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Topological Characterization of Extinction in a Coupled Ricker Patch Model

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Topological Characterization of Extinction in a Coupled Ricker Patch Model

A thesis submitted in partial fulfillment of the requirement for the degree of Bachelor of Science in Mathematics from The College of William and Mary

by

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Accepted for Honors

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Undergraduate Honors Math Project
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Acknowledgments

This section is reserved for the many people who have helped in the creation of this thesis. A separate section gives proper attention to funding sources.

The math department at William & Mary has been very influential in my life for the past four years. When I was forced to take my first math class as a freshman, I hated the subject of mathematics. By the middle of my sophomore year I was converted and became a math major. By the end of my sophomore year I was involved in research which has culminated in this honors project. Such a feat could only have happened in an institution whose faculty are devoted to both teaching and research.

Mostly, I need to thank my advisor Sarah Day who has invested much time, energy, and effort. She has allowed me to attend summer schools, conferences, and countless lectures. She allowed me to use her laptop, workstation, and was a faculty sponsor so that I could obtain a user account on SciClone, William & Mary’s computing cluster. I cannot thank her enough for the countless hours spent in her office talking about mathematics.

I also thank my other three committee members who were chosen because of their help in this project. I took Numerical Analysis I and II from Michael Lewis who has been a valuable resource for questions regarding programming. I took Applied Math I and II from Junping Shi who has organized many of the conferences I have attended. I took both Population Dynamics and Modeling and Random Walks in Biology from Leah Shaw who helped me turn a class project into a portion of this thesis. Also, these four committee members were faced with the daunting task of proofreading this thesis. They found many errors; however, any that remain are entirely mine.
Attributions

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Abstract

Ecologists use Ricker patch models to study meta-population dynamics for populations undergoing growth and dispersal in a patchy environment. This project uses a modified model in which patch-wise extinction thresholds are used to model local extinction events. Computational homology is used to measure shifts in spatial patterns as extinction occurs and to quantify the ways in which dispersal rates affect pattern formation and degradation. Numerical simulations for certain parameters exhibit a decoupling of the system into small regions with periodic dynamics prior to extinction. Lastly, the existence of certain stable periodic orbits which affect population robustness are rigorously proven to exist.
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Chapter 1

Introduction

It is common for biological populations to exist in groups or colonies that are localized around set geographical structures such as forests, lakes, parks, fields, or even suburban yards. Although each individual group interacts primarily within its set region, some portion of the population may disperse to neighboring regions. Ecologists have studied ways to model these types of populations for several decades. A common approach is to use coupled patch models. Every model has its own method for predicting how the population will grow and develop in time; however, most coupled patch models have two main components, (1) equations governing growth within a patch and (2) equations describing the movement of individuals between patches. This project uses a mathematical tool called computational homology to quantify how a population’s spatial pattern changes in time. One particular focus in this project is on shifts in population patterns during global extinction events.

An early investigation of dispersal, or movement of individuals between patches,
revealed that high dispersal can have a stabilizing effect on the population, perhaps making it more tolerant of habitat destruction and less susceptible to extinction \cite{5,6}. Dispersal may also lead to self-synchronization or the formation of characteristic spatial patterns \cite{14}. This stems from what is referred to as the rescue effect, which occurs when extinct patches are reseeded by individuals entering from neighboring patches. Some researchers have noticed that the spatial structure, or topology, of density patterns seems to change in a significant and sometimes characteristic manner prior to extinction \cite{11}. Scheffer, et al. provide examples of shifting patterns in desert vegetation, lakes (which are drawn toward alternative attractors), rangelands, and fisheries. Field data gathered by Rietkerk et al. shows how desert plants tend to clump together and display ‘spotty’ patterns (shown in figure 1.1 panel D) prior to extinction \cite{10}. The main goal of this project is to mathematically model and measure such changes in spatial patterns as a species is driven toward extinction.

The model studied in this project is built on a spatial cubic grid where each grid element is referred to as a patch. On each patch the population experiences a growth phase modeled using a Ricker growth function which is a discrete density dependent nonlinear mapping that exhibits chaotic dynamics for some parameter values. After the growth phase, local patch populations disperse to neighboring patches at a specified dispersal rate. If after the dispersal phase the patch population is below a critical local extinction value then population abundance on that patch is set to zero. At each time step of the simulation a picture of the population’s pattern is created by thresholding the population abundance in each grid patch; if a patch’s population is nonzero then color the patch light blue and if it is zero then color the patch dark blue. More information about these governing equations and the thresholding procedure is provided in Chapter \cite{2}.

Computational homology is used to study connectivity properties of patterns \cite{3} and has been applied to the study of polycrystals \cite{15}, convection currents \cite{9}, and...
and as a method for quantifying spatial temporal chaos [4]. Here, computational homology is used to measure the thresholded spatial pattern at each time step.

In this model, topological transitions have been observed and quantified as extinction events are neared for many different parameter sets in both deterministic and stochastic simulations. Chapter 3 presents the corresponding sample results. Initial simulations suggest the existence of a stable, low dimensional subsystem that appears during the decoupling the model experiences before extinction. A proof that a stable period 2 orbit exists in the subsystem is presented in chapter 4. Simulations suggest that stable periodic orbits of this type could have a strong influence on the smallest global extinction threshold for the system.
Chapter 2

Dynamical Systems Terminology

This chapter has two main goals. The first is to define dynamical systems terminology used throughout this paper and to familiarize the reader with the one-dimensional Ricker Map. The Ricker map will serve as the basic building block for the system of coupled patches presented as our model. The second goal is to define cubical homology as it is used in this project and to explain how it can serve as a valuable tool for studying the high-dimensional coupled patch system.

Proper acknowledgment should be given to three textbooks from which the majority of terms and definitions are taken. Many dynamical systems terms are either taken from Chaos by Alligood, Sauer, and Yorke [1] or from Nonlinear Dynamics and Chaos by Strogatz [12]. Many definitions concerning algebraic topology or computational homology are taken from Computational Homology by Kaczynski, Mischaikow and Mrozek [8].

2.1 One-Dimensional Ricker Map

The one-dimensional Ricker model is initialized with a value, \( p(0) \), which is interpreted as the abundance, or total population size, at time 0. For a discrete time step, \( k = 0, 1, 2, \cdots \), the population value at the next time step, \( k + 1 \), is calculated as

\[
p(k + 1) = f(p(k)).
\]

The nonlinear map \( f : \mathbb{R} \rightarrow \mathbb{R} \) is defined to be

\[
f(p(k)) = rp(k)e^{-p(k)}, \tag{2.1}
\]

where \( r \in \mathbb{R} \) is a fixed parameter which is interpreted as the fitness of the environment. For example, if we were to model a deer population then a prairie would have a higher fitness value than an inner city. Fixed points of this map are found
by setting the output abundance to the input abundance
\[ p(k + 1) = rp(k)e^{-p(k)}. \tag{2.2} \]

The solution \( p(k) = 0 \) is the trivial, or extinction, fixed point. The only other solution to equation (2.2) is the non-trivial fixed point

\[ p_* = \ln r. \tag{2.3} \]

**Definition 2.1.1.** The forward trajectory of a point \( x \) under the map \( f \) is the sequence \((x, f(x), f^2(x), ..., f^j(x))\) where \( j \in \mathbb{Z}^+ \). The orbit of \( x \) under \( f \) is the collection of points \( \{f^j(x) : j \in \mathbb{Z}^+\} \).

**Definition 2.1.2.** A fixed point, \( p_* \), is said to be attracting if points sufficiently close to \( p_* \) are mapped toward \( p_* \). That is, there exists some \( \epsilon > 0 \) such that \( f^n(x) \rightarrow p_* \) whenever \( ||p_* - x|| < \epsilon \). A fixed point is unstable if no such neighborhood exists.

**Theorem 2.1.3.** Let \( p_* \) be a fixed point of a smooth map \( f : \mathbb{R} \rightarrow \mathbb{R} \). Then if \( |f'(p_*)| < 1 \), \( p_* \) is stable.

**Proof.** By the definition of a derivative,
\[ \lim_{x \rightarrow p_*} \frac{|f(x) - f(p_*)|}{|x-p|} = |f'(p_*)|, \]
and we are given that \( |f'(p_*)| < 1 \). Let \( a \) be any number between \( |f'(p_*)| \) and 1. Then there is a neighborhood for some \( \epsilon > 0 \) so that for points \( x \in N_\epsilon(p_*) \setminus \{p_*\} \),
\[ \frac{|f(x) - f(p_*)|}{|x-p|} \leq a. \]
That is \( f(x) \) is closer to \( p_* \) than \( x \) by at least a factor of \( a \) (which is less than 1). This implies two things: First, if \( x \in N_\epsilon(p_*) \) then \( f(x) \in N_\epsilon(p_*) \). Repeating this argument will produce the same result for \( f^2(x), f^3(x) \), and so forth. Second, it follows that
\[ |f^j(x) - p_*| \leq a^j|x - p_*| \]
for all \( j \geq 1 \). Thus \( p_* \) is stable. \( \square \)

**Definition 2.1.4.** Let \( f : \mathbb{R} \rightarrow \mathbb{R} \). We call \( p \) a periodic point of period \( k \) if \( f^k(p) = p \). If \( k \) is the smallest such positive integer then \( k \) is the minimal period. The orbit of \( p \) (which consists of \( k \) points) is called a periodic orbit of period \( k \). The abbreviated forms period-k point and period-k orbit are frequently used.


2.2 Coupled Ricker System

In ecological modeling it is sometimes desired to model populations on more than one environmental patch. This type of modeling is useful in situations where a biological population falls victim to habitat fragmentation or has distinct geographical barriers within the area the population inhabits. For this project, an \( n \times n \) spatial grid is constructed; call it \( \mathcal{G} \).

\[
\mathcal{G} = \mathcal{G}_{n,n} = \{ G_{i,j} = [i, i + 1] \times [j, j + 1] \mid i \leq n, j \leq n \}.
\]

Each point on this grid is a one-dimensional Ricker map and is coupled with its codimension one neighbors resulting in \( n^2 \) coupled equations.

**Definition 2.2.1.** The codimension of two patches is the dimension of the intersection of the two patches.

The local population abundance is stored in a population matrix, \( P \in \mathbb{R}^{n \times n} \), where \( P_{i,j}(k) \) is the population on the \( i^{th}, j^{th} \) patch, \( G_{i,j} \), at (discrete) time step \( k \). We now define \( f : \mathbb{R}^{n^2} \times \mathbb{R}^{n^2} \) modeling how a population abundance configuration \( P \) is mapped to a population abundance configuration \( f(P) \) after one time step.

We now have

\[
P(k + 1) = f(P(k)).
\]

Notationally, we write \( P_{i,j}(k + 1) = f_{i,j}(P(k)) \) where \( f_{i,j}(P(k)) \) is computed according to

\[
P'_{i,j}(k) = R_{i,j}P_{i,j}(k)e^{-P_{i,j}(k)} \quad (2.4)
\]

\[
f_{i,j}(P(k)) = (1 - d)P'_{i,j}(k) + \frac{1}{4}d(P'_{i-1,j}(k) + P'_{i+1,j}(k) + P'_{i,j-1}(k) + P'_{i,j+1}(k)), \quad (2.5)
\]

where \( R \) is the corresponding \( n \times n \) matrix of fitness values so \( R_{i,j} \) is the fitness parameter value of patch \( G_{i,j} \), the dispersal rate \( 0 \leq d \leq 1 \) is the fraction of individuals born in one patch that migrate to one of the four codimension one neighboring patches, and \( P'_{i,j}(k) := 0 \) for \( (i, j) \notin [1, n]^2 \).

In practice, the fitness parameter matrix, \( R \), is assigned values chosen between 5 and 25 and it is common for these values to be the same for all patches in \( \mathcal{G} \). Dispersal values are sometimes drawn from a normal distribution centered at \( d \in [0, 0.5] \) and whose standard deviation is varied.
2.3 Thesholding

When the simulation is iterated forward in time it has a high-dimensional state space $P(k) \in \mathbb{R}^{n \times n}$. The goal is to measure differences in spatial dispersal patterns. For this endeavor both a method relating numerical population values in $P$ to spatial locations stored in $G$ and a mechanism for converting numerical data to a dispersal pattern are required. In this section thesholding is presented as a natural method for reducing the dimensionality of simulation data that still preserves basic geometric features.

It is useful to think of simulation data as belonging to the set $P \times [0, T]$ where $T$ is the number of time steps in the simulation. Bear in mind that by construction $G$ is a finite collection of patches and, because experiments are performed \textit{in silico}, $T$ is finite.

\textbf{Definition 2.3.1.} An elementary interval is a closed interval $I \subset \mathbb{R}$ of the form

$I = [l, l + 1]$ or $I = [l] := [l, l]$

for some $l \in \mathbb{Z}$. The interval $[l, l + 1]$ is nondegenerate and the interval $[l] := [l, l]$ is degenerate. An elementary cube $Q$ is a finite product of $j$ elementary intervals where $j$ is the dimension of the ambient space. The collection of all elementary cubes with $k$ nondegenerate intervals is called the set of $k$-cubes and denoted $K_k$. A cubical set is a finite collection of elementary cubes (all in the same ambient space).

Using this definition of an elementary cube each patch $G_{i,j}$ is treated as an elementary cube. \textit{Thesholding} is used as a simple process by which numerical simulation data can be converted into binary objects.

\textbf{Definition 2.3.2.} At a fixed time step, given a threshold $\varsigma \in \mathbb{R}$, the thesholded image, $P_\varsigma$, is the cubical set

$P_\varsigma = \{[i, i + 1] \times [j, j + 1] \in G | P_{i,j} > \varsigma\}$  \hspace{1cm} (2.6)

thus the image $P_\varsigma$ is the collection of all elementary cubes in $G$ whose corresponding local abundance is above the threshold value $\varsigma$.

$P_\varsigma$ is abbreviated as $P$ when context renders the threshold and time step either clear or irrelevant. Patches in this model are coupled in such a way that there is a strong spatial biological interpretation of local abundance values stored in $P$. Patches are arranged in the spatial grid $G$ and through equation (2.5) populations experience dispersal with codimension one neighbors. Thus patches that are close together in $G$ are coupled together through dispersal. As the simulation is iterated
numerical values on patches undergo growth and dispersal. Thresholding generates a two-dimensional picture which resembles the model population’s spatial configuration. More importantly, after thresholding, data are reduced to a collection of binary objects that have clear boundaries and edges. The importance of this resulting data type is made clear in the following section on algebraic topology, section 2.4.

Often, choosing a threshold value is more of an art than a science. The choice of this value has the ability to greatly affect the associated cubical patterns in this study. In this project, two threshold values, $\varsigma$ in equation (2.6), are used to generate binary objects and pictures. A threshold value of $\varsigma = \ln r$ is used to study spatial patterns in simulations which appear to exhibit persistent chaos. This value was chosen because equation (2.3) says this is a fixed point and it happens to nearly bisect the bifurcation diagram of the one-dimensional Ricker map. From this occurrence a more biological interpretation of this threshold is claimed as it is the value which determines the relative magnitude of the population density. Local abundances above $\ln r$ are higher than the average population which leads to a higher density. A different threshold value, $\varsigma = 0$, is used to study how patterns shift as the population goes extinct.

---

**Example 2.3.3** (Invasive Species). Model an invasive species. Set $n = 201$ and define the spatial grid to be $G$. For simplicity, let all local fitness values be the same, $R_{i,j} = 15$, and fix the dispersal coefficient $d = 0.25$. We will initiate population abundance values such that the center patch is nonzero, $P_{100,100}(k = 0) = 10$, and zero elsewhere. The simulation is iterated according to equation (2.5). Still frames from this simulation are provided below.

---

Example 2.3.3 contains thresholded still frames of simulations stemming from very special initial conditions but it shows the process by-which binary spatial data is obtained from a numerical simulation. When patterns in extinction are investigated in section 3 spatial patterns can be much more complicated. Figure 2.2 provides a thresholded still frame from an extinction simulation.

### 2.4 Computational Homology

There is a strong link between the structure of coupled patches and geometry. Intuitively, spatial patterns are expected to develop as a species interacts with its
Data from Example 2.3.3

Figure 2.1: All figures are still frames from Example 2.3.3 where \( R_{i,j} = 15 \) and \( d = .25 \). A: Thresholded data at time step 10, B: Thresholded data at time step 100, C: Thresholded data at time step 1,000.

environment. We attempt to capture this phenomena by looking at the \( P \) matrix at different time steps in the simulation. Few tools exist that provide an accurate quantitative analysis of this kind of data and even fewer have been applied to biological modeling.

One such tool that can handle this type of analysis is cubical homology. The general idea is to represent spatial temporal data as a union of topological objects. This union of objects is then converted into a collection of cubical sets which provides the algebraic formalism necessary to quantify spatial patterns. Once in this form, elementary collapses and boundary operators can be used to quickly compute homology groups of the system. This section seeks to define these key terms, many of which come from Kaczynski et al. [8], and further explain the way in which computational algebraic topology is used to measure connectivity properties of this system.

The previous section defined thresholding as a process which can be used to reduce numerical spatial data into a binary image denoted by \( P \). We begin by providing an example of the information we retain about objects contained in \( P \).

**Example 2.4.1.** Let \( i, j \in \mathbb{Z} \) and assume that at a fixed time step the population abundance on the \( i^{th} \) \( j^{th} \) patch is above the threshold, that is \( P_{i,j} > \varsigma \). Then the patch \( G_{i,j} \in \mathcal{P}_\varsigma \) is an elementary cube. But this elementary cube also contains four one-dimensional cubes and four zero-dimensional cubes. They are:

\[
K_2 = \{[i, i + 1] \times [j, j + 1]\}
\]

\[
K_1 = \{[i, i + 1] \times [j], [i, i + 1] \times [j + 1],\}
\]
Figure 2.2: Still frame from an extinction simulation of the type investigated in chapter 3.

\[ K_0 = \{ [i] \times [j], [i + 1] \times [j], [i] \times [j + 1], [i + 1] \times [j + 1] \} \]

Now, \( P \) is treated as a finite union of elementary cubes. This finite union can be abstracted as an abelian group.

**Definition 2.4.2.** A group, \((G, +)\), is a set, \( G \), equipped with a binary operation + that satisfies the following:

1. The group operation is associative; that is for \( a, b, c \in G \), \( a + (b + c) = (a + b) + c \).

2. The operation admits the identity element; that is \( \forall a \in G \exists e \in G \) with the property that \( a + e = a \).

3. The operation admits the inverse for every element of \( G \); that is \( \forall a \in G \exists a' \in G \) with the property that \( a + a' = e \).

A finite group is a group that has a finite number of elements. An abelian group is a group where the group operation is commutative.

**Definition 2.4.3.** An algebraic object \( \hat{Q} \) is associated with each elementary \( k \)-cube, \( Q \), that is called an elementary k-chain. \( C^d_k(X) \) is defined as the group of cubical chains. When taken in context, it is common to omit the superscript \( d \) in the expression \( C^d_k(X) \).
In this project the ambient dimension, $d$ in this particular section of the definitions chapter, does not change and to avoid confusion with the dispersal parameter, also $d$, it is frequently omitted.

**Definition 2.4.4** ([8]). *Given $k \in \mathbb{Z}$, the cubical boundary operator or cubical boundary map* 

\[ \partial_k : C_k \to C_{k-1} \]

*is a homomorphism of free abelian groups, which is defined for an elementary chain $\hat{Q} \in \hat{K}^m_k$ by induction on the embedding number $m$.*

Consider the first case $m = 1$. Then $Q$ is an elementary interval and hence $Q = [l] \in K^0_1$ or $Q = [l, l + 1] \in K^1_1$ for some $l \in \mathbb{Z}$. Define

\[ \partial_k \hat{Q} := \begin{cases} 
0 & \text{if } Q = [l], \\
[l + 1] - [l] & \text{if } Q = [l, l + 1].
\end{cases} \]

Now assume that $m > 1$. Let $I = I_1(Q)$ and $S = I_2(Q) \times \cdots \times I_m(Q)$. Then $\hat{Q} = \hat{I} \hat{S}$. Define

\[ \partial_k \hat{Q} := \partial_{k_1} \hat{I} \hat{S} + (-1)^{\dim I} \partial_{k_2} \hat{S}, \]

where $k_1 = \dim I$ and $k_2 = \dim S$. Finally, the definitions is extended to all chains by linearity; that is, if $c = \alpha_1 \hat{Q}_1 + \cdots + \alpha_j \hat{Q}_j$, then

\[ \partial_k c := \alpha_1 \partial_k \hat{Q}_1 + \cdots + \alpha_j \partial_k \hat{Q}_j. \]

It is important to note that by construction,

\[ \partial_{k-1} \circ \partial_k = 0. \] (2.7)

Another important feature of the boundary operator is how it maps from one chain group to another chain group, $\partial(C_k(X)) \subset C_{k-1}(X)$ so that

\[ \cdots \to C_{k+1} \to C_k \to C_{k-1} \to \cdots \] (2.8)

---

**Example 2.4.5** (Unit Square). Compute the boundary of the filled in unit square. For notation, let $A$ be the filled in unit square, in cubical set notation $A = \{[0, 1] \times [0, 1]\}$. $A$ will be compared to the hollow unit square denoted as $B$. Note that $A$ also contains the elementary cubes:
It is instructive to list objects and to classify each object either a topological object or an algebraic object. $Q$ will denote the filled in unit square.

<table>
<thead>
<tr>
<th>Topological Object</th>
<th>Algebraic Object</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_0(A) = {v_1, v_2, v_3, v_4}$</td>
<td>$\hat{K}_0(A) = {\hat{v}_1, \hat{v}_2, \hat{v}_3, \hat{v}_4}$</td>
</tr>
<tr>
<td>$K_1(A) = {e_1, e_2, e_3, e_4}$</td>
<td>$\hat{K}_1(A) = {\hat{e}_1, \hat{e}_2, \hat{e}_3, \hat{e}_4}$</td>
</tr>
<tr>
<td>$K_2(A) = {Q}$</td>
<td>$\hat{K}_2(A) = {\hat{Q}}$</td>
</tr>
</tbody>
</table>

Then

$$\partial_2\hat{Q} = \hat{e}_1 + \hat{e}_2 - \hat{e}_3 - \hat{e}_4 \in C_1(A).$$

Although the table of algebraic and topological objects was not fully used in this example, it will be in example 2.4.11. When $A$ and $B$ are compared, the only difference is that $K_2(B)$ is empty. Correspondingly, $\hat{K}_2(B) = \emptyset$ and $C_2(B) = 0$. 

---

Figure 2.3: On the left is the filled in unit square, $A$, described in example 2.4.5. On the right, $B$ is the hollow unit square in example 2.4.5.
Definition 2.4.6. If \( z \) is a \( k \)-chain with an empty boundary then \( z \) is a \( k \)-cycle. That is \( \partial z = 0 \). The set of all \( k \)-cycles in a cubical topological space \( X \) is defined as
\[
Z_k(X) = \ker \partial_k = C_k(X) \cap \ker \partial_k \subset C_k(X).
\]

Definition 2.4.7. A \( k \)-chain \( z \in C_k(X) \) is called a boundary in \( X \) if there exists \( c \in C_{k+1}(X) \) such that \( \partial c = z \). The set of all boundaries in \( C_k(X) \) is defined as
\[
B_k(X) = \partial_{k+1}(C_{k+1}(X)) \subset C_k(X).
\]

Note that by definitions 2.4.6 and 2.4.7 and since \( \partial \circ \partial = 0 \) (see definition 2.4.4), \( B_k(X) \) is a subgroup of \( C_k(X) \).

Cubical homology groups are defined by utilizing the boundary group, \( B_k(X) \), and cycle group, \( Z_k(X) \), to form quotient groups according to the following:

Definition 2.4.8. The \( k \)th cubical homology group of \( X \) is the quotient group
\[
H_k(X) := Z_k(X)/B_k(X).
\]

The homology of \( X \) is the collection of all homology groups of \( X \).

Corollary 2.4.9 ([8] p.93). Any finitely generated abelian group \( G \) is isomorphic to a group of the form :
\[
\mathbb{Z}^\beta \oplus \mathbb{Z}_{b_1} \oplus \cdots \oplus \mathbb{Z}_{b_k}, \tag{2.10}
\]
where \( \beta \) is a nonnegative integer, \( \mathbb{Z}_b \) denotes the group of integers modulo \( b \), \( b_i > 1 \) provided \( k > 0 \), and \( b_i \) divides \( b_{i+1} \) for \( i \in \{1, 2, \ldots, k-1\} \) provided \( k > 1 \). The numbers \( \beta \) and \( b_1, b_2, \ldots, b_k \) are uniquely determined by \( G \).

Definition 2.4.10. Given a finitely generated abelian group in the form \( \mathbb{Z}^\beta \oplus \mathbb{Z}_{b_1} \oplus \cdots \oplus \mathbb{Z}_{b_k} \), the nonnegative integer \( \beta \) is the rank of the free group \( \mathbb{Z}^\beta \) and is called the Betti number of \( G \). The numbers \( b_1, b_2, \ldots, b_k \) are called the torsion coefficients of \( G \).

In studying homology groups, the \( k \)th Betti number, \( \beta_k \), is defined to be the Betti number of the \( k \)th homology group, \( H_k(X) \). This project has the convenient interpretation of the zeroth Betti number, \( \beta_0 \), as the number of connected components in the topological domain and the first Betti number, \( \beta_1 \), as being the number of one dimensional holes in the topological domain.

Example 2.4.11 (Homology of Unit Square). As an illustration we compute the homology of the filled in unit square. The table of topological and algebraic objects
from example 2.4.5 is useful. Example 2.4.5 shows that
\[ \partial_2 \hat{Q} = \hat{e}_1 + \hat{e}_2 - \hat{e}_3 - \hat{e}_4. \]

The last part of definition 2.4.4 is invoked to claim \( \partial_1 (\partial_2 \hat{Q}) = 0 \), which means that \( \partial_2 \hat{Q} \in \ker(C_1(A)) \). In order to prove that \( \partial_2 \hat{Q} \) is the only element in the kernel of \( C_1(A) \) a less intuitive linear algebra approach is needed. As this example is meant to piece together different structures and terms in computational homology this approach is omitted here but is discussed at length in [8]. Suffice to say that \( \ker(C_1(A)) = <\partial_2 \hat{Q}> = <\hat{e}_1 + \hat{e}_2 - \hat{e}_3 - \hat{e}_4> \) and
\[ H_1(A) = Z_1(A)/B_1(A) = \ker \partial_1 / \text{im} \partial_2 = < \partial_2 \hat{Q} > / < \partial_2 \hat{Q} >= 0. \]

Now, \( \partial C_1(A) = < \hat{v}_2 - \hat{v}_1, \hat{v}_3 - \hat{v}_2, \hat{v}_4 - \hat{v}_3, \hat{v}_1 - \hat{v}_4 > \) and \( \ker C_0(A) = C_0(A) \) by definition. Then
\[
H_0(A) = Z_0(A)/B_0(A) = \ker \partial_0 / \text{im} \partial_1 \\
= < \hat{v}_1 > / < \hat{v}_2 - \hat{v}_1, \hat{v}_3 - \hat{v}_2, \hat{v}_4 - \hat{v}_3, \hat{v}_1 - \hat{v}_4 > \\
\cong \mathbb{Z}
\]

When all homology groups are put together:
\[ H_k(A) \cong \begin{cases} 
\mathbb{Z} & \text{if } k = 0 \\
0 & \text{otherwise.} 
\end{cases} \]

Therefore, \( \beta_0 = 1 \) and all other Betti numbers are zero. This corresponds to \( A \) depicting a topological space with one connected component and no holes. Similar computations show that
\[ H_k(B) \cong \begin{cases} 
\mathbb{Z} & \text{if } k = 0, 1 \\
0 & \text{otherwise.} 
\end{cases} \]

This corresponds to \( B \) depicting a topological space with one connected component and one one-dimensional hole.

The process of actually computing homology groups for large numbers of elementary cubes can be quite involved. For this reason we use prepackaged software from the Computational Homology Project CHomP [2].
This thesis seeks to study topological shifts in spatial patterns of a population as it tends toward extinction. This section lays a foundation of knowledge to help the reader understand how computation of Betti numbers allows for an analysis of topological structures, i.e. connectivity properties, of patterns in our coupled Ricker system of equations. This process is what allows for the quantitative measurement of a biological population’s dispersal pattern.

### 2.5 Chapter Summary

This chapter has explained the coupled system of Ricker equations used in this body of work. It has introduced the reader to computational homology and explained the process of converting numerical simulation data to topological objects. In this project it is common to use a high dimensional systems of equations. The population matrix $P(k)$ at time step $k$ is an $n \times n$ matrix and can be thought of as a point in $\mathbb{R}^{n^2}$. For our studies we typically use $n = 201$, which means that $G$ is composed of over 40,000 coupled patches. We desire to have an accurate measure of this system that is both computationally feasible and informative. The total abundance of the system is saved at each time step,

$$||P(k)|| = \sum_{i,j} |P_{i,j}(k)| = \sum_{i=1}^{n} \sum_{j=1}^{n} P_{i,j}(k),$$

but this measure cannot give information about the geometry of spatial dispersal patterns. The entire $P(k)$ matrix could be recorded at each time step, $k$, but this approach has two set backs. The first setback is computational, the amount of memory and storage necessary to record this amount of information for many long simulations is impracticable. The second setback deals with the lack of an accurate feasible quantitative measure for this amount of data in relation to spatial patterns. For these two reasons, any approach of data analysis must balance the trade-offs of accuracy and practicability.

We desire to use computational homology to quantitatively measure these patterns but in order to use homology we must have topological objects. Thresholding is used to transform numerical data, $P(k) \in \mathbb{R}^{201^2}$, into topological data in the form of a cubical set $\mathcal{P}(k) \subseteq G_{n,n}$. Lastly, CHomP is used to compute the homology of $\mathcal{P}(k)$. This results in two one-dimensional measurements of the connectivity properties of $\mathcal{P}(k)$. Processing data in this manner admits a large amount of reduction in data returned from simulations; nevertheless, this reduced data is still able to facilitate insightful conclusions concerning characteristics of the system as will soon be shown.
Chapter 3

Spatial Patterns in Extinction

In 2009 Scheffer et al. claimed that shifts in a system’s topology are a possible early warning signal of a critical transition toward extinction [11]. Computational homology is used to quantitatively measure these transitions in the coupled Ricker patch model. Also, the preventative influence of dispersal on extinction dynamics is displayed by varying the strength of coupling between patches given by the dispersal parameter and measuring changes in extinction time.

3.1 Modification of Ricker Model

The Ricker model as it was presented earlier is strictly positive for positive initial conditions. Therefore as the model is currently defined it cannot be used to study patterns in extinction. For this reason we modify our model so that it includes a patch-wise extinction threshold, \( e_0 \). At each time step \( k \), the population on each patch \( G_{i,j} \) undergoes Ricker growth and dispersal as before but now if the local abundance is below the extinction threshold after the dispersal phase then the local abundance is reset to zero. We refer to this type of extinction threshold as a local extinction threshold.

\[
P_{i,j}(k+1) = \begin{cases} 
    f_{i,j}(P(k)) & \text{if } f_{i,j}(P(k)) > e_0, \\
    0 & \text{otherwise.}
\end{cases}
\]  

(3.1)

This new system of equations is very similar to the original model defined by equation (2.5). We use extinction thresholds that are small in magnitude when compared to the Ricker growth term, given in (2.1).

To reduce the breadth of our analysis we will let all local fitness values be the same: \( R_{i,j} = 22 \). Future research should further explore parameter space; how-
Figure 3.1: An extinction threshold of $e_0 = 0.70$, red (darker), and the Ricker growth on each patch, equation (2.1), in blue (lighter). In the new model, values less than $e_0$ would be set to zero.

However, its high-dimensionality presents a daunting task. Also, for computational reasons only four different initial conditions are studied. These four initial conditions were created by initializing simulations with pseudo-random population values drawn from a uniform distribution centered at $\ln r$ with a spread of 2 ($P(0)_{i,j} \sim U_{\ln r-1,\ln r+1}$). Then, the simulations were iterated for $T = 5,000$ time steps with parameter values $d = 0.15$, $r = 22$, and $e_0 = 0$ in order to remove transient behavior. Finally, the population matrices were saved and used as initial conditions for this project. These initial conditions can be found electronic form here [7]. When simulation data is presented, the naming convention $IC = \{1, 2, 3, 4\}$ is used to denote which initial condition was used to initialize the simulation.

### 3.2 Spatial Temporal Patterns

The local fitness parameter is fixed at a value ($R_{i,j} = 22$) which would result in chaotic dynamics for the case when patches are decoupled ($d = 0$). When patches are coupled in the modified model with an extinction threshold we find that the coupled system can display three different types of long-term behavior for fixed
Spatial Temporal Patterns

Bifurcation Diagram of 1-D Ricker Map

Figure 3.2: An extinction threshold of $e_0 = 0.70$, red (lighter color), plotted over top the bifurcation diagram of the one dimensional Ricker model, equation (2.1). Trajectories were computed by omitting the first 500 time iterates and then recording 1,000 time steps.

fitness and fixed dispersal values.

One observed behavior from simulations is a decoupling of the system into decoupled subsystems. A decoupled subsystem, $S$, is a collection of connected patches, $S \subseteq \mathcal{S}$, that is completely surrounded by extinct patches. An example of a decoupled four-patch subsystem is provided in figure 3.3. It is important to note that decoupled subsystems can recouple with neighboring patches under iteration of the system.

1. Parameter values exist for which the high-dimensional system decouples into multiple decoupled subsystems but the population rebounds and extinct patches become reseeded thereby re-coupling the patches. As more patches are reseeded and re-coupled the subsystems grow in size and re-couple with other subsystems until there is one coupled system of dimension $n \times n$; that is, there are no extinct patches in the simulation. An example is $r = 22, d = 0.15, e_o = 0.20, IC = 1$, with data provided in figure 6.1.

2. Parameter values exist for which the high-dimensional system decouples into multiple subsystems which persist for all forward time. An example is $r = 22, d = 0.15, e_o = 0.60, IC = 1$ with data provided in figures 6.2.
and [6.3] From this example, notice how although the Betti numbers measuring the system’s topology become fixed the total abundance continues to vary. Furthermore, the patterns themselves may continue to vary while the connectivity properties measured by Betti numbers do not change.

3. Parameter values exist for which the high-dimensional system decouples into subsystems but only as a transient stage prior to extinction. An example is $r = 22, \, d = 0.15, \, e_o = 0.77, \, IC = 1$ with data provided in figures 6.4 and 6.5.

### Four-Dimensional Subsystem

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<thead>
<tr>
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<th>0</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>$P_{i,j}$</td>
<td>$P_{i,j+1}$</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>$P_{i+1,j}$</td>
<td>$P_{i+1,j+1}$</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 3.3: Depiction of a four-dimensional subsystem. Provided that at least one of the interior patches has a nonzero population value, this configuration has one connected component and contributes a “1” to $\beta_0$.

**Definition 3.2.1.** The extinction time is defined as the number of time steps necessary for the system’s total abundance to become zero, that is $\sum_{i,j} P_{i,j} = 0$. The smallest computed extinction threshold for which the system goes extinct is called the global extinction threshold and is denoted $e_o^*$. The extinction time corresponding to $e_o^*$ is denoted $\tau_{e_o^*}$. 
Following Scheffer’s claim, if topological shifts are indeed indicative of critical transitions, we should be able to detect a shift in the system’s Betti time series data when \( e_0 > e_0^* \). Figure 6.5 is an example of Betti time series data obtained from a simulation modeling extinction. One thing noticed in all extinction simulations is that the number of enclosed extinct regions, or holes, measured by \( \beta_1 \), decreases to zero before the number of decoupled subsystems, measured by \( \beta_0 \). A possible hindrance to detecting other topological shifts from extinction simulations is that when global extinction occurs in our model it is a quick process which makes the time series relatively short. Figure 3.4 shows how the extinction time is related to dispersal and local extinction threshold.

**Time to Extinction vs. Global Extinction Threshold**

![Graph showing time to extinction vs. extinction threshold](image)

Values of Extinction Threshold, \( e_0 \geq e_0^* \)

Figure 3.4: Simulations were initialized with same initial condition, \( IC = 1 \), and assigned dispersal parameters \( d = 0.10 \) and \( d = 0.15 \) respectively. Simulation’s using local extinction thresholds above the global extinction threshold are plotted on the horizontal axis and the resulting extinction time is plotted on the vertical axis. The first data point on each graph corresponds to using \( e_0 = e_0^* \), the global extinction threshold.

In figure 3.4 the positive influence of dispersal on the population’s robustness is already visible. Notice how as the dispersal parameter is increased the global extinction threshold \( e_0^* \) also increases. A relatively small increase in dispersal results
in a relatively large increase in the global extinction threshold $e^*_0$. In addition, this relationship between increasing dispersal and the corresponding increase in global extinction threshold has been observed in simulations using the other three initial conditions.

The global extinction values for fixed parameters and the four initial conditions are relatively close to one another, indicating that choice of initial condition should not greatly effect the measured global extinction threshold (addition initial conditions should be further explored to confirm this statement). Also, $\tau e^*_0$, does not seem to exhibit any clear pattern in fluctuations across the four initial conditions. Figure 3.4 shows how the longest extinction times recorded occurred when $e_o = e^*_0$ and even for these values global extinction events occurred in less than 35 time steps for all simulated initial conditions. It is hard to detect statistically significant differences from small amounts of data. For this reason we compare Betti time series of local extinction thresholds slightly smaller than the global extinction threshold in order to have longer time series. More specifically, we compare the computed asymptotic behavior (data recorded after 500 time steps) of the number of connected components ($\beta_0$) and the number of extinct regions ($\beta_1$). Using this approach we have been able to find shifts in the system’s topology for local extinction thresholds for which the population is, in some sense, close to a global extinction event. That is, a small increase in the local extinction threshold would result in a global extinction of the population.

**Example 3.2.2** (Critical Transition). Consider the case when $r = 22$ and $d = 0.15$. For these parameter values the global extinction threshold for initial condition one is $e^*_0 = 0.752$. Slightly prior to this value, when $0.7 < e_0 < e^*_0$, after 500 time steps the number of decoupled subsystems is greater than the number of enclosed extinct regions ($\beta_0 > \beta_1$). As $e_0$ is decreased a transition occurs in the asymptotic behavior. When $e_0 < 0.7$ the number of decoupled subsystems is less than the number of enclosed extinct regions ($\beta_0 < \beta_1$) after 500 time steps. Figure 3.5 provides simulation data for parameter values chosen from these two cases for $e_0$. Notice how the smaller $e_0$ value ($e_0 = 0.70$) resulted in a fixed topological pattern with more enclosed extinct regions then decoupled subsystems and the higher $e_0$ value ($e_0 = 0.71$) resulted in having fewer enclosed regions than decoupled subsystems.
Figure 3.5: Data for example 3.2.2 where dispersal was fixed, \( d = 0.15 \), and \( r = 22, IC = 1 \). The inner plot is the Betti time series generated when \( e_0 = 0.70 \). The outer plot is the Betti time series generated when \( e_0 = 0.71 \). In both plots the number of connected components, \( \beta_0 \), is denoted by blue (darker) and the number of enclosed extinct regions, \( \beta_1 \), is represented by cyan (lighter).

Example 3.2.3 (Asymptotic Topological Pattern). We wish to characterize how the computed asymptotic topological pattern changes with respect to the magnitude of the local extinction threshold, \( e_0 \). Consider the case when \( r = 22 \) and \( d = 0.15 \). Using initial condition one, we begin by iterating the simulation for a variety of different \( e_0 \) values. Each set of parameters will have a Betti time series similar to those computed in example 3.2.2 and displayed in figure 3.5. We notice how the longterm behavior of each Betti number appears to fixate on a single value. After collecting data for a variety of different local extinction thresholds, \( e_0 \), we compare the computed asymptotic behaviors of each simulation by constructing figure 3.6. Notice how for this set of parameters and initial condition there is an increase in the number of connected components and a decrease in the number of enclosed extinction regions which occurs after the critical transition of example 3.2.2.
Asymptotic Topological Pattern vs. Extinction Threshold

Figure 3.6: Depiction of data computed as described in example 3.2.3. Local extinction threshold values (horizontal axis) are $0.65 \leq e_0 \leq 0.76$ with data computed in intervals of 0.01 for most of the region and intervals of 0.001 near $e^*_0$. The computed asymptotic behavior at time step 500 of the number of connected components, $\beta_0$, is in blue (darker) and the computed asymptotic number of enclosed extinct regions, $\beta_1$, is in green (lighter). We observe a critical transition in the system’s topology around $e_0 = 0.7$.

In all investigated parameter sets, a shift in the system’s Betti time series data has been observed. This shift occurs slightly before the smallest global extinction value, $e^*_0$. Computationally where the graphs of $\beta_0$ and $\beta_1$ (both at time step 500) as a function of $e_0$ cross is recorded. This crossing always occurs for values $e_0 < e^*_0$. This shift in the system’s topology might be indicative of an endangered population; however, more research is needed to support such a claim. For now, the value of the crossing, in conjunction with $e^*_0$, is presented to quantify the effect of dispersal on the coupled Ricker system.

Figure 3.4 shows how larger dispersal values require larger local extinction thresholds to cause a global extinction. Similarly, figure 3.7 provides simulation data showcasing the effect of dispersal on the difference between the local extinction value of the critical transition in the system’s topology and the global extinction value. From this observation we claim that robustness of individual subsystems is increased by dispersal. We believe this result originates from dispersal’s positive influence on the likelihood of extinct patches being reseeded. The following section
3.3 Fixed Heterogeneous Dispersal

In an effort to make the model more biologically relevant and to glean more information about dispersal’s effect on the model’s dynamics, the model is modified such that the magnitude of dispersal follows a normal distribution centered at what was previously considered to be the dispersal parameter, $d$, with a standard deviation of $\sigma$. More specifically, dispersal in the four cardinal directions on the spatial grid, $\mathcal{G}$, is to be independent of each other and of all other patches in $\mathcal{G}$. This is further investigates a particular subsystem and the role of dispersal in reseeding extinct patches. In that section there is a surface plot, figure 4.3, displaying dispersal out of a subsystem as a function of dispersal and local population abundance. In that graph, values above the extinction threshold plane would result in reseeding neighboring patches.
accomplished by creating four random matrices, call them \( D^l \in \mathbb{R}^{n \times n}, D^r \in \mathbb{R}^{n \times n}, \)
\( D^u \in \mathbb{R}^{n \times n}, D^d \in \mathbb{R}^{n \times n}, \)
which will store the dispersal values for each patch in the assigned direction. Values are assigned to these matrices according to Matlab’s pseudo random number generator \( \text{randn} \) where \( D^l_{i,j} \sim N(\frac{d}{4}, \sigma^2), \)
\( D^r_{i,j} \sim N(\frac{d}{4}, \sigma^2), \)
\( D^u_{i,j} \sim N(\frac{d}{4}, \sigma^2), \)
\( D^d_{i,j} \sim N(\frac{d}{4}, \sigma^2). \) Notation is made simpler by defining
\[ d_{i,j} = D^l_{i,j} + D^r_{i,j} + D^u_{i,j} + D^d_{i,j}. \]

Now, redefine \( f : \mathbb{R}^{n \times n} \times \mathbb{R}^{n \times n} \) modeling how a population abundance configuration \( P \) is mapped to a population abundance configuration \( f(P) \) after one time step,
\[ P(k+1) = f(P(k)). \]

Notationally, this is \( P_{i,j}(k+1) = f_{i,j}(P(k)) \) where \( f_{i,j}(P(k)) \) is computed according to:
\[ f_{i,j}(P(k)) = (1 - d_{i,j})P'_{i,j}(k) + P'_{i,j-1}(k)D^l_{i,j-1} + P'_{i,j+1}(k)D^r_{i,j+1} + P'_{i+1,j}(k)D^u_{i+1,j} + P'_{i-1,j}(k)D^d_{i-1,j} \]  (3.2)

where \( P'_{i,j}(k) \) is computed according to equation (2.4).

**Remark 3.3.1.** The expected value of \( d_{i,j} \) is \( d \) and the variance of \( d_{i,j} \) is \( \sigma^2 \). This is easily shown by taking advantage of the fact that all dispersal values are independent and identically distributed.
\[ E[d_{i,j}] = E[D^l_{i,j} + D^r_{i,j} + D^u_{i,j} + D^d_{i,j}] = E[D^l_{i,j}] + E[D^r_{i,j}] + E[D^u_{i,j}] + E[D^d_{i,j}] = 4 \frac{d}{4} = d. \]

Similarly,
\[ V[d_{i,j}] = V[D^l_{i,j}] + V[D^r_{i,j}] + V[D^u_{i,j}] + V[D^d_{i,j}] = 4 \frac{\sigma^2}{4} = \sigma^2. \]

This shows that on average the dispersal value for each patch, \( d_{i,j} \), will equal \( d \) and have a standard deviation of \( \sigma \) as desired. More importantly, it is easily shown through the method of moment generating functions that \( d_{i,j} \sim N(d, \sigma) \); this proof is supplied in appendix 6.3.

Initial simulations with random perturbations in dispersal were computed with
varying standard deviations. Data from these simulations is compared with data from simulations with deterministic parameters. Although this project’s progress on simulations with heterogeneous dispersal values is in its infancy, three general trends have already become evident.

1. Computed asymptotic behavior of the total abundance increases with small fluctuations in dispersal values but decreases with large fluctuations. A representative figure is supplied, figure 6.6, with parameter values \(r = 22\) and \(e_0 = 0.6\). Dispersal values for this figure were set to have a mean value of \(d = 0.15\) for all simulations and four different standard deviation values were used, \(\sigma = \{0, 0.01, 0.04, 0.1\}\). This trend in asymptotic behavior of the total abundance has been observed for all simulations performed in the region of parameter space where persistent subsystems exist (data is provided in the online appendix).

![Asymptotic Behavior of Abundance for different σ](image)

**Asymptotic Behavior of Abundance for different σ**

Figure 3.8: Total abundance time series data for \(r = 22\), \(e_o = 0.60\), and \(d = 0.15\). Colors represent different standard deviations with \(\sigma = 0\) (blue), \(\sigma = 0.01\) (red), \(\sigma = 0.04\) (green), \(\sigma = 0.1\) (cyan). Simulations were run for 500 time steps of which the last 100 are plotted.

2. Computed asymptotic behavior of Betti numbers show that both the number of connected components and the number of holes increases for simulations in
the region of parameter space where persistence of subsystems is expected. Representative figures created by plotting topological data from the same simulations as figure 6.6 are figures 6.7 which is a plot of the number of subsystems, $\beta_0$, and figure 6.8 which is a plot of the number of enclosed extinct regions, $\beta_1$. It should be noted that this change in the system’s homology is only observed in non stochastic simulations; a claim that section 3.4 will make clear.

Asymptotic Behavior of $\beta_0$ for different $\sigma$

![Graph showing asymptotic behavior of $\beta_0$ for different $\sigma$.](image)

Figure 3.9: Number of connected components, $\beta_0$, time series data for $r = 22$, $e_0 = 0.60$, and $d = 0.15$ with a fixed initial condition. Colors represent different standard deviations with $\sigma = 0$ (blue), $\sigma = 0.01$ (red), $\sigma = 0.04$ (green), $\sigma = 0.1$ (cyan). Simulations were run for 500 time steps of which the last 100 are plotted.

One factor which could possibly contribute to an increase in the number of enclosed extinct regions, $\beta_1$, is the presence of depleted patches.

**Definition 3.3.2.** A depleted patch is a patch where the dispersal parameter governing flux out of the patch is at least one standard deviation greater than the mean and the dispersal parameter governing flux into the patch is at least one standard deviation less than the mean.

Depleted patches are generated by a patch having an “unlucky” or non-advantageous draw of random dispersal values. Because simulations have
Asymptotic Behavior of $\beta_1$ for different $\sigma$

Figure 3.10: Number of enclosed extinct regions, $\beta_1$, time series data for $r = 22$, $e_0 = 0.60$, and $d = 0.15$ with a fixed initial condition. Colors represent different standard deviations with $\sigma = 0$ (blue), $\sigma = 0.01$ (red), $\sigma = 0.04$ (green), $\sigma = 0.1$ (cyan). Simulations were run for 500 time steps of which the last 100 are plotted.

a large number of coupled patches, $n = 201^2$, many depleted patches are expected in each simulation.

Remark 3.3.3. The expected number of depleted patches generated from each draw of dispersal values can be calculated by taking advantage of the independent nature of the stochastically determined parameters. In order for a patch to be considered depleted, two independent things must happen: dispersal out of the patch must be at least one standard deviation below the average and dispersal into the patch must be at least one standard deviation above the average. The probability of these two independent events happening at the same time is

$$p[d_{i,j} > d + \sigma] \cdot p[D_{i,j+1}^r + D_{i+1,j}^u + D_{i-1,j}^d].$$

In appendix 6.3 it is shown that the probability distribution of dispersal out
of a patch follows a normal distribution, \( d_{i,j} \sim N(d, \sigma) \). Then
\[
p[d_{i,j} > d + \sigma] = p[z > \sigma] = .1587,
\]
where \( z \) is a standard normal variable. The same argument structure used in Appendix 6.3 can be used to show that
\[
D_{i,j-1}^l + D_{i,j+1}^r + D_{i+1,j}^u + D_{i-1,j}^d \sim N(d, \sigma).
\]
From this it follows that
\[
p[d_{i,j} > d + \sigma] p[D_{i,j-1}^l + D_{i,j+1}^r + D_{i+1,j}^u + D_{i-1,j}^d] = .1587^2.
\]
Then the expected number of depleted patches from each draw of dispersal values is the number of patches in the simulation times the probability of each patch being depleted,
\[
n^2.1587^2 \approx 1,020.
\]

The expected number of depleted patches generated from each draw of dispersal values can help explain the large increase in the number of enclosed extinct regions in simulations where dispersal does not vary in time. A more helpful number would be an approximation of the number of enclosed extinction regions generated by depleted patches, but this requires a much more complicated statistical analysis than warranted by the current amount and quality of data. For the present, suffice to say that dead patches are a likely contributor to the observed change in the number of enclosed extinct regions. This possible contributor is also nice in that it would have less of an effect when dispersal values are redrawn after each time step.

3. Global extinction thresholds tend to increase with fluctuations in dispersal despite a decrease in the population’s asymptotic total abundance for simulations with persistent subsystems. A possible explanation of this phenomena is supported through evidence in the following chapter 4 where a particular four-dimensional subsystem is proven to have stable periodic orbits. There is strong evidence to suggest that \( e_* \) is slightly larger than the minimal point on this period-two orbit. The minimal value on the period-two orbit increases as dispersal increases. So if the system has a group of patches with larger than expected dispersal values this will lead to greater stability.
3.4 Heterogeneous Dispersal with Fluctuations in Time

In this step of analysis random dispersal values are changed after each time step and plots similar to those of the previous section are provided in appendix. Admittedly, data of the previous section was rather sparse and that is the reason behind general claims about what has been observed in simulations. Data is even more sparse for the case when dispersal is made to fluctuate in time. Once again, only general observations are reported.

1. When dispersal fluctuates in time, the asymptotic behavior of the total population still displays an increase for small variances in dispersal values and a decrease for large variances in dispersal values when compared to determin-
istic data in a way that is similar to data collected when stochastic variations in dispersal did not fluctuate in time. However, a distinct difference is that populations seem to go extinct more easily.

2. When dispersal fluctuates in time the asymptotic behavior of topological data does not resemble data obtained from simulations where stochastic variations in dispersal did not fluctuate in time.

3. When dispersal fluctuates in time, $e_0^*$, decreases drastically. Similar to how the increase in $e_0^*$ values observed when dispersal did not fluctuate in time, an explanation of this phenomena relies upon information presented in chapter 4.

![Global Extinction Threshold](image)

Figure 3.12: Plot of the global extinction threshold $e_0^*$, depicted by *, for simulations with $\sigma = 0$ (blue), $\sigma = 0.01$ (red), $\sigma = 0.04$ (green), and $\sigma = 0.1$ (cyan) with temporal fluctuations occurring every time step. As with figure 3.7, dispersal is the horizontal axis and local extinction threshold values are the vertical axis. All simulations utilized the same initial condition. Plots with other initial conditions are provided in the on-line appendix.

Although claims in the past two sections about stochastic variations in dispersal have been few, some possible explanations for observed shifts in topological
patterns have been proposed. Something that has not been directly addressed are the observed changes in $e_0^*$ values. The following chapter provides a mechanistic explanation of how $e_0^*$ values change with deterministic dispersal values. The concluding chapter will attempt to answer this question through synthesizing the deterministic findings with the expected behavior of dispersal values.
Chapter 4

Four-Patch Subsystem

Initial numerical simulations of the coupled Ricker model when using extinction
thresholds suggests the existence of a symmetric four-patch subsystem. This sub-
system is interesting because of what must happen in order for the subsystem to
materialize. The simulation begins with an initial condition that under iteration
with an extinction threshold of \( e_0 = 0 \) displays long term behavior that is seemingly
chaotic. In order to model local extinction events the local extinction threshold \( e_o \)
is reset to a positive number. As the simulation progresses in time, if the extinction
threshold is within a certain interval, the \( n \times n \) dimensional system will decouple
into lower dimensional subsystems. The four-patch structure is a subsystem which
appeared in many simulations. The four-patch system is noteworthy in that it is
the smallest stable subsystem discovered. In addition, after decoupling from other
patches, the four-patch system exhibits symmetry and stability. The implication of
this is that the simulation can transition from persistent chaos in \( n \times n \) dimensions
to multiple decoupled symmetric subsystems displaying four dimensional periodic
orbits.

In this section the four-patch subsystem first depicted in figure 3.3 is defined
and constraints are given on parameters that help promote structural stability.
Numerical experimentations suggest the subsystem does indeed have stable peri-
odic orbits for a significant region of parameter space. Lastly, an approach based
on computational topology is used to prove the existence and stability of periodic
solutions in the four patch subsystem for select parameter values.

4.1 Constructing the Four Patch Structure

What renders an in-depth analysis of the four patch subsystem feasible is that the
four-patch subsystem is decoupled from all other non-zero patches in the spatial
grid. This decoupling is caused by the population in surrounding patches going
extinct so there is no dispersal into the four-patch system, and dispersal out of the system will satisfy certain constraints which ensure that the surrounding patches are not repopulated by the subsystem. It is useful to define a function $g : \mathbb{R} \rightarrow \mathbb{R}$ that is the Ricker growth equation devoid of parameters and compute its first and second derivatives as follows,

$$
g(x) = xe^{-x}$$

$$
\frac{d}{dx}g(x) = e^{-x}(1 - x)
$$

$$
\frac{d^2}{dx^2}g(x) = e^{-x}(x - 2).
$$

Using equation (4.1), the four-dimensional subsystem of figure 3.3 is defined by the function $F : \mathbb{R}^4 \rightarrow \mathbb{R}^4$ given by,

$$
F(x) = r \begin{bmatrix}
g(x_1)(1 - d) + g(x_2)\frac{d}{4} + g(x_3)\frac{d}{4} \\
g(x_2)(1 - d) + g(x_1)\frac{d}{4} + g(x_4)\frac{d}{4} \\
g(x_3)(1 - d) + g(x_1)\frac{d}{4} + g(x_4)\frac{d}{4} \\
g(x_4)(1 - d) + g(x_2)\frac{d}{4} + g(x_3)\frac{d}{4}
\end{bmatrix},
$$

where $r$ is the local fitness parameter and $d$ is the dispersal parameter. For this analysis $r$ is assumed to be fixed at $r = 22$. Crucial constraints must be taken into account; subsystems only develop in extinction simulations because a high-dimensional system must decouple through local extinction events. If a subsystem is to remain structurally stable, that is, remain decoupled from extinct codimension-one neighbors, then it cannot be permitted to reseed neighboring patches. In order to help promote isolation, limits are placed on the amount dispersed out of the four-patch system which means that the amount dispersed out of each patch must be below the local extinction threshold $e_o$:

$$
0 < \frac{rd}{4}g(x_i) < e_o, \ i = \{1, 2, 3, 4\}.
$$

Reseeding other patches would help to prevent extinction; however, this makes the system of four equations unstable because the subsystem would recouple with the reseeded patch, thereby destroying the four-dimensional structure.

Numerical simulations suggest the existence of a stable symmetric period-two orbit for a large portion of parameter space. To find these possible periodic orbits the subsystem is assumed to have symmetric population values. Note that the four-dimensional system is projected onto two dimensions by assuming the symmetry depicted in figure 4.1. Because it is possible for an orbit to appear to be stable in
Constructing the Four Patch Structure

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...a projection of a system but be unstable in the original system, all investigations regarding stability are performed in the four-dimensional system. To avoid confusion between whether the two-dimensional or four-dimensional system is in use, new notation is introduced to distinguish the two. Let \( x(k) \) and \( y(k) \) represent the local fitness of the patches at time step \( k \); then the symmetric four-patch structure has the following form:

\[
\begin{align*}
x(k+1) &= r(1-d)g(x(k)) + \frac{d}{2}g(y(k)) \\
y(k+1) &= r(1-d)g(y(k)) + \frac{d}{2}g(x(k)).
\end{align*}
\]

(4.4)

Figure 4.1: Graphical representation of the symmetric four-patch subsystem on a spatial grid. Compare this to figure 3.3.

In order to analyze this system of equations, the same assumptions as before are made, namely that all local fitness values, \( r \), are the same. The dispersal constraints (4.3) reduce to two inequalities,

\[
0 < \frac{rd}{4}g(x(k)) < e_o
\]

and

\[
0 < \frac{rd}{4}g(y(k)) < e_o.
\]

(4.5)

It turns out that this constraint is seldom needed because in the parameter range of investigation, \( r = 22 \) and \( 0.1 < d < 0.2 \), dispersal out of each patch has a relatively small upper bound, \( \frac{d}{4}g(x_i(k)) < 0.45 \). Nevertheless, the constraints (4.5)
Constructing the Four Patch Structure

Effect of Dispersal Constraints

Figure 4.2: Graph of $\frac{rd}{4}g(x(k))$ when $r = 22$ and $d = 0.15$. Values in blue (darker) are below an extinction threshold of $e_0 = 0.23$ and values in red (lighter) are above the threshold. Thus red values are those for which the stable four-dimensional subsystem cannot have with an extinction threshold of $e_0 = 0.23$.

prevent the four-patch structure from repopulating neighboring patches. This by itself does not ensure the structure’s isolation for all time. It is possible for other subsystems to repopulate the codimension-1 neighbors of the four-patch structure which would allow for dispersal into the structure and re-coupling it with a higher-dimensional system. This cannot be accounted for in a lower-dimensional analysis.

Numerical simulations predict that this structure displays stable periodic behavior for a range of parameter values. More specifically, period two dynamics are expected to exist which would satisfy

$$x(k + 1) = y(k) = x(k - 1),$$
$$y(k + 1) = x(k) = y(k - 1).$$

For clarification in notation, let $A$ and $B$ represent the two fixed values in the periodic orbit, namely, $x(0) = A$ and $y(0) = B$. This information can be used to
Dispersal Constraint

Figure 4.3: A surface plot of the dispersal constraints $\frac{rd}{2}g(x)$ for all possible $d$ and $x$ combinations when $r = 22$. The plane on top represents the extinction threshold for $e_o = .23$. Values of $(x, d)$ where the graph is below the plane are allowed under the inequality constraints (4.5) and values of $(x, d)$ where the graph is above the plane would reseed extinct neighboring patches.

relate $A$ and $B$ to the $r$ and $d$ parameters.

\[
A = Bre^{-B}(1 - d) + \frac{dB}{2(1 - d)}(1 + \frac{d}{2}re^{-B})
\]

\[
B = Are^{-A}(1 - d) + \frac{dA}{2(1 - d)}(1 + \frac{d}{2}re^{-A})
\]  (4.6)

Equations (4.6) can be solved numerically to find points which might be period-two points of the four-dimensional system. The following section provides methods for investigating the stability of these points.

4.2 Jacobian and Floquet Multiplier

The stability for particular periodic orbits of the four-patch structure needs to be determined. Here, a linearization technique is presented which works as a mechanism to numerically estimate stability. The stability of fixed points is determined
through an eigenvalue analysis of the system’s Jacobian when evaluated at the fixed point. Stability of periodic orbits is determined through the use of Floquet multipliers.

**Definition 4.2.1.** The Jacobian of a four-dimensional system of equations \( F(x) \) is

\[
DF(x) = \begin{bmatrix}
\frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \frac{\partial f_1}{\partial x_3} & \frac{\partial f_1}{\partial x_4} \\
\frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \frac{\partial f_2}{\partial x_3} & \frac{\partial f_2}{\partial x_4} \\
\frac{\partial f_3}{\partial x_1} & \frac{\partial f_3}{\partial x_2} & \frac{\partial f_3}{\partial x_3} & \frac{\partial f_3}{\partial x_4} \\
\frac{\partial f_4}{\partial x_1} & \frac{\partial f_4}{\partial x_2} & \frac{\partial f_4}{\partial x_3} & \frac{\partial f_4}{\partial x_4}
\end{bmatrix}.
\]  

(4.7)

**Theorem 4.2.2.** [1] If all eigenvalues of the Jacobian matrix, when evaluated at a fixed point, are less than one in magnitude, then the fixed point is stable.

**Definition 4.2.3.** Period-two Floquet multipliers are defined as the eigenvalues of the linearization:

\[
DF^2(x) = DF(y) \times DF(x)
\]

\[
= \begin{bmatrix}
\frac{\partial f_1}{\partial y_1} & \frac{\partial f_1}{\partial y_2} & \frac{\partial f_1}{\partial y_3} & \frac{\partial f_1}{\partial y_4} \\
\frac{\partial f_2}{\partial y_1} & \frac{\partial f_2}{\partial y_2} & \frac{\partial f_2}{\partial y_3} & \frac{\partial f_2}{\partial y_4} \\
\frac{\partial f_3}{\partial y_1} & \frac{\partial f_3}{\partial y_2} & \frac{\partial f_3}{\partial y_3} & \frac{\partial f_3}{\partial y_4} \\
\frac{\partial f_4}{\partial y_1} & \frac{\partial f_4}{\partial y_2} & \frac{\partial f_4}{\partial y_3} & \frac{\partial f_4}{\partial y_4}
\end{bmatrix} \times \begin{bmatrix}
\frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \frac{\partial f_1}{\partial x_3} & \frac{\partial f_1}{\partial x_4} \\
\frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \frac{\partial f_2}{\partial x_3} & \frac{\partial f_2}{\partial x_4} \\
\frac{\partial f_3}{\partial x_1} & \frac{\partial f_3}{\partial x_2} & \frac{\partial f_3}{\partial x_3} & \frac{\partial f_3}{\partial x_4} \\
\frac{\partial f_4}{\partial x_1} & \frac{\partial f_4}{\partial x_2} & \frac{\partial f_4}{\partial x_3} & \frac{\partial f_4}{\partial x_4}
\end{bmatrix},
\]  

(4.8)

where \( y = F(x) \) and \( x = F(y) \).

**Definition 4.2.4.** [1] If all period-two Floquet multipliers are less than one in magnitude then the period-two orbit is stable.

The Jacobian of equations (4.2) is

\[
DF(\tilde{x}) = r \begin{bmatrix}
g'(x_1)(1 - d) & g'(x_2)\frac{d}{4} & g'(x_3)\frac{d}{4} & 0 \\
\frac{g'(x_1)\frac{d}{4}}{4} & g'(x_2)(1 - d) & 0 & g'(x_4)\frac{d}{4} \\
\frac{g'(x_1)\frac{d}{4}}{4} & 0 & g'(x_3)(1 - d) & g'(x_4)\frac{d}{4} \\
0 & \frac{g'(x_2)\frac{d}{4}}{4} & \frac{g'(x_3)\frac{d}{4}}{4} & g'(x_4)(1 - d)
\end{bmatrix}.
\]

(4.9)

In the previous notation, let \( x = [ABBA]^T \) and \( y = [BAAB]^T \); then the Floquet multipliers are the eigenvalues of

\[
DF^2(x) = DF(y) \times DF(x).
\]

(4.10)
4.3 Numerical Computations

The motivation of the previous two subsections has been to develop a means of determining whether the four-patch system is stable for various parameter values. Unfortunately, at this stage it is too difficult to find analytical solutions of equation (4.6) so stability of this system using Jacobians and Floquet multipliers will have to be performed using numerical approximations of values rendering our findings non-rigorous. The next subsection focuses on a different type of analysis which is rigorous but computationally more costly. For now, we begin by finding numerical solutions to equation (4.6). This means that $r$ and $d$ must be discretized.

Once this has been done approximate $A$ and $B$ values for each set of $r, d$ parameters can be computed. For each set of parameters there could be up to three $A$ and $B$ combinations. The first set of $A, B$ pairs always exists as it is the trivial fixed point of $A = B = 0$; these values are omitted from all diagrams. The second set of $A, B$ pairs also always exists as it is the non-trivial fixed point of $A = B \neq 0$.

Lastly, the third set of $A, B$ pairs, which does not always exist, are points that are possibly on a period two orbit. Some example $A, B, r, d$ pairings are provided in figure 4.4. Although these values are for the four-dimensional vectors, because of symmetry and periodicity the $A$ and $B$ values can be plotted in two dimensions. Until now the fitness parameter, $r$, has been held fixed. In figure 4.4 this is not the case because it is desirable to display the similarity of this behavior with a two-dimensional pitchfork bifurcation. Stability of values is determined through the use of the system’s Jacobian given in (4.9) for the plane of fixed points and Floquet multipliers given in (4.10) are used to determine the stability of possible periodic points. Points numerically determined to be stable are labeled as the green points in figure 4.4.

The calculations necessary to produce data represented in figure 4.4 had to be performed insilico. By performing these calculations numerical round-off error and numerical eigenvalue estimation errors have been introduced to the data. This error is relatively small; however, it is large enough to question the stability of regions where blue and green colors seem to mix in figure 4.4. Thus the task of finding regions of parameter space for which the four-patch structure is stable has not been rigorously accomplished. For this reason a discrete representation of phase space is now introduced and used to rigorously find and classify dynamical structures.

4.4 Discrete Representation of Phase Space

Our motivation is to find dynamical properties of the four-patch structure and determine the stability of different dynamical modes. This goal is realized through
Figure 4.4: A 3-D scatter plot of $A, B$ pairs (numerical values that satisfy equations (4.6)) for different fitness, $r$, and dispersal, $d$, parameters. Plotted values also satisfy the constraints (4.5). Points have been color coded green (lighter) if numerical Jacobian (4.9) or Floquet (4.10) analysis determined them to be stable and are blue (darker) otherwise.

the creation of a box around one of the points on the period-two orbit.

**Definition 4.4.1.** A box, $\tilde{x}$, is defined by a vector coordinate, $c$, that is the center of the box in phase space and a radius vector, $r$, that specifies the box radius in each coordinate direction.

The image of a box is computed by using interval arithmetic. Notationally, equation (4.2) takes an input vector $x$ and maps it to another vector $y$. When interval arithmetic is used, equation (4.2) will take an input $\tilde{x}$ and compute the maximum and minimum values of $F(x)$ for $x \in \tilde{x}$ and return a value $\tilde{y}$. Because calculations are performed using computers, a certain amount of bounded error is introduced with each binary operation. These errors are accounted for by taking the computed outer enclosure $\tilde{y}$ and rounding outward by an amount that will overcompensate for any numerical roundoff error.
Example 4.4.2. To illustrate interval arithmetic consider the function \( rg(x) \). The first example will be of a large interval. Let \( \hat{x} \) be a box centered at 1 with a radius of 1. To find the interval image of \( \hat{x} \) we first find the local maximum of \( g(x) \) across the interval \( x \in \hat{x} \). The derivative is used to find a maximum at \( x_{\text{max}} = 1 \). Because \( g \) is unimodal and concave we know that the local minimum must occur at an end point which in this case is \( x_{\text{min}} = 0 \). From here we can find an upper bound on \( g(x) \) as \( g(x) \leq rx_{\text{max}}e^{-x_{\text{max}}} = \frac{r}{e} \). Similarly, a lower bound of \( g(x) \) is \( g(x) \geq rx_{\text{min}}e^{-x_{\text{min}}} = 0 \). In practice much smaller intervals are used to improve accuracy. A more useful example is that of \( x \in [1.8, 2] \implies r(0.27) \leq g(x) \leq r(0.3) \).

Figure 4.5: Graphical representation of computing the outer enclosure of a box. The teal color is the actual image of a box, green represents what might have been returned from interval arithmetic, and yellow represents boxes that are added to the interval image through outward rounding.

Definition 4.4.3. For a map \( F : X \to X \), the Lipschitz constant, \( k \), is a nonnegative real-valued constant that satisfies:

\[
d(F(x), F(y)) \leq kd(x, y) \quad \forall x, y \in X.
\]

Theorem 4.4.4. [1] A contracting map is a map \( F : \hat{x} \to \hat{x} \) for which there exists a Lipschitz constant, \( k \), such that \( k < 1 \).

As with the numerical analysis of the four patch subsystem a Jacobian and Floquet multiplier approach is used. However, the Lipschitz constant is now used to determine stability over a specified region, or box, rather than using eigenvalues.
to determine stability in the neighborhood a single point. An upper bound of the Lipschitz constant for a period two orbit is found as the row sum of the Floquet multiplier,
\[ k \leq \|DF(F(\bar{x}))DF(\bar{x})\|_\infty, \quad (4.11) \]

**Example 4.4.5** (Contracting Neighborhood). Determine the stability of the period-two orbit numerically observed when \( d = 0.15 \) and \( r = 22 \). Simulations indicate that the point \((6.63, 0.747, 0.747, 6.63)\) is near the orbit. First, construct a box, \( \bar{x} \), around this expected point with center \( c=(6.63, 0.747, 0.747, 6.63) \) and radius \( r=[.1 .1 .1 .1] \). One condition that must be met is for \( F : \bar{x} \rightarrow \bar{x}, \) which is easily checked by mapping \( \bar{x} \) twice (using interval arithmetic) and seeing if \( F^2(\bar{x}) \subseteq \bar{x} \). To use the formula for a Lipschitz estimate \((4.11)\), values for \( DF(\bar{x}) \) and \( DF^2(\bar{x}) \) must be known. Begin by using interval arithmetic and outward rounding to find an outer enclosure of the maximum values for all 16 entries of \( DF(\bar{x}) \) (the second derivative of \( g(\bar{x}) \) provided in equation \((4.1)\) is helpful). Next, compute the image of \( \bar{x} \) under equation \((4.2)\) using interval arithmetic and outward rounding, which will return a new vector of values for the center box and a new vector of box radii. Now, use interval arithmetic and outward rounding to find an outer enclosure of the maximum values for all 16 entries of \( DF^2(\bar{x}) \) by using the new center and radii vectors. The upper bound of the Lipschitz constant is \( \|DF(F(\bar{x}))DF(\bar{x})\|_\infty = 0.464 < 1 \), which means that there is a stable period two contained within the box \( \bar{x} \). When this process is repeated for different radius values it is discovered that a box centered at \( c \) (with slightly more significant digits) can have a radius as large as 0.118 in all dimensions or as small as \( 10^{-13} \) in all dimensions.

**Example 4.4.6** (Undetermined Point). Determine the stability of the period-two orbit numerically observed when \( d = 0.10 \) and \( r = 22 \). Simulations indicate that the point \( c=(0.567, 6.38, 6.38, 0.567) \) is near the orbit which will be the center of our box with a radius \( r = [.01 .01 .01 .01] \). To use the formula for a Lipschitz estimate \((4.11)\), values for \( DF(\bar{x}) \) and \( DF^2(\bar{x}) \) must be known. Begin by using interval arithmetic and outward rounding to find an outer enclosure of the maximum values for all 16 entries of \( DF(\bar{x}) \). Next, compute the image of \( \bar{x} \) under equation \((4.2)\) using interval arithmetic and outward rounding, which will return a new vector of values for the center box and a new vector of box radii. Now, use interval arithmetic and outward
rounding to find an outer enclosure of the maximum values for all 16 entries of $DF^2(\tilde{x})$ by using the new center and radii vectors. The upper bound of the Lipschitz constant is $\|DF(F(\tilde{x}))DF(\tilde{x})\|_\infty = 0.864 < 1$. However, this does not imply the existence of a period-two point. It was never shown that $F : \tilde{x} \rightarrow \tilde{x}$, which would be done by mapping $\tilde{x}$ twice (using interval arithmetic) and seeing if $F^2(\tilde{x}) \subseteq \tilde{x}$. Outward rounding results in too much error for this condition to be satisfied so the existence and stability of a periodic orbit when $d = 0.10$ and $r = 22$ cannot be proven.

Example 4.4.5 proves the existence of a stable period-two orbit when $r = 22$ and $d = 0.15$. The four-patch subsystem was proposed as a possible deterrent to extinction. Strong evidence for this claim is drawn from the values of confirmed periodic orbits. According to example 4.4.5, two periodic points are approximately $x_1 = (6.63, 0.747, 0.747, 6.63)$ and $x_2 = (0.747, 6.63, 6.63, 0.747)$. Recall from figures 3.4 and 3.7 that the smallest global extinction threshold for $r = 22$ and $d = 0.15$ is $e_0^* = 0.752$, which is suspiciously close to the minimum entries of $x_1$ and $x_2$. This trend is reflected in other periodic orbits that have been rigorously proven to exist such as $d = 0.20$ and $r = 22$, where the minimum orbit value is approximately 0.9819 and $e_0^* = 0.9820$.

Using the method outlined in example 4.4.5, the existence of period-two orbits has been rigorously proven for selected parameter values. Figure 4.4 shows how as dispersal increases, the point on the period-two orbit of smaller magnitude grows larger, which means that a higher local extinction threshold, $e_0$, is needed in order to eliminate the subsystem. However, figure 4.3 displays graphically how large dispersal values affects the structural integrity of the subsystem because dispersal out of the subsystem is large enough to reseed codimension-one neighbors. These findings about the four-patch subsystem provide a dynamical mechanism to explain topological data computed in the previous chapter.
Chapter 5

Conclusion

In this project a coupled patch model is used to simulate a population’s growth and dispersal in a patchy environment. The evolution of patterns generated by this model are tracked and measured using computational topology. Some of our findings are reminiscent of the work of Sheffer et al. [11] describing shifts in population patterns as populations near extinction. We further investigate subsystems that develop near extinction in order to understand more of the mathematics of how global extinction occurs in this model.

In chapter 4 the existence and stability of period-two orbits for a four-patch subsystem are proved. This four-patch system emerges in simulations as a decoupled subsystem that appears to be very resistant to extinction. Furthermore, numerical simulations conducted in chapter 3.2 suggest that this subsystem is the smallest stable subsystem. We have observed subsystems of this type for larger dispersal values but have not for smaller dispersal values. Given an initial condition and appropriate parameter values (where the existence of a stable period-two orbit in the four-patch subsystem has been proven) it is not clear whether we should expect to see the emergence of the stable period-two orbit in a decoupled four-patch subsystem. This is due to the fact that along the trajectory of the initial condition used for the simulation, the system must decouple in a way that produces a four-patch subsystem (connected as in figure 3.3) and then population values on this four-patch subsystem must be attracted to the stable period-two orbit. Although proven to exist for the general system, stable period-two behavior has not been observed for some initial conditions. However, when it is observed, as is the case with many systems and initial conditions studied, the stable period-two behavior prevents extinction and therefore gives a lower bound on the global extinction threshold.

In chapter 3 the positive influence of dispersal on population robustness is displayed through the use of numerical simulations. Figure 3.7 displays how a sys-
tem’s global extinction threshold is affected by the dispersal parameter. The same relationship between dispersal and global extinction threshold is observed when dispersal values are non-homogeneous as well as in simulations where dispersal varies stochastically in time. Also, figure 3.7 displays observed transitions in the asymptotic topological behavior of systems that are, in a sense, close to extinction. Like the relation between dispersal and global extinction threshold, dispersal appears to directly influence the observed topological transition. In all simulated extinction events, the number of enclosed extinct regions, $\beta_1$, decreases significantly before the number of connected components, $\beta_0$. The importance of where these two time series cross and the topological shift that it represents should be further investigated.

It is hypothesized that stable periodic orbits in decoupled subsystems offer one explanation for why higher dispersal parameters lead to higher global extinction thresholds; however, more evidence is necessary to support such a claim. Future research should investigate stable periodic orbits in decoupled subsystems other than the four-patch subsystem presented. Also, future research should investigate attracting neighborhoods of stable periodic orbits to determine if there are characteristics of initial conditions which would make the trajectory of the initial condition more resistant to extinction. The investigation of attracting neighborhoods for stable orbits in lower-dimensional decoupled subsystems would also serve to further explain changes observed in topological data for simulations with heterogeneous dispersal parameters.
Bibliography


Chapter 6

Appendices

6.1 Definitions Appendix

This appendix supplies additional information about the programming techniques used to optimize computation of the Ricker model. Simulations are coded in Matlab and all scripts needed to run simulations and reproduce figures are provided in the on-line appendix. For the purpose of completeness, we provide a sketch of how the simulation’s dispersal phase is coded.

Recall how $R \in \mathbb{R}^{n \times n}$ stores local fitness values and $P(k) \in \mathbb{R}^{n \times n}$ stores local abundance values. Also, recall equation (2.4),

$$P'_{i,j}(k) = R_{i,j}P_{i,j}(k)e^{-P_{i,j}(k)}.$$

Computations are made more efficient by recasting the coupled Ricker equations into matrix form. Let $D$ be a matrix whose off-diagonal elements have a value of one and zero elsewhere:

$$D_{i,j} = \begin{cases} 1 & i = j \pm 1 \\ 0 & \text{otherwise} \end{cases}. \tag{6.1}$$

Using this matrix $D$ the process of summing all neighbors of a patch can be reduced to two matrix multiplications, $D \times P'(k) + P'(k) \times D$. The $D$ matrix is sometimes referred to as the dispersal matrix. Now, we define $F : \mathbb{R}^{n^2} \times \mathbb{R}^{n^2}$. Similar to before,

$$P(k + 1) = F(P(k)),$$

but we now make use of matrix notation:
\( P'_{ij}(k) = RP(k)e^{-P(k)} \)

\[ F(P(k)) = (1 - d)P'(k) + \frac{d}{4}(D \times P'(k) + P'(k) \times D). \]  \hspace{1cm} (6.2)

There is a difference between traditional matrix multiplication and entry-wise operations that are common in programming situations. In our notation, if two matrices are side-by-side with no operand between them then the implied operation is entry-wise multiplication; an example is \( RP(k) \). If two matrices are separated by a \( \times \) symbol then the implied operation is matrix multiplication, such as \( D \times P'(k) \). This notation, although it is used in actual computation of the model, was omitted from the main body of the thesis because the lack of an operand is not standard notation within the mathematic community.
6.2 Practical Computation of Stochastic Simulations

Simulations are coded in Matlab and all scripts needed to run simulations and reproduce figures are provided in the on-line appendix. For the purpose of completeness, we provide a sketch of how the simulation’s dispersal phase is coded.

Recall how $R \in \mathbb{R}^{n \times n}$ stores local fitness values and $P(k) \in \mathbb{R}^{n \times n}$ stores local abundance values and that we created random matrices to store pseudo-random dispersal values, $D_{i,j}^l \sim N(d^l_4, \sigma^2)$, $D_{i,j}^r \sim N(d^r_4, \sigma^2)$, $D_{i,j}^u \sim N(d^u_4, \sigma^2)$, $D_{i,j}^d \sim N(d^d_4, \sigma^2)$.

We now turn to matrix notation to optimize the computation process. We begin by creating two new matrices (for which superscripts do not imply powers):

\[
D_{i,j}^1 = \begin{cases} 
1 & i = j + 1 \\
0 & \text{otherwise} \end{cases} \quad (6.3)
\]

and

\[
D_{i,j}^2 = \begin{cases} 
1 & i = j - 1 \\
0 & \text{otherwise} \end{cases} \quad (6.4)
\]

With these additional matrices the process of summing neighboring patches is given more compact notation. The more compact notation is both easier to code and has a run time that is significantly faster than a loop method implied by the previous formulation. Now, we define $F : \mathbb{R}^{n^2} \times \mathbb{R}^{n^2}$. Similar to before,

\[P(k+1) = F(P(k)),\]

but we now make use of matrix notation:

\[
P'_{i,j}(k) = RP(k)e^{-P(k)} \\
F(P(k)) = (1 - D^l - D^r - D^u - D^d)P'(k) + \\
P'(k)D^l \times D^2 + P'(k)D^r \times D1 + D^2 \times P'(k)D^d + D^l \times P'(k)D^u. \quad (6.5)
\]

There is a difference between traditional matrix multiplication and entry-wise operations that are common in programming situations. In our notation if two matrices are side by side with no operand between them then the implied operation is entry-wise multiplication; an example is $P'(k)D^l$. If two matrices are separated by a $\times$ symbol then the implied operation is matrix multiplication, such as $D^l \times D^2$. This notation, although it is used in actual computation of the model, was omitted.
from the main body of the thesis because the lack of an operand is not standard notation within the mathematic community.

6.3 Proof that \( d_{i,j} \sim N(d, \sigma) \)

Each value in stochastically generated dispersal matrices discussed in section 3.4 is defined such that \( D_{l,i,j} \sim N(\frac{d}{4}, \frac{\sigma}{2}) \), \( D_{r,i,j} \sim N(\frac{d}{4}, \frac{\sigma}{2}) \), \( D_{u,i,j} \sim N(\frac{d}{4}, \frac{\sigma}{2}) \), \( D_{d,i,j} \sim N(\frac{d}{4}, \frac{\sigma}{2}) \). The moment generating functions of the dispersal matrices are:

\[
\begin{align*}
    m_{D_{l,i,j}}(t) &= e^{\frac{d}{4}t + \frac{\sigma^2 t^2}{8}} \\
    m_{D_{r,i,j}}(t) &= e^{\frac{d}{4}t + \frac{\sigma^2 t^2}{8}} \\
    m_{D_{u,i,j}}(t) &= e^{\frac{d}{4}t + \frac{\sigma^2 t^2}{8}} \\
    m_{D_{d,i,j}}(t) &= e^{\frac{d}{4}t + \frac{\sigma^2 t^2}{8}}.
\end{align*}
\] (6.6)

Also, recall that \( d_{i,j} \) was defined to be

\[
d_{i,j} = D_{l,i,j} + D_{r,i,j} + D_{u,i,j} + D_{d,i,j}.
\]

Then, the moment generating function of \( d_{i,j} \) is simply the product of the moment generating functions of the independent random variables that are summed to create \( d_{i,j} \), which is:

\[
m_{d_{i,j}}(t) = \left( e^{\frac{d}{4}t + \frac{\sigma^2 t^2}{8}} \right)^4 = e^{dt + \frac{\sigma^2 t^2}{2}}. \] (6.7)

Moment generating functions uniquely define probability distributions and this moment generating function has the form of a normal distribution with mean \( d \) and variance \( \sigma^2 \). [13]
6.4 Additional Figures for Deterministic Simulations

Section 3.2 mentions how there are three different types of expected long term behavior for simulations when an extinction threshold is used. One of these expected behaviors had representative figures within the text. Here, figures depicting data obtained from extinction simulations is provided as well as data from simulations where no longterm subsystems develop.

Figure 6.1: Graph of time series data recording the total abundance of the Ricker simulation for parameter values: \(d = 0.15, r = 22, e_o = 0.2, IC = 1\). A Betti time series is not provided for these parameter values because the system’s topology changes very quickly.
Figure 6.2: Graph of time series data recording the total abundance of the Ricker simulation for parameter values: \( d = 0.15, r = 22, e_o = 0.6, IC = 1 \). It should be noted that the total abundance is not period two as it might appear; this is a result of the scale being in terms of \( 10^5 \).

Figure 6.3: Graph of time series data recording the homology of the Ricker simulation for parameter values: \( d = 0.15, r = 22, e_o = 0.6, IC = 1 \). Blue (darker) denotes \( \beta_0 \) and cyan (lighter) denotes \( \beta_1 \). It should be noted that \( \beta_0 \neq 0 \) but it is close, asymptotic value is 5.
Figure 6.4: Graph of time series data recording the total abundance of the Ricker simulation for parameter values: $d = 0.15, r = 22, e_o = 0.77, IC = 1$.

Figure 6.5: Graph of time series data recording the homology of the Ricker simulation for parameter values: $d = 0.15, r = 22, e_o = 0.77, IC = 1$. Blue (darker) denotes $\beta_0$ and cyan (lighter) denotes $\beta_1$. 
6.5 Additional Figures for Stochastic Simulations

Section 3.3 presented representative figures of how stochastic dispersal effects different regions of parameter space. This appendix supplies representative figures for the effect of redrawing new stochastically generated dispersal values after each time step. Like the representative figure of section 3.3, all simulations used the same initial condition. Figures and data from other initial conditions are available through the online appendix.

**Long term Behavior of Abundance for different $\sigma$**

![Graph showing total abundance time series data for $r = 22$, $c_o = 0.60$, $IC = 1$, and $d = 0.15$. Colors represent different standard deviations with $\sigma = 0$ (blue), $\sigma = 0.01$ (red), $\sigma = 0.04$ (green), $\sigma = 0.1$ (cyan). Dispersal values were redrawn after each time step. Simulations were run for 500 time steps of which the last 100 are plotted. If the simulation went extinct before 500 time steps then the last 100 iterates are plotted.]

Figure 6.6: Total abundance time series data for $r = 22$, $c_o = 0.60$, $IC = 1$, and $d = 0.15$. Colors represent different standard deviations with $\sigma = 0$ (blue), $\sigma = 0.01$ (red), $\sigma = 0.04$ (green), $\sigma = 0.1$ (cyan). Dispersal values were redrawn after each time step. Simulations were run for 500 time steps of which the last 100 are plotted. If the simulation went extinct before 500 time steps then the last 100 iterates are plotted.
Longterm Behavior of $\beta_0$ for different $\sigma$

Figure 6.7: Number of connected components, $\beta_0$, time series data for $r = 22$, $e_o = 0.60$, $IC = 1$, and $d = 0.15$. Colors represent different standard deviations with $\sigma = 0$ (blue), $\sigma = 0.01$ (red), $\sigma = 0.04$ (green), $\sigma = 0.1$ (cyan). Dispersal values were redrawn after each time step. Simulations were run for 500 time steps of which the last 100 are plotted. If the simulation went extinct before 500 time steps then the last 100 iterates are plotted.
Figure 6.8: Number of enclosed extinct regions, $\beta_1$, time series data for $r = 22$, $e_o = 0.60$, $IC = 1$, and $d = 0.15$. Colors represent different standard deviations with $\sigma = 0$ (blue), $\sigma = 0.01$ (red), $\sigma = 0.04$ (green), $\sigma = 0.1$ (cyan). Dispersal values were redrawn after each time step. Simulations were run for 500 time steps of which the last 100 are plotted. If the simulation went extinct before 500 time steps then the last 100 iterates are plotted.
6.6 Simulation Code

%%%%%%% Ben Holman %%%%%

%% MatLab script can reproduce data cited in my senior thesis, April 2011
for simplicity this script has reduced functionality and assumes that local fitness
values are fixed at the same value for all patches for all time steps (a preliminary
version allowed for fitness values to be modified much like the dispersal values
can be) a function to compute the coupled Ricker system of equations based upon
inputs of :

% d := average dispersal value, coupling between patches
% dspread := variance of the normal random distribution from which
% dispersal values are drawn
% freq := how often to draw new dispersal values
% T := length of time to run the simulation,
% will stop early if global extinction occurs
% thres := threshold for topology
% ethres := local extinction threshold
% IC := initial condition that is imported, assumes a value in {1,2,3,4}

% calls CHomP which is available for free on the computational homology
% project website, http://chomp.rutgers.edu/
% calls saveData.m which is available through the online appendix
% imports initial conditions available through the online appendix

% data is saved in two text files where the name is reflective of the
% parameter values used.

function exThres(d,dspread,freq,T,thres,ethres,IC)

tnn = sprintf('exThres_%g_%g-%g_%g_%g.txt',d,dspread,freq,ethres,IC);
tn = sprintf(tnn);
% temporary files to save data that is exported to CHomP

% parameters
n=201; % size of spatial grid
D1 = diag(diag(ones(n),1),1);
D2 = diag(diag(ones(n),-1),-1);
Dr1 = (d + dspread*randn(n))*.25;
Dr2 = (d + dspread*randn(n))*.25;
Dr3 = (d + dspread*randn(n))*.25;
Dr4 = (d + dspread*randn(n))*.25;
R = 22*ones(n);
storage = ";
abundance = zeros(1,T);

tmp = sprintf('IC_%g.mat',IC);
N = importdata(tmp); %import the chosen initial condition

% ————Simulation code——————
for t = 1:T

  %———Extinction——————
  N(N<ethres)=0;

  %———Betti Calculations ——
  %this is not efficient, it would be faster to run CHomP from .mex files
  [I,J,K]=find(N>thres);
  if(size(I) == 0)
    tmpid = fopen(tn,'w');
    fprintf(tmpid,'(%g,%g)\n',[I,J])
    fclose(tmpid);
    command = sprintf('chomp %s',tn);
    [status, betti] = unix(command);
    storage = [storage betti];
  else
    storage = [storage '0 0 0\n'];
  end

end

%———check if dispersal should be changed ———
if mod(t,freq) == 0
  Dr1 = (d + dspread*randn(n))*.25;
  Dr2 = (d + dspread*randn(n))*.25;
  Dr3 = (d + dspread*randn(n))*.25;
  Dr4 = (d + dspread*randn(n))*.25;
end
%——-Abundance data ———-
abundance(t) = sum(sum(N));

%——-Check for Extinction ——
if abundance(t) == 0
    saveData(d,dspread,freq,ethres,IC,storage,abundance);
    command = sprintf('rm %s',tnn);
    unix(command);
    return;
end

%——-iterate simulation ——
N = R.*N.*exp(-N);
N = (1-(Dr1+Dr2+Dr3+Dr4)).*N+(N.*Dr1)*D1+D1*(Dr2.*N)+(N.*Dr3)*D2 + D2*(Dr4.*N);
end

saveData(d,dspread,freq,ethres,IC,storage,abundance);
%will save data to text files
command = sprintf('rm %s',tnn); %remove temporary files
unix(command);
end

6.7 Contracting Neighborhood Code

%takes the input vectors c and r that are the center and radii of boxes and
%computes what the Lipschitz constant is for the four dimensional subsystem
%if the point is on a period 2 orbit

%outward rounding is performed. Machine accuracy is 10^-16 and I over
%compensate for this by rounding out by 10^-15 in strategic places.

%if r=22 and d=.1 then
%c = [0.5675808573958 6.3826868193922 6.3826868193922 0.5675808573958]
%is on the period 2 orbit, and stable for box size of r=ones(1,4).*12

function L=lip(c,r,d,R)
Y = compY(c,r);
Yim = ricker(c’,r’,d,R);
Yim = compY(Yim(1:4),Yim(5:8));
DF1 = jac(Y,d);
DF2 = jac(Yim,d);

%find row sum of norm
L = R*(norm(DF1*DF2,Inf)+10^(-15));

function Y=compY(c,r)
%find maximum of entries in Jacobian over specified interval
ylower = abs(fprime(c-r))+10^(-15);
yupper = abs(fprime(c+r))+10^(-15);
tmp1 = ylower < yupper;
tmp2 = abs(1-tmp1);
tmp3 = c-r-10^(-15) < 2 < c+r+10^(-15);
tmp4 = abs(1-tmp3);
Y = ylower.*tmp2 + yupper.*tmp1;
Y = Y.*tmp4 + exp(-2).*tmp3+tmp3.*10^(-15);
end

%function to compute derivative of growth term
function y=fprime(x)
y = exp(-x).*(1-x);
end

%computes the interval image of box (c,r)
function y=ricker(c,r,d,R)
%get x values
xl = c-r-10^(-15);
xu = c+r+10^(-15);
%map growth term
[ygl, ygu] = intSort(xl,xu,R);
ygltmp1 = (ygl(2) + ygl(3))*d/4;
ygltmp2 = (ygl(1) + ygl(4))*d/4;
ygutmp1 = (ygu(2) + ygu(3))*d/4;
ygutmp2 = (ygu(1) + ygu(4))*d/4;
yl = ygl*(1-d)+[ygltmp1; ygltmp2; ygltmp2; ygltmp1];
yu = ygu*(1-d)+[ygutmp1; ygutmp2; ygutmp2; ygutmp1];
y = [(yu+yl)*.5; (yu-yl)*.5+10^(-15)];
end

% handy dandy helper function
function [ygl, ygu]=intSort(xl,xu,R)
ygl = R.*xl.*exp(-xl)-10^(-15);
ygu = R.*xu.*exp(-xu)+10^(-15);
tmp1 = ygl < ygu;
tmp2 = abs(1-tmp1);
tmp3 = ygl;
ygl = ygl.*tmp1 + ygu.*tmp2;
ygu = tmp3.*tmp2 + ygu.*tmp1;
for j=1:4
    if xl(j)<1 && xu(j)>1
        ygu(j)=R*exp(-1)+10^(-16);
    end
end
end

% enter values into Jacobian
function J = jac(x,d)
J(1,1) = (1-d)*x(1);
J(1,2) = d*x(2)/4;
J(1,3) = d*x(3)/4;
J(4,4) = (1-d)*x(4);
J(4,2) = d*x(2)/4;
J(4,3) = d*x(3)/4;
J(2,1) = d*x(1)/4;
J(2,2) = (1-d)*x(2);
J(2,4) = d*x(4)/4;
J(3,1) = d*x(1)/4;
J(3,3) = (1-d)*x(3);
J(3,4) = d*x(4)/4;
end