx_0 + ax_0 = 2 \Rightarrow x_0 = \frac{1}{a-r} \Rightarrow a > r \\
r(1-x_0) &= ay_0 \Rightarrow y_0 = \frac{r(1-x_0)}{a} \Rightarrow y_0 = \frac{r(a-r-1)}{a(a-r)} \Rightarrow a > r + 1 \\
y_0 &= x_0[e^{a y_0} - 1] \Rightarrow e^{a y_0} = \frac{y_0 + x_0}{x_0}
\end{align*}
\]

By eliminating $x_0$, $y_0$, and $a$, we get an equation in $r$

\[
\frac{r^2}{er+1} = \frac{(r+1)^2}{2r+1}
\]

Let $f(r) = e^{r+1}$, $g(r) = \frac{(r+1)^2}{2r+1}$, then

\[
F(r) = f(r) - g(r) \Rightarrow F'(r) \geq 0
\]

In addition, the equality holds exactly when $r = 0$. Hence when $r > 0$, we have $F(r) > 0$. Therefore, there is no fixed point satisfying all the conditions, i.e., there doesn’t exist an interior equilibrium point with eigenvalues $\lambda_1 = 1$ and $\lambda_2 = 1$. 

\[\text{Figure 4.22: Case one: } \lambda_1 = 1, \lambda_2 = -1\]

\[\text{Figure 4.23: Case two: } \lambda_1 = \lambda_2 = 1\]
(iii) \( \lambda_1 = -1 \) and \( \lambda_2 = -1 \). Then we have the following four equations:

\[
\det(J_i) = ax_0 e^{ay_0}(1 - rx_0) = 1 \tag{1.53}
\]

\[
\text{trace}(J_i) = 1 - rx_0 + ax_0 = -2 \Rightarrow x_0 = \frac{3}{r - a} \Rightarrow r > a \tag{1.54}
\]

\[
r(1 - x_0) = ay_0 \Rightarrow y_0 = \frac{r(1 - x_0)}{a} \Rightarrow y_0 = \frac{r(r - a - 1)}{a(r - a)} \Rightarrow r > a + 1 \tag{1.55}
\]

\[
y_0 = x_0[e^{ay_0} - 1] \Rightarrow e^{ay_0} = \frac{y_0 + x_0}{x_0} \tag{1.56}
\]

By eliminating \( y_0 \) and \( a \), we get an equation in \( r \) and \( x_0 \):

\[
r > 4 \tag{1.57}
\]

\[
a = \frac{r - 3r(r - 3)}{r - 4} = \frac{r^2 - 4r - 3r^2 + 9r}{r - 4} = \frac{r(5 - 2r)}{r - 4} \tag{1.58}
\]

Since \( a > 0 \), this implies \( r < \frac{5}{2} \), which it is a contradiction to the condition \( r > 4 \).

Therefore, there is no fixed point satisfying all the conditions, i.e., there doesn’t exist an interior equilibrium point with eigenvalues \( \lambda_1 = -1 \) and \( \lambda_2 = -1 \).

From the argument above we have the following theorem:

**Theorem 4.1.** The codimension two bifurcation happens at the boundary equilibrium \( (1,0) \) when \( r = 2 \) and \( a = 1 \).

4.3. **Codimension one: Neimark-Sacker bifurcation.** The condition for a Neimark-Sacker bifurcation are that \( \lambda \cdot \bar{\lambda} = 1 \) and \( \lambda \) is not a real number. Hence the interior equilibrium \( E_i = (x_0,y_0) \) should satisfy the following three equations:

\[
\det(J_i) = ax_0 e^{ay_0}(1 - rx_0) = 1 \Rightarrow e^{ay_0} = \frac{1}{ax_0(1 - rx_0)} \tag{1.59}
\]

\[
|\text{trace}(J_i)| = |1 - rx_0 + ax_0| \leq 2 \tag{1.60}
\]

\[
r(1 - x_0) = ay_0 \Rightarrow y_0 = \frac{r(1 - x_0)}{a} \tag{1.61}
\]

\[
y_0 = x_0[e^{ay_0} - 1] \Rightarrow e^{ay_0} = \frac{y_0 + x_0}{x_0} \Rightarrow \frac{y_0}{x_0} + 1 = \frac{r(1 - x_0)}{ax_0} + 1 = \frac{1}{ax_0(1 - rx_0)} \tag{1.62}
\]
From these equations, we get the following two equations describing the relationship between $x_0$, $a$ and $r$.

\[
det(J) = ax_0e^{a_0}(1-rx_0) = (r-rx_0+ax_0)(1-rx_0) = 1 \tag{1.63}
\]

\[
e^{a_0} = e^{r(1-x_0)} = \frac{r(1-x_0)}{ax_0} + 1 \tag{1.64}
\]

which gives the following:

\[
(r-rx_0+ax_0)(1-rx_0) = 1 \tag{1.65}
\]

\[
e^{r(1-x_0)} = \frac{r(1-x_0)}{ax_0} + 1 \tag{1.66}
\]

From the first equation, we can solve for $x_0$ in terms of $a$ and $r$ to get

\[
x_0 = \frac{-r^2 + a - r + \sqrt{r^4 + 2ar^2 - 2r^3 + a^2 - 6ar + 5r^2}}{2r(-r+a)} = f_1(r,a)
\]

or

\[
x_0 = \frac{-r^2 + a - r - \sqrt{r^4 + 2ar^2 - 2r^3 + a^2 - 6ar + 5r^2}}{2r(-r+a)} = f_2(r,a)
\]

Hence we have

\[
e^{r[1-f_1(r,a)]} = \frac{r[1-f_1(r,a)]}{af_1(r,a)} + 1
\]

or

\[
e^{r[1-f_2(r,a)]} = \frac{[1-f_2(r,a)]}{af_2(r,a)} + 1
\]

Therefore,

**Theorem 4.2.** A necessary condition for a Neimark-Sacker bifurcation to occur at an interior equilibrium point is

If

\[
e^{r[1-f_1(r,a)]} = \frac{r[1-f_1(r,a)]}{af_1(r,a)} + 1 \text{ and } |\text{trace}(J)| = |1-rf_1 + af_1| \leq 2
\]
If the necessary conditions for a Neimark-Sacker bifurcation are satisfied, then the solutions for the four equations (1.59), (1.60), (1.61) and (1.62) are the bifurcation curves for a Neimark-Sacker bifurcation in the parameters space \((a, r)\).

4.4. **Codimension one: period doubling bifurcation.** A period doubling bifurcation occurs when one of the eigenvalues \(\lambda_1\) is equal to \(-1\). Hence we have the following four equations:

\[
\begin{align*}
    r(1-x_0) &= ay_0 	o y_0 = \frac{r(1-x_0)}{a} \\
    y_0 &= x_0[e^{ay_0} - 1] 	o e^{ay_0} = \frac{y_0}{x_0} + 1 \\
    \det(J_i) &= ax_0e^{ay_0}(1 - rx_0) = \lambda_1\lambda_2 = -\lambda_2 \\
    \text{trace}(J_i) &= 1 - rx_0 + ax_0 = \lambda_1 + \lambda_2 = -1 + \lambda_2
\end{align*}
\]

From the last two equations, we get the equality:

\[
\det(J_i) + \text{trace}(J_i) = (ax_0 + ay_0)(1 - rx_0) + 1 - rx_0 + ax_0 = -1
\]

Therefore,

\[
[ax_0 + r(1 - x_0)][1 - rx_0] - (r - a)x_0 + 2 = 0
\]

Solving this equation for \(x_0\) in terms of \(r\) and \(a\), we get

\[
x_0 = \frac{2r - 2a + r^2 + \sqrt{r^4 + 4a^2 - 4r^2}}{2r(r - a)} = k_1(r, a)
\]

or

\[
x_0 = \frac{2r - 2a + r^2 - \sqrt{r^4 + 4a^2 - 4r^2}}{2r(r - a)} = k_2(r, a)
\]

Therefore,

\[
y_0 = \frac{r[1 - k_1(r, a)]}{a}, \text{ or } y_0 = \frac{r[1 - k_2(r, a)]}{a}
\]
Substituting the expressions for $x_0$ and $y_0$ into the equation $y_0 = x_0[e^{a_0y_0} - 1]$, we get the following relation for $a$ and $r$ when the system has period doubling bifurcation:

$$\frac{r[1 - k_1(r, a)]}{a} = k_1(r, a)[e^{r[1 - k_1(r, a)]} - 1]$$

or

$$\frac{r[1 - k_2(r, a)]}{a} = k_2(r, a)[e^{r[1 - k_2(r, a)]} - 1]$$

**Theorem 4.3.** A necessary condition for a period doubling bifurcation to occur at an interior equilibrium point is

$$\frac{r[1 - k_1(r, a)]}{a} = k_1(r, a)[e^{r[1 - k_1(r, a)]} - 1]$$

or

$$\frac{r[1 - k_2(r, a)]}{a} = k_2(r, a)[e^{r[1 - k_2(r, a)]} - 1]$$

If the necessary conditions for a period doubling bifurcation are satisfied, then the solutions for the four equations (1.67), (1.68), (1.69) and (1.70) are the bifurcation curves for a period doubling bifurcation in the parameters space $(a, r)$.

4.5. **Codimension one: saddle-node bifurcation.** Geometrically we see that a saddle-node bifurcation occurs when the nullcline $x = 1 - \frac{ay}{r}$ is tangent to the nullcline $x = \frac{y}{e^{ay} - 1}$ at the interior equilibrium point $E_i = (x_0, y_0)$. Let $b = \frac{a}{r}$. We have the following equations

$$x_0 = 1 - by_0 \quad \text{(1.71)}$$

$$x_0 = \frac{y_0}{e^{ay_0} - 1} \quad \text{(1.72)}$$

$$-b = \frac{\partial(\frac{y_0}{e^{ay_0} - 1})}{\partial y_0} = \frac{e^{ay_0} - 1 - ay_0e^{ay_0}}{(e^{ay_0} - 1)^2} \quad \text{(1.73)}$$
From the first two equations, we get

\[ 1 - by_0 = \frac{y_0}{e^{ay_0} - 1} \rightarrow e^{ay_0} = \frac{y_0}{1 - by_0} + 1 \]

Substituting this relation into the third equation, we have:

\[ -b = \frac{y_0}{1 - by_0} - ay_0 \left( \frac{y_0}{1 - by_0} + 1 \right) \left( \frac{y_0}{(1 - by_0)^2} \right) \rightarrow 1 - ay_0 + aby_0^2 - a + 2aby_0 - ab^2y_0^2 = 0 \]

Solve for \( y_0 \) in terms of \( b \) and \( a \), we get

\[ y_0 = \frac{-a + 2ab + \sqrt{a^2 - 4ab + 4a^2}}{2ab(b - 1)} = h_1(a,b) \]

or

\[ y_0 = \frac{-a + 2ab - \sqrt{a^2 - 4ab + 4a^2}}{2ab(b - 1)} = h_2(a,b) \]

Hence

**Theorem 4.4.** We have saddle node bifurcation at interior equilibrium point \( E_i = (x_0, y_0) \) if

\[ 1 - \frac{ah_1(r,a)}{r} = \frac{h_1(r,a)}{e^{ah_1(r,a)} - 1} \tag{1.74} \]

or

\[ 1 - \frac{ah_2(r,a)}{r} = \frac{h_2(r,a)}{e^{ah_2(r,a)} - 1} \tag{1.75} \]

**Theorem 4.5.** The saddle node bifurcation at the interior equilibrium point \( E_i = (x_0, y_0) \) happens when it has one eigenvalue with 1.

**Proof.** We have the following equalities in the case where the interior equilibrium point \( E_i = (x_0, y_0) \) has one eigenvalue \( \lambda_i = 1 \).
\[
\begin{align*}
    r(1 - x_0) &= ay_0 \quad y_0 = \frac{r(1 - x_0)}{a} \quad (1.76) \\
    y_0 &= x_0[e^{ay_0} - 1] \rightarrow e^{ay_0} = \frac{y_0}{x_0} + 1 \quad (1.77) \\
    \det(J_i) &= ax_0e^{ay_0}(1 - r x_0) = \lambda_1 \lambda_2 = \lambda_2 \quad (1.78) \\
    \text{trace}(J_i) &= 1 - rx_0 + ax_0 = \lambda_1 + \lambda_2 = 1 + \lambda_2 \quad (1.79)
\end{align*}
\]

By eliminating \(x_0\) and \(y_0\), we get the relationships (1.74) and (1.75). Hence getting the relation between \(r\) and \(a\) which is exactly the same in the case of saddle node bifurcation. □

5. Global stability of the boundary equilibrium

In (Wang, 2004), has studied the global stability of the following two dimensional model:

\[
\begin{align*}
    x_{n+1} &= x_ne^{r_{1-x_n}-a_1x_n-a_2y_n} \quad (1.80) \\
    y_{n+1} &= kx_n(1 - e^{-a_2y_n}) + y_ne^{-b_1-b_2y_n} \quad (1.81)
\end{align*}
\]

The biggest difference between the model studied by (Wang, 2004) and our model is that our model has an extra term \(e^{r[1-x_n]}\) in the population of parasite \(y_{n+1}\), which makes it more difficult to prove the global stability. In this section, we are going to show global stability of the boundary equilibrium \((1,0)\) for the system

\[
\begin{align*}
    x_{n+1} &= x_ne^{r[1-x_n]-a_1x_n} \quad (1.82) \\
    y_{n+1} &= x_ne^{r[1-x_n]}[1 - e^{-a_2y_n}] \quad (1.83)
\end{align*}
\]

when \(0 < r < 2 \) and \(0 < a < 1\).

For any initial condition \(x(0) > 0, y(0) \geq 0\), we have

\[
x_n + y_n = x_{n-1}e^{r[1-x_{n-1}]} \leq \frac{e^{r-1}}{r}
\]
for \( n \geq 1 \). By adding the equation (1.82) and the equation (1.83), we get

\[
x_{n+1} + y_{n+1} = x_n e^{r[1-x_n]} \tag{1.84}
\]

\[
\frac{y_{n+1}}{x_{n+1}} = e^{ay_n} - 1 \tag{1.85}
\]

\[
\frac{y_{n+1}}{y_n} = x_n e^{r[1-x_n]} \left[1 - e^{-ay_n}\right] < a x_n e^{r[1-x_n]} \tag{1.86}
\]

\[
\ln \frac{x_{n+1}}{x_n} = r[1 - x_n - \frac{ay_n}{r}] \tag{1.87}
\]

Define operator \( F_n := \frac{y_{n+1}}{y_n} < ax_n e^{r(1-x_n)} \), then with Equation (1.86) we have

\[
y_{n+m} = \prod_{i=n+1}^{n+m} \frac{y_i}{y_{i-1}} = \prod_{i=n}^{n+m-1} F_i < a^m \prod_{i=n}^{n+m-1} x_i e^{r(1-x_i)} \tag{1.88}
\]

By the equation (1.87), we have:

\[
\ln \frac{x_{n+m}}{x_n} = \sum_{i=n}^{n+m-1} \ln \frac{x_{i+1}}{x_i} = \sum_{i=n}^{n+m-1} r[1 - x_n - \frac{ay_n}{r}] \tag{1.89}
\]

\[
\sum_{i=n}^{n+m-1} r[x_n + \frac{ay_n}{r}] = mr - \ln \frac{x_{n+m}}{x_n} \tag{1.90}
\]

\[
\sum_{i=n}^{n+m-1} \frac{x_n + \frac{ay_n}{r}}{m} = 1 - \frac{\ln \frac{x_{n+m}}{x_n}}{mr} \tag{1.91}
\]

**Lemma 5.1.** If \( 0 < r < 2, 0 < a < 1 \), then it falls into the one of the following three cases

(i) \( 0 < r \leq a < 1 \).

(ii) \( \frac{ae^{r-1}}{r} < 1 \).

(iii) \( 0 < a < 1 < r < 2, \frac{ae^{r-1}}{r} \geq 1 \).

Note: case one and case two are not disjoint, i.e., has overlapping.
Proof

If $0 < r < 2$, $0 < a < 1$, then it belongs to:

$$0 < r \leq a \text{ or } 0 < a < r < 1 \text{ or } 0 < a < 1 = r, \text{ or } 0 < a < 1 < r < 2$$

If

$$0 < a < r < 1 \text{ or } 0 < a < 1 = r,$$

then

$$\frac{ae^{r-1}}{r} < \frac{a}{r} < 1$$

In the case $0 < a < 1 < r < 2$, then it is either $\frac{ae^{r-1}}{r} < 1$ or $\frac{ae^{r-1}}{r} \geq 1$. Hence, we have the result of the lemma. See figure 5.24, where the case one has regions 1 and 2, the case two has regions 2 and 3 and the case three has region 4.

Figure 5.24: Three cases for different values of $r$ and $a$

5.1. Persistence of the host. We need the persistence theory to show the global stable for our model. Hence, we are going to define some basic terminology which will be used in
Definition 5.1 (Isolated Invariant Set). A compact subset $N \subset \mathbb{R}^2$ is called an isolating neighborhood for the flow $\Phi_t$ if the maximal invariant set $S(N)$ in $N$ is contained in the interior of $N$. An invariant set $S$ of the flow $\Phi_t$ called an isolated invariant set if $S = S(N)$ is the maximal invariant set in some isolating neighborhood $N$.

Definition 5.2 (Weakly $\rho$-persistent). A semiflow $\Phi : J \times X \to X$ is called weakly $\rho$-persistent, if
\[
\lim_{t \to \infty} \sup \rho(\Phi(t, x)) > 0 \quad \forall x \in X, \rho(x) > 0.
\]

Definition 5.3 (Strongly $\rho$-persistent). A semiflow $\Phi : J \times X \to X$ is called Strongly $\rho$-persistent, if
\[
\lim_{t \to \infty} \inf \rho(\Phi(t, x)) > 0 \quad \forall x \in X, \rho(x) > 0.
\]

Definition 5.4 (Weakly uniformly $\rho$-persistent). A semiflow $\Phi : J \times X \to X$ is called weakly uniformly $\rho$-persistent, if there exists some $\epsilon > 0$ such that
\[
\lim_{t \to \infty} \sup \rho(\Phi(t, x)) > \epsilon \quad \forall x \in X, \rho(x) > 0.
\]

Definition 5.5 (Uniformly $\rho$-persistent). A semiflow $\Phi : J \times X \to X$ is called strongly uniformly $\rho$-persistent, if there exists some $\epsilon > 0$ such that
\[
\lim_{t \to \infty} \inf \rho(\Phi(t, x)) > \epsilon \quad \forall x \in X, \rho(x) > 0.
\]

Definition 5.6 (Point Dissipative). Let $\Phi : J \times X \to X$ be a semiflow. $\Phi$ is called point-dissipative (or ultimately bounded) if there exists a bounded subset $B$ of $X$ which attracts all points in $X$. 
Definition 5.7 (Repellor). $M \subset X$ is an repellor if there is a neighborhood $U$ of $M$ such that for all $x \notin M$, there exists $t_x \in J, t_x > 0$ such that $\Phi_t(x) \notin U, t \geq t_x$. $U$ is called a repellor neighborhood of $M$.

Definition 5.8 (Attractor). $\emptyset \neq M \subset X$ is an attractor if there is a neighborhood $U$ of $M$ that is attracted to $M$. $U$ is called an attractor neighborhood of $M$.

Definition 5.9 (Cyclic). Let $C, B \subset X_0$. $C$ is said to be chained to $B$ in $X_0$, written $C \rightarrow B$, if there exists a total trajectory $\varphi$ through some $x \notin C \cup B$ with $\varphi(-J \cup J) \subset X_0$ such that $\omega(x) \subset B$ and $\alpha(\varphi) \subset C$. A finite sequence $\{M_1, \ldots , M_k\}$ of subsets of $X_0$ is called cyclic if, after possibly renumbering, $M_1 \rightarrow M_1$ in $X_0$ or $M_1 \rightarrow M_2 \rightarrow \cdots \rightarrow M_j \rightarrow M_1$ in $X_0$ for some $j \in \{2, \ldots , k\}$. Otherwise it is called acyclic.

Define

$$X = \{(x, y) : x \geq 0, y \geq 0\}$$

$$X_{10} = \{(x, y) \in X, x > 0\}$$

$$\partial X_{10} = X \setminus X_{10}$$

Lemma 5.2. The system of equations (1.82) and (1.83) is uniformly persistent with respect to $(X_{10}, \partial X_{10})$.

Proof

We have shown that both $X$ and $X_{10}$ are positively invariant in Chapter four. In addition, $\partial X_{10}$ is relatively closed in $X$. For any positive solution of $(x_n, y_n)$ of (1.82) and (1.83), observe that

$$x_{n+1} < x_ne^{r(1-x_n)} \leq \frac{e^{r-1}}{r} = M.$$ (1.92)
This also applies to \( y_{n+1} \), hence \( y_{n+1} < M \) for \( n \) large enough. Therefore, both \( x_n \) and \( y_n \) are bounded and the system is point dissipative.

Let

\[
M_\theta = \{(x_0, y_0) : (x_n, y_n) \text{ satisfies (1.82) and (1.83) and } (x_n, y_n) \in \partial X_{10}, \forall n \geq 0\}
\]

We can check that

\[
M_\theta = \{(0, y) : y \geq 0\} = \partial X_{10}.
\]  

(1.93)

In addition \((0, 0)\) is the unique equilibrium in \( M_\theta \). Let \( W^s((0, 0)) \) to be the stable set for \((0, 0)\). We now want to show that

\[
W^s((0, 0)) \cap X_{10} = \emptyset.
\]

Suppose that it is not true. Then there exists a solution \((x_n, y_n)\) of the system with \( x_n > 0 \) such that

\[
(x_n, y_n) \rightarrow (0, 0) \text{ as } n \rightarrow \infty.
\]  

(1.94)

Then for large \( n \), by the equation (1.82) we have

\[
x_{n+1} > x_ne^{r/2}.
\]

Since \( r > 0 \), it follows that \( x_n \rightarrow \infty \) as \( n \rightarrow \infty \). Therefore, we have a contradiction. Note that every orbit in \( M_\theta \) tends to \((0, 0)\) as \( n \rightarrow \infty \). This shows that \((0, 0)\) is an isolated invariant set in \( X \) and \((0, 0)\) is acyclic in \( M_\theta \). By (Thieme, 1993) and (Hirsch, Smith, & Zhao, 2001) for a stronger repelling property of \( \partial X_{10} \), we conclude that \( \partial X_{10} \) repels uniformly the solutions of system (1.82) and (1.83) with positive \( x_n \). It follows that there is an \( c > 0 \) such that \( x_n > c \) for \( n \) large enough.
Theorem 5.1. There exists \( c > 0 \), such that for any \( x_0 > 0 \) the following inequalities hold

\[
c < x_n < \frac{e^{r-1}}{r}.
\] (1.95)

Proof. Obvious consequence of Lemma 5.2.

5.2. First case. The first case is \( 0 < r \leq a < 1 \). From equation (1.88), we can see that:

\[
\frac{y_{n+m}}{y_n} < a^m \prod_{i=n}^{n+m-1} x_i e^{r(1-x_i)}
\] (1.96)

\[
= a^m \prod_{i=n}^{n+m-1} [x_{i+1} + y_{i+1}]
\] (1.97)

By the inequality

\[
\prod_{i=1}^{m} F_i \leq \left( \sum_{i=1}^{m} \frac{F_i}{m} \right)^m
\] (1.98)

we have the following inequalities:

\[
\frac{y_{n+m}}{y_n} < a^m \prod_{i=n}^{n+m-1} [x_{i+1} + y_{i+1}]
\] (1.99)

\[
= a^m \left( \sum_{i=n+1}^{n+m} \frac{x_i + y_i}{m} \right)^m
\] (1.100)

\[
< a^m \left( \sum_{i=n+1}^{n+m} \left[ \frac{x_i + ay_i}{m} \right] \right)^m
\] (1.101)

Using Equation (1.91), we get

\[
\frac{y_{n+m}}{y_n} < a^m \left( 1 - \frac{\ln x_{n+1}}{x_{n+1} \frac{r}{m}} \right)^m
\] (1.102)

By theorem 5.1, we know that \( 0 < c < x_n < \frac{e^{r-1}}{r} \), then there exists \( m \) big enough, such that
\[ a \left( 1 - \frac{\ln \frac{x_{n+m+1}}{x_{n+1}}}{mn} \right) = \eta < 1 \quad (1.103) \]

Therefore,

\[ \frac{y_{n+m}}{y_n} < \eta^m \quad (1.104) \]
\[ y_{n+m} < y_n \eta^m \quad (1.105) \]
\[ y_n < y(0) \eta^n \quad (1.106) \]

Hence

\[ 0 \leq \lim_{n \to \infty} y_n < \lim_{n \to \infty} y(0) \eta^n = 0 \quad (1.107) \]

Therefore,

\[ \lim_{n \to \infty} y_n = 0. \]

5.3. Second case. From the equation (1.86), we have the following:

\[ y_{n+1} = x_n e^{r[1-x_n]} \frac{[1 - e^{-\eta y_n}]}{y_n} \]
\[ < a x_n e^{r[1-x_n]} y_n \quad (1.108) \]
\[ < ae^{r-1} y_n \quad (1.109) \]
\[ < \frac{ae^{r-1}}{r} y_n \quad (1.110) \]
\[ < \left( \frac{ae^{r-1}}{r} \right)^{n-1} y(1) \quad (1.111) \]

Hence,

\[ \lim_{n \to \infty} y_n = \lim_{n \to \infty} \left( \frac{ae^{r-1}}{r} \right)^{n-1} y(1) = 0 \quad (1.112) \]
5.4. Third case.

**Proposition 5.1.** If $0 < a < 1 < r < 2$ and $y_n \geq 1$, then

$$y_{n+1} < 1$$

with initial condition such as:

$$x_0 > 0, \quad y_0 \geq 0$$

**Proof.** From the equation (1.84),

$$x_n + y_n = x_{n-1}e^{r(1-x_{n-1})} \leq \frac{e^{r-1}}{r}$$  \hspace{1cm} (1.113)

Since $y_n > 1$, then

$$x_n < \frac{e^{r-1}}{r} - 1 \leq 0.36 \Rightarrow x_ne^{r(1-x_n)} \leq 1.294$$

Therefore,

$$y_{n+1} = x_ne^{r(1-x_n)}(1 - e^{-a\cdot y_n})$$  \hspace{1cm} (1.114)

$$\leq x_ne^{r(1-x_n)}(1 - e^{r-1/r})$$ \hspace{1cm} (1.115)

$$\leq 1.294 \times 0.7432 < 1$$ \hspace{1cm} (1.116)

**Proposition 5.2.** If $0 < a < 1 < r < 2$ and $y_n < 1$, then

$$y_{n+1} < 1$$

with initial condition such as:

$$x_0 > 0, \quad y_0 \geq 0$$
Proof. Since \( a < 1 \) and \( y_n < 1 \), then we have \( ay_n < 1 \), hence:

\[
1 - e^{-ay_n} < 1 - e^{-1}.
\]

\[
y_{n+1} = x_n e^{r(1-x_n)} [1 - e^{-ay_n}]
\]

\[
\leq \frac{e}{2} [1 - e^{-1}] < 0.86 < 1
\]

(1.117)

(1.118)

Therefore, for any \( k > n \), we have the following:

\[
y(k) < 1.
\]

Recall that:

\[
f_1(y) = 1 - \frac{ay}{r}, f_2(y) = \frac{y}{e^a - 1}
\]

Then we want to show that if \( r < 2 \), then \( f_2(y) - f_1(y) > 0 \) for any \( y \geq 0 \). Define

\[
F(y) = f_2(y) - f_1(y) = \frac{y}{e^a - 1} + \frac{ay}{r} - 1 = \frac{y + \frac{ay}{r} (e^{ay} - 1) - (e^{ay} - 1)}{e^{ay} - 1}
\]

Using a Taylor expansion, we have the following equality:

\[
F(y) = \frac{y + \frac{ay}{r} \sum_{i=1}^{\infty} \frac{(ay)^i}{i!} - \sum_{i=1}^{\infty} \frac{(ay)^i}{i!}}{e^{ay} - 1}
\]

Hence,

\[
F(y) = \frac{y - ay + \sum_{i=2}^{\infty} \frac{(ay)^i}{r(i-1)!} - \sum_{i=2}^{\infty} \frac{(ay)^i}{i!}}{e^{ay} - 1}
\]

\[
= \frac{(1-a)y + \sum_{i=2}^{\infty} \frac{(ay)^i}{r(i-1)!} - \frac{(ay)^i}{i!}}{e^{ay} - 1}
\]

\[
= \frac{(1-a)y + \sum_{i=2}^{\infty} \frac{(ay)^i}{r!} (i-r)}{e^{ay} - 1}
\]
Since we already assumed that $a < 1$, and $r < 2$, we have $(1 - a)y > 0$ and $(i - r) > 0$ for any $i \geq 2$ and $y > 0$. Therefore,

$$F(y) > 0, y \in R^+$$

In addition, from Lemma 4.1, we know that,

$$\lim_{y \to o} F(y) = \lim_{y \to o} f_2(y) - f_1(y) = \frac{1}{a} - 1 > 0$$

since $a < 1$. Thus we have

$$F(y) > 0, y \geq 0.$$ 

Therefore, we do not have any interior equilibrium points for our discrete dynamical system, and the only equilibrium points are

$$(x, y) = (0, 0) \text{ and } (x, y) = (1, 0)$$

We can check their local stability by looking at their Jacobian matrix (1.1) and (1.8). Hence (0, 0) is a saddle whenever $r > 0$. In addition, since $|1 - r| < 1$ and $0 < a < 1$, the boundary equilibrium point $(1, 0)$ is locally stable. According to the discussion in the section, we can conjecture that

**Conjecture 5.1.** If $0 < a < 1 < r < 2$, then

$$\lim_{n \to \infty} x_n = 1, \lim_{n \to \infty} y_n = 0$$

for any initial condition $x_0 > 0, y_0 \geq 0$.

6. **Stability and bifurcation**

6.1. **Stability of the synchronized steady state.** In this section, we study the stability of the synchronized steady state. Model (4.1) and (4.2) at the steady state $(P, H)$ has the
Jacobian matrix

\[
J_{(P,H)} = \begin{bmatrix}
1 - r_P & -a_P \\
(1 - r_P)(e^{a_H} - 1) & a_P
\end{bmatrix}
\]  

(1.119)

with eigenvalues

\[
\lambda_1 = \frac{a_P + 1 - r_P + \sqrt{a^2 P^2 + 2 a_P - 2 r P^2 a + 1 - 2 r P + r^2 P^2 - 4 a_P e^{a_H} + 4 a P^2 r e^{a_H}}}{2},
\]

and

\[
\lambda_2 = \frac{a_P + 1 - r_P - \sqrt{a^2 P^2 + 2 a_P - 2 r P^2 a + 1 - 2 r P + r^2 P^2 - 4 a_P e^{a_H} + 4 a P^2 r e^{a_H}}}{2}.
\]

The Jacobian matrix of the coupled system (4.5)-(4.8) can be represented as

\[
J_{P(P,H,P,H)} = \begin{bmatrix}
1 - r_P & -a_P & 0 & 0 \\
(1 - r_P)(e^{a_H} - 1) & a_P & 0 & 0 \\
0 & 0 & 1 - r_P & -a_P \\
0 & 0 & (1 - r_P)(e^{a_H} - 1) & a_P
\end{bmatrix}
\]

with eigenvalues

\[
\lambda_1 = \frac{h(P) + \sqrt{k(P,H)}}{2},
\]

\[
\lambda_2 = \frac{h(P) - \sqrt{k(P,H)}}{2},
\]

\[
\lambda_3 = \frac{h(P) - 2 a_P l + \sqrt{k(P,H) + s(P,H,l)}}{2},
\]

and

\[
\lambda_4 = \frac{h(P) - 2 a_P l - \sqrt{k(P,H) + s(P,H,l)}}{2}
\]

where

\[
h(P) = a_P + 1 - r_P,
\]
\[ k(P, H) = a^2P^2 + 2aP - 2rP^2a + 1 - 2rP + r^2P^2 - 4aPe^{aH} + 4aP^2re^{aH} \] and

\[ s(P, H, l) = 4Pal(-aP + Pal + rP - 1 - 2Pre^{aH} + 2e^{aH}). \]

**Theorem 6.1.** If the model (4.1) and (4.2) has a stable steady state at \((P, H)\), then the synchronized steady state \((P, H, P, H)\) of the coupled system (4.5)-(4.8) is stable if

\[ 2 > |h(P) - 2Pal| > 1 + (h(P) - 2Pal)^2 - k(P, H) - s(P, H, l). \] (1.120)

**Remark:** This theorem shows that even if the original single patch model has a steady state, the coupled two patch model needs the additional condition (1.120) to keep the stability of the synchronized steady state. It is possible that for some values of \(l\) the synchronized steady state becomes unstable hence the coupled system can possibly have more complicated dynamics. It seems that two-patch spatial structure can destabilize the system. However, if the barrier \(l\) is small enough, then the two-patch model mainly behaves like two independent patches.

### 6.2. Proof of Theorem 3.3.

**Proof.** Assume the map \(F(U)\) undergoes a period doubling bifurcation at \((U, l^*)\), then when \(l > l^*\), the map \(F(U)\) has period two solutions, i.e., \(U = F(F(U))\) has two solutions \(U^I\) and \(U^H\) such that \((P^I, U^I, P^H, U^H)\) is a steady state of the system (4.9)-(4.12) with \(U^I = F(U^H)\) and \(U^H = F(U^I)\) and \(P^I \neq P^H, U^I \neq U^H\). We need to show that the map \(F(U)\) satisfies the conditions of a period doubling bifurcation at \((U, l^*)\):

(i) \(F(U^*) = U^*\) implies that

\[ \frac{(1 - l)U^*}{l} + \frac{(2l - 1)f(U^*)}{l} = U^* \Rightarrow f(U^*) = U^*. \]
(ii) \( \frac{\partial F(U)}{\partial U}|_{U=U^*} = -1 \), i.e.,

\[
\frac{\partial F(U)}{\partial U} = \frac{1}{l} + (2 - \frac{1}{l}) \frac{\partial f(U)}{\partial U}|_{U=U^*} = -1
\]

which implies

\[
\frac{\partial f(U)}{\partial U}|_{U=U^*} = \frac{1}{1 - 2l}
\]

(1.121)

Since \( 0 < l < 1 \), the range of \( \frac{1}{1 - 2l} \) is \((-\infty, -1)\) and \((1, \infty)\). Then there exists \( l^* \) such that the equality (1.121) holds if we choose the parameter region \((r, a)\) such that

\[|\frac{\partial f(U)}{\partial U}|_{U=U^*}| > 1.\]

(iii) \( F_l(U)F_{UU}(U) + 2F_{Ul}(U) \neq 0 \)

\[
F_l(U) = -\frac{U - f(U)}{l^2} \Rightarrow F_l(U)|_{U=U^*} = 0
\]

(1.122)

\[
F_{Ul}(U) = -\frac{1 - \frac{\partial f(U)}{\partial U}}{l^2} \Rightarrow F_{Ul}(U)|_{U=U^*, l=l^*} = \frac{2}{l(1 - 2l)} \neq 0
\]

(1.123)

Therefore, \( F_l(U)F_{UU}(U) + 2F_{Ul}(U)|_{U=U^*, l=l^*} = \frac{2}{l(1 - 2l)} \neq 0 \)

(iv) \( c = -2F_{UUU}(U) - 3(F_{UU}(U))^2 \neq 0 \)

\[
F_{UU}(U) = \frac{(2l - 1)f_{UU}(U)}{l}
\]

(1.124)

\[
F_{UUU}(U) = \frac{(2l - 1)f_{UUU}(U)}{l}
\]

(1.125)

Since \( 2f_{UUU}(U) + 3\frac{2l-1}{l}(f_{UU}(U))^2|_{U=U^*} \neq 0 \), then \( c = -2F_{UUU}(U) - 3(F_{UU}(U))^2|_{U=U^*} = -2f_{UUU}(U) - 3\frac{2l-1}{l}(f_{UU}(U))^2|_{U=U^*} \neq 0 \)


