The Mathematics of Critical Shifts in Ecological Networks with Alternative Stable State Theory, A Potential Framework for Early Warning Indicators

by

Michael Kupperman

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Honors Bachelors of Science in Mathematics
(Honors Scholar)

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A long running problem in mathematical biology is the prediction of extinction events, a specialized case of the larger global stability problem found in differential equations and dynamical systems theory. A central technical question is how to introduce the randomness observed in real ecological systems not accounted for in deterministic models. This work introduces the SP-system as a new mathematical object in which ecological parameters are treated as sequences of random variables that attain values over intervals of random lengths of time. The SP-system characterization of ecological networks leads to two different novel approaches for the simulation and extinction prediction. The first approach uses a construct new to modeling literature to describe the probability of a parameter transition event into an extinction event. The second approach utilizes Markov chains for both simulation and extinction prediction. A constructive technique for the associated probability kernel is demonstrated as the basis of the Markov chain approach. An example of each application is presented.

Keywords: Mathematical Biology, Probability and Simulation, Stochastic Parameters, Applied Random Dynamical Systems, Alternative Steady State Theory

Corresponding email address: kuppermm@oregonstate.edu

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APPROVED:

David Koslicki, Mentor, representing Mathematics

Patrick De Leenheer, Committee Member, representing Mathematics

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Mark Novak, Committee Member, representing Integrative Biology

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Toni Doolen, Dean, Oregon State University Honors College

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my project to any reader upon request.

Michael Kupperman, Author

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1 Introduction

Theoretical ecology attempts to construct and analyze abstract mathematical models that describe physical ecological systems [18, 26, 27, 20, 23]. As such, describing model parameters in terms of the underlying ecological system is often necessary to begin quantifying parameters in structured models. However, gathering independent observations of an ecological system for parameter estimation is quite difficult as parameters in ecological systems tend to be highly autocorrelated [32, 44, 15] and have a large number of simultaneous nonlinear interactions with multiple feedback pathways (see [48] for a review). As a result, direct estimation is quite difficult, requiring high-powered statistical analyses to generate robust estimates of underlying parameter distributions [31, 30]. As a result, classical analytical methods in mathematical biology have emphasized the mathematical and ecological relationships between model parameters, rather than relying on good estimates of the parameter values from which to begin an analysis (see [28] for a comprehensive discussion of classical techniques and case studies, [25] for a classical technique, and [8, 46] for modern deterministic and stochastic techniques respectively).

After reading the above, one may have the impression that the statistical complications which may appear as noise in ecological systems is at best another layer of experimental complexity, and at worst a significant technical challenge in the study and analysis of ecological systems. However, one quickly realizes that across the life sciences, the structural complexity, stochasticity, and nonlinearity that complicate the analysis are essential characteristics of biological systems [18]. The complexity required to maintain robust biological systems provides numerous opportunities to study the underlying interactions and structure from both an ecological and mathematical standpoint. If real systems were only as robust as our smooth and continuous deterministic approximations, their comprehension would not present nearly an interesting challenge.

Classical modeling methodologies assume that parameter values are unknown, but obey fixed algebraic relationships (e.g. $a < b$). This allows for the application of standard methods in dynamical systems analysis, both discrete and continuous, to be utilized. However, these methods rely on the assumption that the parameters that describe the ecological system are fixed while independent of the state of the population. As a result, these methods offer a limited framework to describe the interplay between stability of models and the randomness in the underlying system not explicitly depicted in deterministic models.

This thesis seeks to determine the potential significance of stochastic parameter variations on model end-behavior and examines the possibility of the application of the framework we will develop to extinction prediction within the existing ecological framework of alternative stable state theory [13, 14, 40].

1.1 A biological description of the problem

Parameters in mechanistic models of biological systems attempt to reduce complex phenomenon down to a numerical value, often this value will be selected from an empirical distribution computed by measurements of a system. Direct parameter estimation from observational data is quite difficult, resulting in the generation of multiple distributions of data from which a single *best* point estimate is extracted (see [30]). Statistical techniques have been employed to attempt to reduce the variability of parameter estimates, but no technique to date directly incorporates parameter variability directly into the mechanisms encapsulated in an ODE model. In measurements of materials, often seen in chemistry, physics, and material science, assumptions about the behavior of the system allow for homogeneity assumptions which result in parameters that are often exact within a small error bound. Error in the estimate is primarily a source of measurement error or approximations of behavior made in the model rather than variability within the object being measured.

In biological systems, parameters may themselves be described by a distribution with a non-negligible variance [47]. For example, a birth or death rate process on an intermediate sized population may exhibit variance between measurements of process, where the process may occur at some rate over some interval of time, $(t_0, t_0 + (\Delta t)_0)$, and then occur at a

different rate over another interval of time $(t_1, t_1 + (\Delta t)_1)$. We can state that the observed process exhibits some degree of stochasticity.

The effect I am describing is not to be confused with demographic stochasticity or environmental stochasticity. These processes are described as stochastic, but are perhaps better characterized as a deterministic modification to the system as a result of an unpredictable or random event, such as a flood impacting a habitat or a mutation impacting the birthrate. The ecological effects we are attempting to model in these works are intrinsic phenomenon to the population that describes an underlying process that may appear stochastic. This will be further explored in section 2.2.2.

1.2 A mathematical description of the problem

This thesis examines the question of the stability of a dynamical system when parameter values are fixed for short intervals of time, and attain new random values from a known underlying distribution. Standard mathematical modeling techniques and analytical methods in literature largely avoid addressing this situation due to both its limited parallels with other physical systems and the difficulty of potentially novel technical challenges that must be overcome. Ecological systems are often investigated either statistically through statistical analyses of population data or theoretically with the usage of bifurcation theory to identify critical parameters in bifurcations and describe the associated transitions. The problem I have introduced can be viewed as a novel variation on the premise of control theory, in which model parameters are controlled directly by dials which are all randomly changed independent of each other.

The reader may notice that these observations echo those similar to those developed by early mathematical biologists [24, 26] of the applicability of classical dynamical systems theory. Random dynamical systems theory offers stochastic differential equations as a method to describe the population. However, the overwhelming majority of stochastic models used in modeling literature assume that populations have a continuous random rate of change coupled with a randomly occurring deterministic modification to the rate of change. This is a primarily due to historical factors, rather than the difficulty of associated technical

challenges. Much of the probabilistic development of random dynamical systems can be traced back to stochastic analysis and the pursuit of understanding stochastic differential equations [1].

As we are interested primarily in the stability of the system, we introduce a method to relate the distribution of the stochastic parameter(s) of interest to the probability that a solution trajectory originating at a known initial condition transitions from one region of stability to another as the parameters change randomly over time. Classical methods for introducing noise with stochastic processes rely on introducing a white-noise term to represent some stochastic noise acting on the system in addition to the deterministic term. This rests on the validity of the assumption that the parameters for both the deterministic term and stochastic term are known to within a small error bound. Rather than attempting to introduce and define a new stochastic term [12], we introduce and develop a new modeling technique that incorporates stochasticity at the parameter level. This approach can be implemented with less parameters while incorporating the variance of parameter distributions directly into the model. This approach begins from a relatively simple observation about the fundamental nature of global stability as it applies to alternative stable state theory. This approach gives rise to a new method to investigate regime changes and transitions across a critical threshold.

Simulation strategies for ordinary differential equation and stochastic ordinary differential equation models often utilize a combination of Monte-Carlo methods and direct numerical simulation to obtain results. These experiments are limited by available computing capabilities. To perform parameter sweeps over high dimensional parameter state spaces often requires large amounts of time and computer storage space. We will then develop an alternative method to describe the behavior of systems with stochastic parameters explicitly. We show that these systems can be described as a Markov chain and demonstrate how to construct a Markov Kernel under mild assumptions.

1.2.1 Approach

The approach described in this thesis, in broad terms, is to treat model parameters as random variables, then proceed by analyzing the systems as a result of new probabilistic behavior. In sections 3, we develop the method of stochastic parameters as a technique to directly compute theoretical probabilities of a regime change event within a simulation. We consider the population as deterministic, with randomly occurring changes in the parameters, which may or may not cause a regime change event (see figure 1.1). In section 4, we develop a theorem which encapsulates this technique. In section 5, we observe that a Markov chain can be produced by constructing a sequence of transition points and provide a constructive technique to define the associated transition kernel.

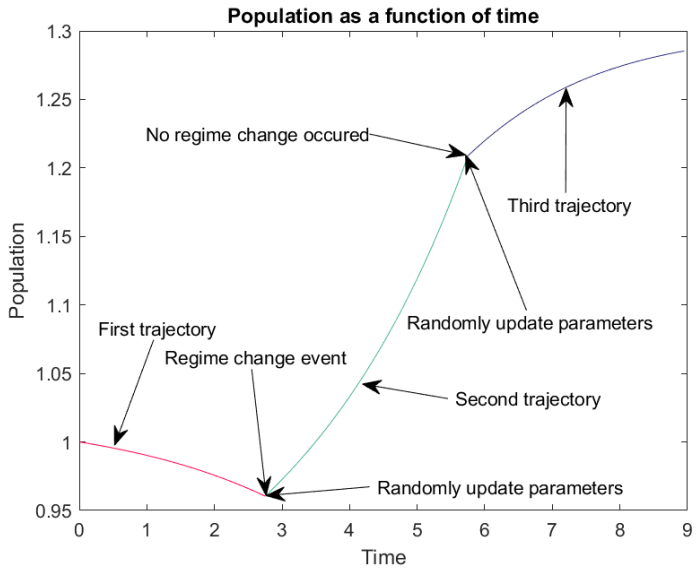

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Figure 1.1: A depiction of the general scheme by which the population trajectory can be described. An initial state and set of parameters are fixed, then the population is simulated forward in time. This occurs until a randomly selected time, at which all parameters are redrawn from their respective distributions. This may or may not cause a regime change event. The population is forward simulated until another parameter change event occurs. This process can be iterated until an extinction event occurs, the population stabilizes at an equilibrium, or a stopping time is reached on the simulation.

2 Preliminaries

This section presents an overview of the relevant mathematics and ecology for this thesis.

2.1 Mathematics

2.1.1 Population modeling

When constructing a population model, there are three significant decisions that must be made before any equations can constructed:

1. Is the spatial distribution of the population a significant contributor to the system of interest? Can we make the assumption that the population is spatially homogeneous?

2. Is a discretization appropriate for the population size and time variable? This determines if a difference equation or differential equation framework is to be used.

3. Can we assume that all members of a species can be attributed to the same population? Are there significant factors or attributes that can be used to partition the population?

A classic example of a system where the spatial homogeneity cannot be assumed is in the study of wolf-moose systems as *Canis lupis* are social but territorial species - packs compete with other packs for territory and the resources that they contain. The age or sex of a member within a population may significantly influence the population dynamics. On a finer note, populations may be partitioned by non-karyotype genetic factors that influence preferences and/or behavior.

A standard approach in mathematical biology is to assume that populations are large enough to be approximately spatially homogeneous [7] unless there is explicit evidence to the contrary [19]. This approach is common in systems governed by the principle of mass action and is often found in well mixed populations, including microbial ecosystems, biochemical systems, (historical) fisheries models, and susceptible-infected-recovered (SIR) models.

This permits the construction of compartment model for populations. In a compartment model, the behavior of the population is entirely characterized by births, deaths, immigration, emigration, nutrient flux, and predation effects. All models of this type can be summarized into the following equation (2.1).

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \text{births}(t) - \text{deaths}(t) + \text{feeding}(t) - \text{predation}(t) + \text{immigration}(t) - \text{emigration}(t) \quad (2.1)$$

The right-hand side of this equation is often summarized into the generic form $f(N)$ or $f(t, N)$ to preserve generality. We will assume that f is a continuous function on $\mathbb{R}_+$ with an infinity of derivatives ($f \in C^\infty(\mathbb{R}^n_+)$). There are multiple expressions used by modelers to represent different phenomena, however linear or constant functional forms are preferred where possible. The usage of linear terms is two-fold: linear representations of systems may permit algebraic manipulation into a matrix model and/or decrease the computational difficulty of finding or approximating solutions. The introduction of nonlinear behavior is required to commonly reflect a saturation effect in which per-capita returns are diminishing, or to reflect a decrease in per-capita rates at low population density. Examples of the five main functional forms used within this thesis are described in table 2.1.

The interaction between two species: prey N and predator P can be described in the algebraic form given within equation (2.2), for a functional form f. Several common examples of functional forms are given in Table 2.1. This is not a representative sample or exhaustive list of functional forms in literature, these are due to Holling [18] and are commonly accepted algebraic generalizations of these functional forms.

$$Nf(N, t)P \quad (2.2)$$

Population models can have two additional qualities. They can be well-defined and well-posed.

Definition 2.1.1.1 (Well-defined model)**.** *A mathematical model given by the function $f : X \to Y$ is well defined if and only if $\forall x \in X, f(x) \equiv y$ for only one $y \in Y$.*

Definition 2.1.1.2 (Well-posed model)**.** *A model is well-posed if and only if it is both well-*

Table 2.1: A table of commonly found functional forms in mathematical models for interaction terms. The functions $f(N,t)$ are used within a mass action functional framework, see equation 2.2.

	Functional form	Parameters	Description
Constant rate	$f(N,t) = \frac{k}{N}$	k	Note that $Nf(N,t) = k$, describing a constant rate independent of time and population. Often used for immigration or emigration.
Linear (Holling type I)	$f(N,t) = aN$	a	Dependent linearly on population size, a commonly describes the interaction strength.
Holling Type II	$f(N,t) = \frac{aN}{1+ahN}$	a, h	Describes saturation behavior at $N = \frac{1}{h}$, where a describes the interaction strength.
Holling type III	$f(N,t) = \frac{aN^n}{1+ahN^n}$	a, h, n	One generalization of the type II response. The same end behavior as in type II is also found, this functional form imposes a penalty for 'low' densities. Commonly, $n \in [1,3]$, but there is no rule governing this.

defined, where there exists a unique solution for a given set of allowed initial conditions, and all populations are always non-negative.

Remark 2.1.1.3. *Many well-defined models can be written down that are not well posed. To ensure that the model is well-posed, we wrap the function f that describes the population within a maximum argument, to obtain $\tilde{f}(N) = \max\{f(N), 0\}$.*

All models posed in this thesis will be well-defined.

We next transition to a discussion of a more abstract mathematics. The remainder of this section is centered around the discussion of dynamics and probability theory. We begin by introducing an algebraic structure in preparation for dynamical systems. We then will continue our development of ordinary differential equation models into dynamical systems, where we will utilize the algebra we next introduce. The details presented here are primarily used in section 5.

2.1.2 Algebra

Our discussion of algebra is limited to a discussion of groups and monoids.

Definition 2.1.2.1 (Group)**.** *A group G is a pair $(S, +)$, where S is a set and $+ : S \times S \to S$ is a binary operation such that*

1. *for any $a, b \in S$, $a + b \in S$, $b + a \in S$ (closure)*
2. *for any $a, b, c \in S$, $(a + b) + c = a + (b + c)$, (associativity)*
3. *there exists some $i_S \in S$ named the identity element which for all $a \in S$ satisfies $i_S + a = a = a + i_S$ (identity)*
4. *for any $a \in S$, there exists some element $b \in S$ which satisfies, $b = a^{-1}$ (ie $ab = i_S$) (invertibility)*

We often abuse notation and write $a + b$ rather than $+(a, b)$. Note that condition 1 of the prior definition follows trivially from the definition of the binary operation, and thus

is often omitted. We introduce groups as an algebraic object in advance of introducing dynamical systems. We will later observe that the flow operator φ forms a group on the time index.

The second algebraic structure we will introduce is the monoid. A monoid is a group where assumption 4 does not hold. Note that property 1 is obtained from a totality axiom on the map + in some texts, rather than being obtained from this definition. Formally,

Definition 2.1.2.2 (Monoid)**.** *A monoid M is a tuple $(S, +)$, where S is a set and $+ : S \times S \to S$ is a binary operation such that*

1. *for any $a, b \in S$, $a + b \in S$, $b + a \in S$ (closure)*
2. *for any $a, b, c \in S$, $(a + b) + c = a + (b + c)$, (associativity)*
3. *there exists some $i_S \in S$ named the identity element which for all $a \in S$ satisfies $i_S + a = a = a + i_S$ (identity)*

A monoid time index set can preserve one direction of dynamical behavior. We next introduce a specific monoid constructed from the real line.

Definition 2.1.2.3. *Let $\mathcal{T}_{t_0} = [t_0, \infty)$ for some $t_0 \in \mathbb{R}$ be a set. Then the associated monoid $M = (\mathcal{T}, +_{\mathcal{T}})$ is **homomorphic** to the submonoid $S = ([0, \infty), +)$ of the monoid $R = (\mathbb{R}, +)$. The definition of the binary operation $+_{\mathcal{T}}$ follows from this characterization. The operation is defined $+_{\mathcal{T}}(a, b) = a + b - t_0$, where operations on the right side are inherited from the group $(\mathbb{R}, +)$. $\mathcal{T}$ can be thought of as a forward time index set for dynamical behavior, which we will introduce formally in the next subsection. If $\mathcal{T}$ is used without reference to a specific t_0, then t_0 is assumed to be arbitrary in $\mathbb{R}$.*

2.1.3 Function spaces

In this section, we introduce the space of bounded continuous functions on X.

Definition 2.1.3.1 (Space of bounded continuous functions C)**.** *The space $C(X)$ is a*

metric space of continuous functions is given as

$$C(X) = \{f : X \to \mathbb{R} : f \text{ is continuous}, \sup_{x \in X} |f(x)| \leq M \text{ for some } M \in \mathbb{R}\} \tag{2.3}$$

Where $\sup_{x \in X} |f(x)| = ||f||_\infty$ *is the uniform norm.*

2.1.4 Dynamical systems and ordinary differential equations

The study of dynamical systems lends itself well to providing both vocabulary and theory to describe the behavior of populations. Differential equations are but one type of dynamical system, however we will first limit our discussion of dynamical systems to that which can be described deterministically as differential equations (as opposed to stochastic differential equations). A robust conversation can be found here [34] (or for a *much* more abstract approach see [22]).

Let

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x) \tag{2.4}$$

be an autonomous (possibly) nonlinear system where $f(x)$ is defined in (2.1). The solutions of (2.4) are called flows or flow functions, and are denoted a φ. This flow is sometimes interchangeably referred to as the flow of the differential equation (2.4) or the solution flow operator. Solution flows to differential equations are useful as they satisfy multiple algebraic properties.

Definition 2.1.4.1 (Flow)**.** *Let $E \subset X$ where E is a nonempty open subset of X containing an identity element of X, $\varphi : T \times E \to X, (t, x) \mapsto \varphi(t, x)$ as a flow over X on the group $(\mathbb{T}, +_{\mathbb{T}})$. This in fact defines a group when $\mathbb{T} = \mathbb{R}$ equipped with $+$, or a monoid when we relax T to a monid where $\mathbb{T} = \mathcal{T}$ equipped with the binary operation $+_{\mathcal{T}}$. The flow function*

φ satisfies the following properties

$$\varphi(0, x) = x \tag{2.5}$$

$$\varphi(t, \varphi(s, x)) = \varphi(t + s, x) \tag{2.6}$$

$$\varphi(t, \varphi(-t, x)) = \varphi(0, x) \tag{2.7}$$

The map φ is also referred to as the group action of the system (2.4).

Remark 2.1.4.2. *The flow φ is referred to as a local flow if* $\mathrm{E} \subsetneq X$*, or a global flow if* $\mathrm{E} = X$*.*

Remark 2.1.4.3. *In literature, the flow $\varphi(t, x)$ is often written as $\varphi^t(x)$ or simply φ^t for brevity if a specific x is assumed.*

Formal proofs that the solution of a differential equation (*solution flow*) is in fact a flow, and satisfies the above criteria can be found in [34]. Often, statements before some starting time t_0 may describe behavior outside of the observable time frame of ecological interest (history). As such, we are often only interested in the forwards behavior of the system, where $t \in [t_0, \infty) \subset \mathbb{R}$. To adjust accordingly, we select a monoid (definition 2.1.2.2) instead of a group by removing the requirement for the existence of additive inverses from our group structure. This results in the removal of the third statement (2.7). Thus, we may restrict our time index space to the subspace of all time values greater than an arbitrary initial condition, $t_0 \in \mathbb{R}$. We will later show that the restriction to $[t_0, \infty)$ induces several useful properties, namely that many flows on $\mathbb{R}_+$, are now bounded functions.

Corollary 2.1.4.4. *The map $\varphi(t_0, \cdot)$ defines an identity map $id_X : X \to X$.*

The proof of this corollary follows from the definition of a dynamical system with a monoid index. These properties can be extended to form an algebraic structure known as a cocycle. Loosely, a cocycle is a structure within a dynamical system that has a group-like structure which preserves some semblance of the dynamical action and which obeys the cocycle equation.

Definition 2.1.4.5 (Cocycle of a dynamical system)**.** *The map $\varphi : \mathbb{T} \times X \to X$ is a cocycle if it satisfies the following*

$$\varphi(g + h, x) = \varphi(g, \varphi(h, x)) \circ \varphi(h, x) \tag{2.8}$$

Such a map is said to satisfy the cocycle equation (2.8)*.*

This characterization allows for the operation of the action of a dynamical system to be decomposed into the composition of the sequential actions of many random dynamical systems. The study of objects characterized by this is the study of skew products, which include objects other than a dynamical system.

A practical discussion of the application of cohomological algebra to abstract dynamical systems can be found here [43].

2.1.5 Equilibria, stability analysis, and regions of attraction

Stability and the existence or nonexistence of regions of attraction are significant properties of dynamical systems. An equilibrium state for a system occurs at $x^\star$ if and only if $x^\star$ satisfies

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x^\star) = 0 \tag{2.9}$$

where $f(x)$ is defined in 2.4. This construction permits a parallel construction from functional analysis. Define $\ker(f) = \left\{x^\star \in \mathbb{R}^n_+ | f(x^\star) = 0\right\}$. The elements of $\ker(f)$ are indexed if $\ker(f)$ is finite or countably infinite. Once $\ker(f)$ is known, every element of $\ker(f)$ may be characterized as stable or unstable.

Nonlinear systems can be approximated with a linear approximation for some ϵ-neighborhood around a point of interest. The system 2.4 can be approximated by the linear system 2.10, where $D[f(x)](x^\star)$ is defined as the jacobian matrix at the point $x^\star$ (definition 2.1.5.1).

$$\frac{\mathrm{d}z}{\mathrm{d}t} = J(x^\star)\ (z),\ z = x - x^\star \tag{2.10}$$

Definition 2.1.5.1 (Jacobian matrix of a system)**.** *The jacobian matrix $J(x)$ of a system*

(formula (2.4)) at a point $x^\star$ is given component-wise by $J(x^\star)_{i,j} = \left.\frac{\partial f_i(x)}{\partial x_j}\right|_{x=x^\star}$.

Remark 2.1.5.2. *The Jacobian matrix $J(x^\star)$ is equivalent to* $\left.D[f(x)]\right|_{x=x^\star}$ *and is sometimes referred to in this form. The later form arises through series approximations of f.*

Note that the matrix $J(x^\star)$ is square as the size of f and x are the same in biological models. Then the system (2.10) can be diagonalized and decoupled, resulting in a similar constant-coefficient differential equation $\dot{x}_j = \lambda_j x_j$, where λ_j is the j^{th} eigenvalue. If all eigenvalues $\lambda_j < 0$, then every 1-dimensional flow φ defined by the decoupled system approaches the origin. This follows from theorem 2.1.5.5, which we will soon introduce.

Definition 2.1.5.3 (Spectrum of a matrix)**.** *Let $\sigma_s : V \to \mathbb{C}$ where V is the space of all square matrices. Then the spectrum a matrix A is given by $\sigma_s(A)$, the elements of $\sigma_s(A)$ are the eigenvalues of A.*

The following definition is from [34] and is the most general definition.

Definition 2.1.5.4 (Stable equilibrium point of an autonomous differential equation)**.** *Let φ denote the flow of the differential equation $\dot{x} = f(x)$ defined over all $t \in \mathbb{R}$. A point $x^\star$ is a stable equilibrium point if $f(x^\star) = 0$ and if for all $\epsilon > 0$ there exists some $\delta > 0$ such that for some open neighborhood of radius ϵ N_ϵ containing $x^\star$, all $x \in N_\epsilon$ and $t \geq t_0$,*

$$\varphi(t, x) \in N_\epsilon(x^\star) \tag{2.11}$$

This definition is not ideal due to both the number of components involved and the analytical requirement of proving convergence. Rather, we introduce the following theorem as a more practical working definition of a stable equilibrium.

Theorem 2.1.5.5 (Stable equilibrium point)**.** *A point $x^\star$ is a stable equilibrium of the system 2.4 if and only if all of the following hold.*

1. $x^\star \in \mathbb{R}^n_+$.
2. $x^\star \in \ker(f)$.
3. $\forall \lambda \in \sigma_s(J(x^\star)), Re(\lambda) < 0$.

A full derivation and proof of theorem 2.1.5.5 can be found in many textbooks (see [34]). However, this leaves an ambiguity as we have not formally defined a maximal subset of the space $\mathbb{R}^n_+$ where this characterization can be extended. To do so, we turn to the theory of regions of attraction.

Definition 2.1.5.6 (Region of attraction)**.** *A region of attraction (RoA) is defined for an equilibrium state $x^\star$ of the system 2.4 as $Z \subset \mathbb{R}^n_+$, where $Z = \left\{x_0 \in \mathbb{R}^n_+ : \lim_{t\to\infty} \varphi(x_0, t) = x^\star\right\}$. Each region of attraction is denoted $Z_{x^\star}$,*

$$Z_{x^\star} = \left\{x_0 \in \mathbb{R}^n_+ | \lim_{t\to\infty} x(t) = x^\star \text{ where } x_0 := x(t_0)\right\} \text{ for } x^\star \in \ker(f) \tag{2.12}$$

Methods for determining the existence and definitions of RoA vary depending on the dimension (number of species). Exact characterizations are algebraically complicated to compute for high dimensional spaces, and even in two dimensions.

Method for one dimension

In the one-dimensional case, exact characterizations of $Z_{x^\star}$ are possible when $\ker(f)$ is sufficiently easy to obtain. Suppose the model f is well-posed and that $\ker(f)$ contains some $x^\star > 0$ that is stable. Then $0 \in ker(f)$ also. As $x^\star$ is a 1-dimensional stable equilibrium, $f(x - \epsilon_-) > 0$ and $f(x + \epsilon_+) < 0$, where $\epsilon_+, \epsilon_- \in \mathbb{R}_{>0}$. If $\epsilon_+ = \epsilon_-$, then the interval $(x - \epsilon_-, x + \epsilon_+)$ is a ϵ-ball at x. However, we can find a maximal ϵ by identifying the largest values of ϵ_- and ϵ_+ such that $f(x - \epsilon_-) > 0$ and $f(x + \epsilon_+) < 0$. As a consequence of the intermediate values theorem (recall that $f \in C^\infty$), only some other $y^\star \in ker(f)$ for $y^\star \neq x^\star$. While the existence of some $y^\star$ as a lower bound is guaranteed by $y^\star = 0$ (for a sufficiently well-posed biological system), the existence of a second $y^\star > x^\star$ is not guaranteed. Then $\epsilon_- = x^\star - ys$. However, should such $y^\star > x^\star$ exist, then $\epsilon_+ = y^\star - x^\star$. This method is used to construct exact characterizations of RoA in 3.1.

Method for higher dimensions

An optimal method to compute an exact characterization of the region of attraction in two or more dimensions is through the usage of Lyapunov functions. However, since a criterion for the existence has not been proven, we shall instead use computational approximations or indirect estimation from observation. For dimensions greater than two, notably with nonlinear functions, computational approximations are a primary method for identifying regions of attraction. The Matlab global optimization toolbox contains implementations of standard algorithms for finding and approximating regions of attraction.

Note that these are sometimes referred to as basins of attraction, however the difference is nontrivial. A basin of attraction is a general term defined for all types of attractors including limit cycles and fixed points, whereas a region of attraction is defined only for an equilibrium state. As we shall see, no significant theoretical issue arises from the application of these methods or the application of relevant ecological theory. Construction of these objects for limit cycles requires minimal deviation from theoretical methods. The application to limit cycles is not within the scope of this thesis.

A comprehensive discussion of the details of these search methods and convex hull algorithms are largely beyond the scope of this thesis. An implementation of Qhull [2] can be found within the standard functions of Matlab (R2018a) to construct a convex approximation of the region of attraction.

2.1.6 Probability theory

We partition our discussion of probability theory into distributions and stochastic topics.

2.1.6.1 Random variables and distributions

Let $X : \Omega_X \to E$ be a random element. Then roughly speaking, Ω_X is defined as the sample space for random element X and E is a measurable space containing the values that can be mapped to by X for some $\omega \in \Omega_X$. Elements of the σ-algebra of Ω_X are referred to

as events. If E is discrete, X is said to be a discrete random element. Likewise, if E is a continuous measurable space, X is said to be a continuous random element. If $E \subset \mathrm{E}^n$ where E is a euclidean space, then X is said to be a euclidean-valued random variable. Often $E = \mathbb{R}$, $E = \mathbb{R}_+$ or $E = V$ for some vector space V. Then X is said to be a real-valued random variable or random vector respectively. This is not to say that random variables cannot have $E = \mathbb{C}$, however the case of $E = \mathbb{C}$ has no direct biological or mathematical application within the scope of this thesis.

Definition 2.1.6.1 (Sampling from a random variable)**.** *The parameter a is said to be sampled from the random variable A if any of the following are true*

- *a is said to be drawn from A.*
- *a is a realization of A.*
- *$a = A(\omega)$ for some $\omega \in \Omega_A$.*
- *a is an observation of A.*

The last definition is primarily used in the context of statistics, however we will refer to it within the context of collected data.

Let $\mathbb{P} : \mathrm{E} \to \mathbb{R}_+$ be the probability measure on Ω. As $\mathbb{P}$ is a probability measure it must be non-negative. The probability of an event $S \subseteq E$ occurring is given by

$$Pr_X(S) = \mathbb{P}(\{\omega \in \Omega : X(\omega) \in S\}) \tag{2.13}$$

where $Pr_X : E \to [0, 1]$. If E is a continuous space, the map is defined with an integral equation

$$Pr_X(S) = \int_S r_X(\vec{x})\mathrm{d}\vec{x} \tag{2.14}$$

Where $r_X(x)$ is the probability density function $r_X : E \to \mathbb{R}_+$ (if such a function exists). Note that for the one-dimensional case, if we fix $S = (-\infty, s]$, then

$$Pr_X(S) = Pr_x(X < s) = \int_{-\infty}^{s} r(x)\mathrm{d}x \tag{2.15}$$

The above discussion centers around distributions that return a single value. If the $\dim(S) >$

1, then X is a multivariate distribution and can be written as

$$Pr_X(S) = \int_S \cdots \int r_X(\vec{x}) \mathrm{d}\vec{x} \tag{2.16}$$

where $r_X(\vec{x})$ is the joint density function. If $E = (\mathbb{R}_+^n)$ for some fixed $n \in \mathbb{N}$, then the computation of $Pr_X(s)$ can be accomplished directly or approximated with numerical methods. Multivariate distributions are one way to compact the notation for the sequence of integral operations that commonly occurs in multivariate distributions.

Every non-trivial differential equation model for an ecological system has more than one parameter before any change of variables occurs. We are primarily interested in distributions that define parameters of the form:

$$\Theta : \Omega_0 \to \mathbb{R}^n, \quad F_\Theta : \mathbb{R}^n \to [0,1]^n, \quad r_\Theta : \mathbb{R}^n \to \mathbb{R}_+, \quad r_\Theta(\mathbf{x})_i := r_\alpha(\mathbf{x}_i) \tag{2.17}$$

$$T : \Omega_T \to \mathbb{R}_+, \quad F_T : \mathbb{R} \to [[0,1], \quad r_T : \mathbb{R}_+ \to \mathbb{R}_+, \quad r_T(x) = \frac{1}{\tau} e^{\frac{x}{\tau}} \tag{2.18}$$

where T and $\Omega_0 = \prod_{\alpha \in I} \Omega_\alpha$, where I is an index set for all random variables in a given model, $n = |I| < \infty$.

Remark 2.1.6.2. *The definition of r_T is a nonstandard definition. This is done such that the distribution parameter τ satisfies $\tau = \mathrm{E}T$, where* E *is the expectation function.*

We may construct a sequence of Ω_n, denoted as $\{\Omega_n\}_{n \in \mathbb{N}_0}$, and associated sequence Θ_n denoted as $\{\Theta_n\}_{n \in \mathbb{N}_0}$ to describe a sequence of random variables. Often, this sequence will be i.i.d.

2.1.7 Stochastic processes, random dynamical systems, and Markov chains

To proceed, we require more general notion of a random variable. This generalization is called a random element.

Definition 2.1.7.1 (Random element)**.** *Let $(\Omega, \mathcal{F}, P)$ be a probability space and (E, ε) be a measurable space. A random element X is a map $X : \Omega \to E$ that is $(\mathcal{F}, \varepsilon)$ measurable, where*

- *Ω is a (nonempty) space called a sample space,*
- *$\mathcal{F}$ is a σ-algebra on Ω,*
- *P is a probability measure on Ω.*

Remark 2.1.7.2. *A real valued random variable is a random element where $E = \mathbb{R}$. Likewise, a random vector is a random element where $E = V$ where V is some vector space. A random function is a random element where E is a set of ε-measurable functions.*

Stochastic processes are a common method for characterizing a sequence of random events that with respect to a time variable. We consider here stochastic processes that are defined on real spaces.

Definition 2.1.7.3 (Stochastic process)**.** *Let (E, σ) be a measurable space along with a probability triple $(\Omega, \beta, \mathbb{P})$. Let $\mathbb{T}$ be an arbitrary set, called the index (or time) set. For each $s \in \mathbb{T}$, the random variable X_s are functions $x_n : \Omega \to E$. The collection of these random variables $\{X_s : s \in \mathbb{T}\}$ defines a stochastic process.*

Remark 2.1.7.4. *Often $\mathbb{T} = \mathbb{N}, \mathbb{N}_0, \mathbb{R}, \mathbb{R}_+$ or is finite. We are primarily interested in stochastic processes in which $\mathbb{T} \subset \mathbb{R}_+$, $Card(\mathbb{T}) = Card(\mathbb{N})$, such that for all $i \in \mathbb{N}_0$, $t_i \in \mathbb{T}$ satisfies $t_i - t_{i-1} \sim T$, where T is an exponential random variable.*

The class of object we introduce in this section is the random dynamical system (RDS). Random dynamical systems are derived from dynamical systems with the introduction of a probability space. The theory of random dynamical systems were first developed for a more abstract approach to stochastic differential equations, however the theory has found broad applicability within the study of Markov chains and applied stochastic processes due to the applicability of ergodic theory. The following definitions of a random dynamical system is from [1].

Definition 2.1.7.5 (Random Dynamical system)**.** *A measurable random dynamical system on the space (X, B) covering a metric dynamical system $(\Omega, \mathcal{F}, P\ (\theta(t))_{t\in\mathbb{T}})$, where $\mathbb{T}$ is the time set, is a mapping*

$$\varphi : \mathbb{T} \times \Omega \times X \to X,\ (t, \omega, x) \mapsto \varphi(t, \omega, x)$$

which satisfies the following properties

1. *measurability: φ is $B(\mathbb{T}) \bigotimes \mathcal{F} \bigotimes B, B$-measurable.*
2. *Cocycle property: The mappings $\varphi(t, \omega) \equiv \varphi(t, \omega, \cdot) : X \to X$ form a cocycle over $\theta(\cdot)$, i.e. they satisfy*

$$\varphi(t_0, \omega, \cdot|t_0) = id_X \text{ for all } \omega \in \Omega \text{ if } t_0 \in \mathbb{T} \tag{2.19}$$

where t_0 is the identity element of the group (or monoid) $\mathbb{T}$, and

$$\varphi(t + s, \omega) = \varphi(t, \theta(s)\omega) \circ \varphi(s, \omega) \forall s, t \in \mathbb{T},\ \omega \in \Omega \tag{2.20}$$

Definition 2.1.7.6 (Continuous random dynamical system)**.** *A random dynamical system φ is said to be continuous if the map*

$$\varphi(\cdot, \omega, \cdot) : \mathbb{T} \times X \to X, (t, x) \mapsto \varphi(t, \omega, x) \tag{2.21}$$

is continuous.

The reader may notice that the cocycle of an RDS resembles a skew product, or skew dynamical system, in addition to the algebraic structure. This is similar to that of a (classical) random dynamical system.

Definition 2.1.7.7 (Smooth random dynamical system)**.** *A smooth random dynamical system of class C^k, or a C^k random dynamical system, for $1 \leq k < \infty$ on a $d-$dimensional (C^∞) manifold X is a topological RDS which in addition satisfies the following property: for each $(t, \omega) \in \mathbb{T} \times \Omega$, the corresponding random flow $\varphi(t, \omega, \cdot) : X \to X$ is C^k.*

2.2 Biological

2.2.1 Ecological Regimes

Definition 2.2.1.1 (Ecological state)**.** *An ecological state is a unique set of biotic and abiotic environmental conditions. This includes the habitat, population sizes and spatial distributions, pollution, resource availability, and inter-species interactions found in the ecosystem at a moment in time. We notate the population state as* $\mathbf{x}$ *and collect the environmental and biological interactions into* $\mathbf{y}$*. An ecological state is characterized by the tuple* $(\mathbf{x}, \mathbf{y})$*.*

Remark 2.2.1.2. *An ecological state assumes that the interactions between populations can be perfectly described by a set of parameters. These parameters are constant with respect to time within a given interval* $[a, b)$ *for* $a < b, a, b \in \mathbb{R}$*. Classically this interval is* $[0, \infty)$*, where the time of the observation is set to zero. A more apt characterization for this interval within the context investigated in this work is* $[0, \Delta t)$*, where* Δt *is exponentially distributed.*

Due to experimental constraints in the observation of ecosystems, ecological states are better characterized experimentally over an interval of time.

Definition 2.2.1.3. *An ecological regime* $\mathfrak{A}$ *is a set of ecological states* $\{(\mathbf{x}, \mathbf{y})\}$ *characterized by the following:*

- *There exists a subset of ecological states which can be reached from any other ecological state in the regime. Such a subset is said to be connected.*
- *All ecological states in the regime have the same parameters, captured by* $\mathbf{y}$*.*

The set of all ecological regimes is denoted $\mathbf{\Omega}$*.*

Often, multiple ecological regimes will exist which contain similar population states with different parameter values. Algebraically, these are described by the same region of attraction with different parameter values. Ecological regimes of a system can be partitioned by an equivalence relation.

Definition 2.2.1.4 (Equivalent Ecological regimes)**.** *Two ecological regimes* $\mathfrak{A}$ *and* $\mathfrak{B}$ *are said to be equivalent under the equivalence relation* $\dot{\sim}$ *if both ecological regimes can be described algebraically with the same region of attraction but with different parameter values. The class of equivalent regimes is denoted by* $[\mathfrak{A}]_{Er} = \{\mathfrak{B} \in \mathbf{\Omega} : \mathfrak{B} \dot{\sim} \mathfrak{A}\}$*. The elements of* $[\mathfrak{A}]_{ER}$ *are pairs expressed as* $(\mathbf{x}_0, \mathbf{y}_0)$*.* $\mathbf{x}_0$ *is an ecological state with the associated parameter vector* $\mathbf{y}_0$*.*

Note that all possible population states may not be represented by an ecological state in any ecological regimes. Such populations are said to be not stable (or unstable).

2.2.2 Intrinsic parameter variations

Observed ecological networks are generally highly structured [33, 41, 21, 42], with significant variation in species phenotype and behavioral preferences within populations. Large variations can result in the formation of subpopulations identified by a common phenotype or behavioral preference. Fluctuations in subpopulations across spatial and time dimensions can drive within-population variation of interactions by modifying the rate at which members of both predator and prey subpopulations encounter each other, the probability that an encounter results in an interaction, and the regulation of this interaction by environmental factors [36, 35].

The distillation of ecological interactions from the highly structured underlying networks constructed around interactions between subpopulations characterized by different phenotypes or behavioral preferences into a network assuming homogeneity within populations can be aptly characterized by a single set of parameters [36]. This assumption may not always be possible for an arbitrary biological system [33]. For large ecosystems or ecosystems that present multiple generalist predators, this presents challenges that are statistical [47] and/or experimental [3, 30] in nature.

These network-derived models describe populations as the fundamental units of study, where feeding experiments, longitudinal capture/tag/release studies, and patch-observation studies are used to elucidate and approximate the mathematical representations of the underlying mechanisms. While such studies provide robust data on population level inter-

actions, they rarely capture information on sub-populations and individuals at the genomic level as this data is not incorporated directly into the model. Historically, the cost of genomic data collection and analysis has presented additional financial barriers to collection of rich datasets. These obstacles have only recently been overcome to provide meaningful results and contributions to the field [37, 16, 6, 38, 5]. This recent work suggests that within-population and within-subpopulation variation can contribute to parameter variation that appears intrinsic at the population level.

2.2.3 The extinction prediction problem

A major goal of theoretical ecology is the prediction of extinction events and the development of early warning indicators for extinction events. This question is in essence, a simplification of the problem of predicting regime change events. Predicting extinction events and ecological regime changes experimentally is a difficult task [39, 41]. Previous works have examined compositional disorders in biodiversity [11], random matrix steady state models [42, 21], and bifurcation theory [10, 39, 18]. None of these previous methods directly address population level parameter variation within the developed deterministic mathematical framework at the population level. Of the above techniques, bifurcation theory provides an analytical framework which can aid in the analysis of transient or near-steady state behavior. However, this method fails to provide a robust integration of parameter variation, allowing for the study of transient behavior of such systems. Multi-species models may possess multiple stable equilibria, bifurcation theory does not afford systemic method to describe the transition between stable states.

2.3 General terminology and notation

Throughout this work, we will refer to a transition between ecological regimes as a regime change, a regime change event, or a transition between regions of attraction. These terms are equivalent, different usages are used to emphasize the ecological, probabilistic, or deterministic aspects.

3 Motivating and Worked Examples

3.1 Example I

3.1.1 The model

Consider the 1-dimensional C^∞ system

$$\dot{x} = (x)(r_1)\left(-ab + ax + bx - x^2\right) \tag{3.1}$$

which permits the mapping given by $f : \mathbb{R}_+ \to \mathbb{R}$,

$$f(x) = r_1 x(x - a)(b - x) \tag{3.2}$$

where $a, b, r \in \mathbb{R}_+$ without loss of generality and are drawn from representative distributions as $a \sim A, b \sim B$, and $r_1 \sim R_1$ respectively where each random variable is determined statistically from system data. This is a nice equation, but (3.1) does not immediately correspond to an interpretation of a physical system. Instead, consider equation (3.3).

$$\dot{x} = r_1 x^2(b - x) + r_1 ax(x - b) \tag{3.3}$$

The first term can be interpreted as a variation on the logistic growth function. The second term can be viewed as a state dependent immigration function, in which population flow in or our is described with the unique parameter a with population growth r_1, carrying capacity b. Specifically, the rate of immigration is a product of the $r_1 ax$ and the 'distance' to the carrying capacity b. If the population is less than the carrying capacity b, there is outward emigration, but if the population is above the carrying b capacity, there is immigration. We will then assume that $a \ll b$ biologically, so any choice of a or b selected from their corresponding distribution obeys $a < b$.

The representation of the system in the form in equation (3.1) is more insightful analytically and we will default to this form.

3.1.2 Equilibria and Stability Analysis

As (3.1) can be written as a single polynomial, it follows that $ker(f) = \{0, a, b\}$ so the equilibria are $x^\star \in ker(f)$. We can index these equilibria as $x_1^\star = 0$, $x_2^\star = a$, and $x_3^\star = b$.

We can then compute the stability of each equilibrium by linearization. As f is a C^∞ polynomial, f' must exist, so

$$f'(x) = \frac{\mathrm{d}f}{\mathrm{d}x} = r_1\left(2x(a+b) - ab - 3x^2\right) \tag{3.4}$$

Then

$$f'(x_1^\star) = f'(0) = -r_1 ab < 0 \tag{3.5}$$

$$f'(x_2^\star) = f'(a) = r_1(2a(a+b) - ab - 3a^2) = r_1 a(b-a) > 0 \tag{3.6}$$

$$f'(x_3^\star) = f'(b) = r_1(2b(a+b) - ab - 3b^2) = r_1 b(a-b) < 0 \tag{3.7}$$

We are able to conclude the last inequality in (3.6-3.7) from the observation that $a < b$. We have shown that $x_1^\star = 0$ and $x_3^\star = b$ are stable, and $x_2^\star = a$ is unstable. Then $x_1^\star = a$ is the stability bound between the two regions of attraction.

3.2 Probabilistic State Transition

We must define the random variables from which a, b, and r_1 are drawn from as A, B, and R_1 before proceeding. Let $A = \{A_n\}_{n=1}^\infty$, $B = \{B_n\}_{n=1}^\infty$, and $R_1 = \{R_{1n}\}_{n=1}^\infty$ be sequences of i.i.d. random variables. Note that our only requirement is that all values attained by these distributions is strictly positive. Let r_A, r_B, and r_{R_1} be the respective probability distributions of A, B, and R_1. For simplicity, let all distributions be uniform with mean

parameters μ_A, μ_B, and μ_{R_1}. Let each distribution have width $2\epsilon_X$ for each $X = A, B, R_1$, such that all $\mu_A - \epsilon_A > 0, \mu_B - \epsilon_B > 0$, $\mu_{R_1} - \epsilon_{R_1} > 0$, and $\mu_A - \mu_B > \epsilon_A + \epsilon_B$, so any value chosen from the distribution satisfies the conditions on the parameters for this model.

Formally,

$$A_n : \Omega_A \to \mathbb{R}, \quad F_A : \mathbb{R} \to [0,1] \quad r_A : \mathbb{R} \to \mathbb{R}_+, \qquad r_A(a) = \begin{cases} \frac{1}{2\epsilon_A} & a \in \text{supp}(A_n) \\ 0 & \text{elsewhere} \end{cases} \tag{3.8}$$

$$B_n : \Omega_B \to \mathbb{R}, \quad F_B : \mathbb{R} \to [0,1] \quad r_B : \mathbb{R} \to \mathbb{R}_+, \qquad r_B(b) = \begin{cases} \frac{1}{2\epsilon_B} & b \in \text{supp}(B_n) \\ 0 & \text{elsewhere} \end{cases} \tag{3.9}$$

$$R_{1n} : \Omega_{R_1} \to \mathbb{R}, \quad F_{R_1} : \mathbb{R} \to [0,1] \quad r_{R_1} : \mathbb{R} \to \mathbb{R}_+, \quad r_{R_1}(r_1) = \begin{cases} \frac{1}{2\epsilon_{R_1}} & r_1 \in \text{supp}(R_{1_n}) \\ 0 & \text{elsewhere} \end{cases} \tag{3.10}$$

We can thus describe parameter space with a joint probability distribution Θ, whose event space is given by

$$\Omega_0 = \Omega_A \times \Omega_B \times \Omega_{R_1} \tag{3.11}$$

and the random variable Θ is defined with

$$\Theta_n : \Omega_0 \to \mathbb{R}^3 \qquad F_\Theta : \mathbb{R}^3 \to [0,1] \qquad \Theta : \mathbb{R}^3 \to \mathbb{R}^3_+ \qquad r_\Theta(a, b, r_1) = \begin{bmatrix} r_A(a) \\ r_B(b) \\ r_{R_1}(r_1) \end{bmatrix} \tag{3.12}$$

For notational simplicity, we use $r_\Theta(\theta)$ and $r_\Theta(a, b, r_1)$ interchangeably, as we can define $\theta = (a, b, r_1)^T$. Where each probability density function is defined as above. Thus, we have defined a multivariate random variable that describes the model parameters.

3.2.1 Regions of Attraction

Let $Z_{x^\star}$ be the region of attraction for the equilibrium point $x^\star$. As the population is one-dimensional, it follows that the regions of attraction for each equilibrium (for arbitrary a and b as defined above) are given by

$$x_1^\star : Z_{x_1^\star}(\Theta) = [0, x_2^\star) = [0, a) \tag{3.13}$$

$$x_2^\star : Z_{x_2^\star}(\Theta) = \{x_2^\star\} = \{a\} \tag{3.14}$$

$$x_3^\star : Z_{x_2^\star}(\Theta) = (x_2^\star, \infty) = (a, \infty) \tag{3.15}$$

We will abuse notation and drop the dependence of $Z_{x^\star}$ on Θ. It then follows from this construction that the probability of changing regimes can be characterized by parameter space and the population state at time t. We then must define the subset of parameter space ($\mathbb{R}^3$, equation (3.12)) 'different enough' such that drawing a new parameter triple Θ_{n+1} results in $x_0 \in Z_{x^\star}(\Theta_n) \wedge x_0 \notin Z_{x^\star}(\Theta_{n+1})$. Further, notice that this can be generalized for every x_0. Thus, for a given position $x_0 \in \mathbb{R}_+$,

$$S_B(x_0|\Theta_n) = \text{supp}(\Theta_n) \setminus \{Z_{x^\star} | x_0 \in Z_{x^\star} \forall x^\star \in ker(f), \text{ for fixed } \Theta_n\} \tag{3.16}$$

where $\text{supp}(\Theta_n)$ is the region of support of the random variable Θ_n. Notice that every region of attraction is invariant of the parameters r_1 and b. In fact, any value of r_1 and b do not impact any region of attraction.

3.2.2 Probabilistic State Transition

Note that as the distribution is invariant of r_1 and b, then $S_B(x_0|\Theta_n)^c \cap \text{supp}(B_n) = \text{supp}(B_n)$ and $S_B(x_0|\Theta_n)^c \cap \text{supp}(R_{1n}) = \text{supp}(R_{1n})$. For brevity, define $A^* = (S_B(x_0|\Theta_n))^c \cap \text{supp}(A_n)$. Thus, the probability of a regime change event (denoted R_C) at a fixed position in phase space is given by

$$\mathbb{P}(R_C|\Theta(\omega)) = \iiint_{S_B(x_0|\Theta_n)} r_\Theta(\theta)\mathrm{d}\theta = 1 - \iiint_{(S_B(x_0|\Theta_n))^c} r_\Theta(\theta)\mathrm{d}\theta \tag{3.17a}$$

$$= 1 - \int_{A^*} r_A(u) \left(\int_{\mathrm{supp}(B_n)} r_B(v) \int_{\mathrm{supp}(r_1)} r_{R_{1_n}}(s)\mathrm{d}s\mathrm{d}v \right) \mathrm{d}u \tag{3.17b}$$

$$= 1 - \int_{A^*} r_A(u) \left(\int_{\mathrm{supp}(B_n)} r_B(v)(1)\mathrm{d}v \right) \mathrm{d}u \tag{3.17c}$$

$$= 1 - \int_{A^*} r_A(u) \left((1)(1) \right) \mathrm{d}u \tag{3.17d}$$

$$= 1 - \int_{A^*} r_A(u)\mathrm{d}u \tag{3.17e}$$

Further simplification is case-dependent. First, note that if $x_0 \in Z_{x_2^\star}$, then $x_0 = a$, then

$$\mathbb{P}(R_C|a = A_n(\omega), x_0 \in Z_{x_2^\star}) = 1 - \int_{u=a} r_A(u)\mathrm{d}u = \int_a^a r_A(u)\mathrm{d}u = 1 - 0 = 1 \tag{3.18}$$

as a consequence of the Riemann integral. (Note that this calculation may encounter problems with numerical implementations of random number generations). For the remaining two cases, we can further simplify this integral by applying the same invariant property used to evaluate the inner integrals. Next, consider the nontrivial cases, where $x_0 \in Z_{x_1^\star}$ or $x_0 \in Z_{x_3^\star}$. Suppose $x_0 \in Z_{x_1^\star}$. Then

$$\mathbb{P}(R_C|a = A_n(\omega), x_0 \in Z_{x_1^\star}) = 1 - \int_{u\in[0,a)} r_A(u)\mathrm{d}u \tag{3.19a}$$

$$= 1 - \int_0^a r_A(u)\mathrm{d}u \tag{3.19b}$$

$$= 1 - P(A_n < a) \tag{3.19c}$$

$$= 1 - F_{A_n}(a) \tag{3.19d}$$

Likewise,

$$\mathbb{P}(R_C|a = A_n(\omega), x_0 \in Z_{x_3^\star}) = 1 - \int\limits_{u\in[(a,\infty)} r_A(u)\mathrm{d}u \tag{3.20a}$$

$$= 1 - \int\limits_{a}^{\infty} r_A(u)\mathrm{d}u \tag{3.20b}$$

$$= 1 - P(A_n > a) = 1 - (1 - F_{A_n}(a)) \tag{3.20c}$$

$$= F_A(a) \tag{3.20d}$$

These are well defined as the associated cumulative density functions are well defined on $\mathbb{R}$. Then the probability $\mathbb{P}(R_C)$ can be described as

$$\mathbb{P}(R_C|\Theta_n(\omega), x_0) = \begin{cases} 1 - F_{A_n}(x_0) & x_0 \in Z_{x_1^\star} \\ 1 & x_0 \in Z_{x_2^\star} \\ F_{A_n}(x_0) & x_0 \in Z_{x_3^\star} \end{cases} \tag{3.21}$$

Thus we have a closed form equation that describes the probability of a regime change event at a specified position. A natural question is how to extend this construct when the time that the regime change occurs is either not known, or is random. Let us set aside the experimental question of detecting these events for now. Computing closed form explicit flows that are insightful is often impossible, but a close numerical approximation often is. A numerical approximation to the solution of the differential equation (3.2) is easily available. A numerical simulation where parameters are held constant is shown in figure 3.1, where the parameters are set at $a = 1.005$, $b = 3$, $r_1 = 0.25$. We use the uniform distributions specified above. These correspond to the expected value for the uniform distribution where $\mu_A = 1.005$ and $\epsilon_A = 1$. This strategy provides sufficient information to characterize regime change events that occur randomly, given that we know the state $x(t^\star) = x_1$ when and where the transition occurs. We can then construct $\mathbb{P}(R_C)$ for the new parameter values and determine if a regime change occurs.

The alternative question, what if the regime changes occur randomly, provides a more

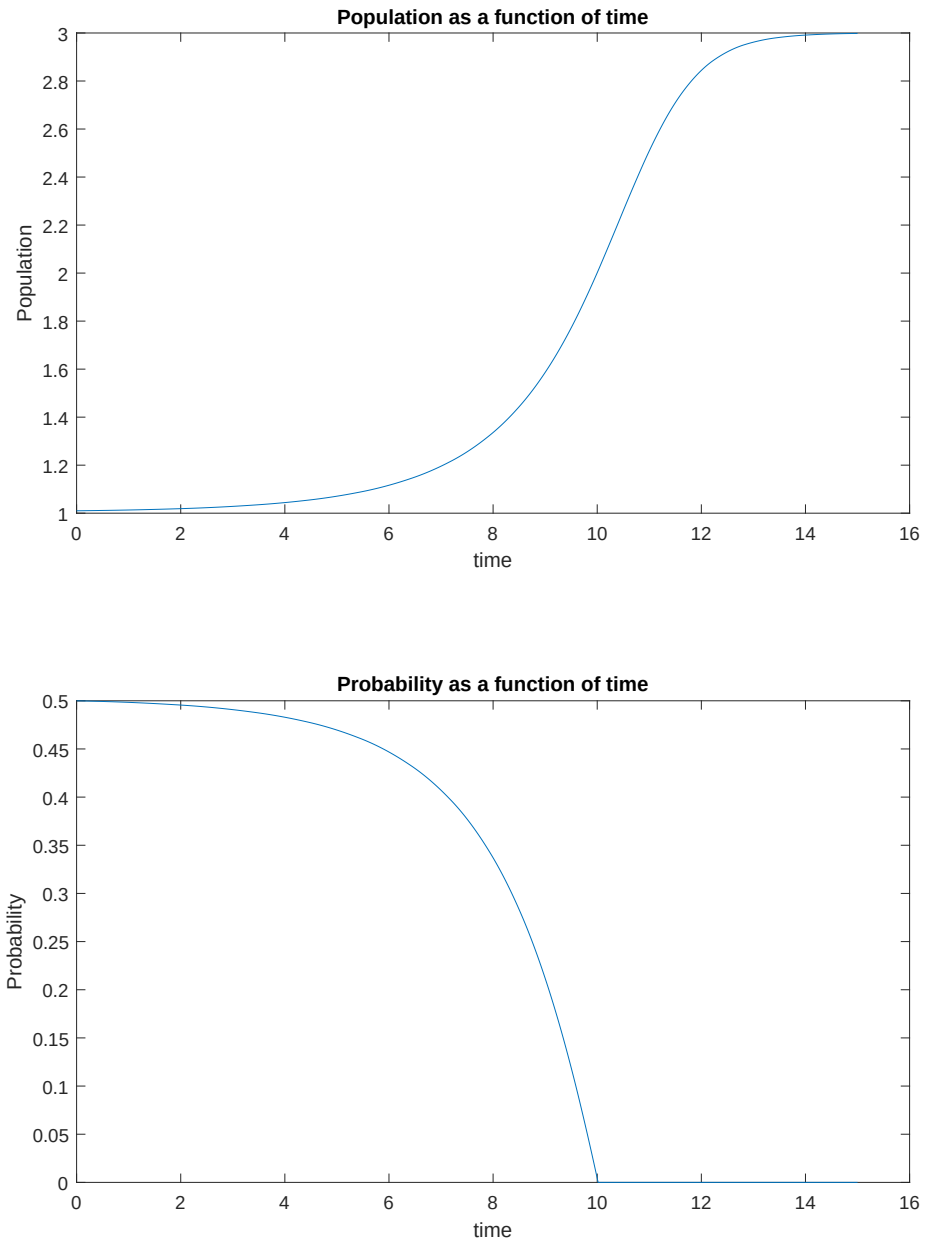


Figure 3.1: A plot of the numerical approximation of the solution (top) and associated $\mathbb{P}(R_C)$ (bottom) when the initial condition is set at $x_0 = 1.01$. Note that the associated transition probability is zero when $x(t) > 2.01$. This is consistent with our intuition, as no parameters can be drawn such that changing the parameter values changes the region of stability. Also note that the curvature of the associated transition probability (bottom) appears similar to the curvature of the position function $x(t)$ (top). This follows from the linear relationship described by the cumulative density function of the uniform distribution.

interesting path forward. Rather than considering the question of when does the next transition occur we may instead ask the equivalent question: what is the 'length' of the time interval that a parameter tuple Θ maintains one value before changing? There are several candidate distributions that are well known for describing this type of behavior, depending on what additional properties we ascribe to this 'length'. All obvious candidates are within the family of generalized extreme value distributions. This includes the exponential, Weibull, Frechet, and Gumbel distributions, all of which are well understood with physically meaningful parameters within the context of waiting times or life expectancy. We select the exponential distribution as requires the least number of parameters and has the simplest algebraic form. The benefit of selecting a compact algebraic form that is easily integrable will become apparent in the next section.

3.2.3 Generalized Probabilistic State Transitions

In this subsection, we consider the question posed at the end of the prior section. We will consider an exponential distribution T that describes the time between transitions. We introduce an additional parameter τ which is the scale parameter for an exponential distribution T. The following definition of T generalizes

$$\bar{T} : \Omega_T \to \mathbb{R}_+, \quad F_T : \mathbb{R} \to [0,1] \quad r_T : \mathbb{R}_+ \to \mathbb{R}_+, \quad r_T(x|t_0) = \tau^{-1} e^{\frac{-(t-t_0)}{\tau}}, t \geq t_0 \quad (3.22)$$

Then we can construct the probability of a regime change event occurring in the interval $[t_n, t_{n+1}]$. To do so, we must define R_C with respect to time. Let $P\mathbb{P}(R_C \in [t_n, t_{n+1})|\Theta(\omega)) \equiv \mathbb{P}(\bar{R}_C|\Theta(\omega))$ to denote the implicit dependence on the interval. We make the dependence of the regime change probability on the time value explicit within the construction,

$$\mathbb{P}(\bar{R}_C|\Theta(\omega)) = \int_{t_n}^{t_{n+1}} r_T(t)\mathbb{P}(R_C|\Theta(\omega), x(t))\mathrm{d}t \quad (3.23)$$

As we already have a closed form for $\mathbb{P}(R_C)$, then computing this integral is dependent

upon which $Z_{x^\star}$ each $x(t)$ is contained in. To proceed, we invoke a closure property of regions of attraction: For every state $x_0 \in Z_{x^\star}$, the forwards trajectory $\{x(t)\}_{(t\in\mathcal{T})}$.

To construct $\mathbb{P}(\bar{R}_C|\Theta(\omega))$, we evaluate the integral by cases. Before we do so, we note that each case corresponds entirely to one region of attraction and as such is not a piecewise function in the traditional sense.

First, suppose that $x_0 \in Z_{x_1^\star}$ Then $\mathbb{P}(R_C|\Theta(\omega)) = 1 - F_{A_n}(x(t))$, so

$$\mathbb{P}(\bar{R}_C|\Theta(\omega)) = \int_{t_n}^{t_{n+1}} r_T(t)\mathbb{P}(R_C|\Theta(\omega), x(t))\mathrm{d}t \tag{3.24a}$$

$$= \int_{t_n}^{t_{n+1}} r_T(t)(1 - F_{A_n}(x(t)))\mathrm{d}t \tag{3.24b}$$

$$= \int_{t_n}^{t_{n+1}} r_T(t)\mathrm{d}t - \int_{t_n}^{t_{n+1}} r_T(t)F_{A_n}(x(t))\mathrm{d}t \tag{3.24c}$$

$$= (F_T(t_{n+1}|t_n) - F_T(t_n|t_n)) - \int_{t_n}^{t_{n+1}} r_T(t)F_{A_n}(x(t))\mathrm{d}t \tag{3.24d}$$

Computing the remaining integral requires knowledge of the solution, $x(t)$. The next case $x(t) \in Z_{x_2^\star}$ does have a closed form, as

$$\mathbb{P}(\bar{R}_C|\Theta(\omega)) = \int_{t_n}^{t_{n+1}} r_T(t)\mathbb{P}(R_C|\Theta(\omega), x(t))\mathrm{d}t \tag{3.25a}$$

$$= \int_{t_n}^{t_{n+1}} r_T(t)(1)\mathrm{d}t \tag{3.25b}$$

$$= F_T(t_{n+1}|t_n) - F_T(t_n|t_n) \tag{3.25c}$$

The final case $x(t) \in Z_{x_3^\star}$ is similar to the case of $x(t) \in Z_{x_1^\star}$.

$$\mathbb{P}(\bar{R}_C|\Theta(\omega)) = \int_{t_n}^{t_{n+1}} r_T(t)\mathbb{P}(R_C|\Theta(\omega), x(t))\mathrm{d}t \tag{3.26a}$$

$$= \int_{t_n}^{t_{n+1}} r_T(t)(F_{A_n}(x(t)))\mathrm{d}t \tag{3.26b}$$

The primary obstacle here is not complexity introduced by the cumulative density functions, but rather the algebraic complexity induced by $x(t)$. However, a numerical approximation of $x(t)$ is easily accessible. To do so, construct a numerical approximation of the solution trajectory. There are two canonical approaches that can be implemented depending on the desired output. The first approach is to construct a polynomial approximation of the solution, and then distribute. To do so would generate integrals of the form $\int e^{-\alpha t}\left(\sum_{i=0}^{j} a_i t^i\right)\mathrm{d}t$ for some $j \gg 1$. This can be decomposed into a difference of sums of $j+1$ incomplete gamma functions, after applying a unique affine transformation to every term in the polynomial. Alternatively, we could numerically integrate the function and sample the polynomial interpolation for values of $x(t)$. This is easier to implement with generality with many numerical software packages. With implementation, we omit the second case as $\mathbb{P}(a = A_n(\omega)) = 0$.

3.2.4 Sequences of Generalized Probabilistic State Transitions

Once the parameters update, the system 'resets', and we can then repeat the previous protocol, recording the time of each transition. The first value in the sequence is $\mathbb{P}(R_C \in [t_0, t_1))$, the second value is $\mathbb{P}(R_C \in [t_1, t_2))$, etc. The sequence of regime change probabilities is a new measurement of stability to describe and predict regime change events or extinctions. With simulations, we can record the sequence of ecological regimes (RoA) attained and compare how well the prediction of a change does predict the change. Further, we can separate the transition probabilities by those that are followed by a transition event and those that are not. Figure 3.3 and figure 3.4 depict two instances of the time series generated through this simulation technique. Figure 3.3 depicts the result of four different simulations. The top depicts the population time series, the bottom depicts the associated

transition probabilities. The probabilities plotted below correspond to the population data of the same color plotted above. No clear pattern emerges with only 500 steps. In figure 3.4, two simulations with the same initial condition $x_0 = 1.01$ are plotted. With ≥ 600 iterations a pattern now becomes clear. The noise in the dataset subsides as the trajectory approaches an equilibrium. Near an equilibrium, the transition probabilities more accurately correlate to correct predictions. That is, near an equilibrium, high values more likely predict a transition and low probabilities predict no transition. Thus if the ecological state is near the equilibrium state for the current ecological regime with the average associated parameter values, a high transition probability is a good indicator of the system. However, when near an equilibrium, most regime changes do not result in a transition event. Near a 'tipping point', many regime change events occur in sequence, often with a probability near 0.5.

Identifying an optimal critical threshold for classification remains an open problem not addressed in this thesis.

A good question to ask is there structure to this data? Is the distribution of probabilities that correctly predict a change different that the distribution of probabilities that do not predict a change? Additionally, if the distributions are different, if we collect a single transition probability, might it be possible to determine if this data comes from the distribution of probabilities that correctly predicted a change or the distribution of probabilities that correctly predicted no change.

The latter of these problems is statistical in nature and is beyond the scope of this thesis. The development of the statistical machinery to further analyze this data further remains an open problem.

The first of these problems could generally be answered by a Kolmogorov-Smirnov (KS) test. This is not an ideal strategy as continued iteration of the simulation inevitably results in the population converging to one of the two equilibrium, resulting in the probability sequence saturating with zeros or near zero values, skewing the distribution towards zero. These distributions have similar regions of support and are practically indistinguishable

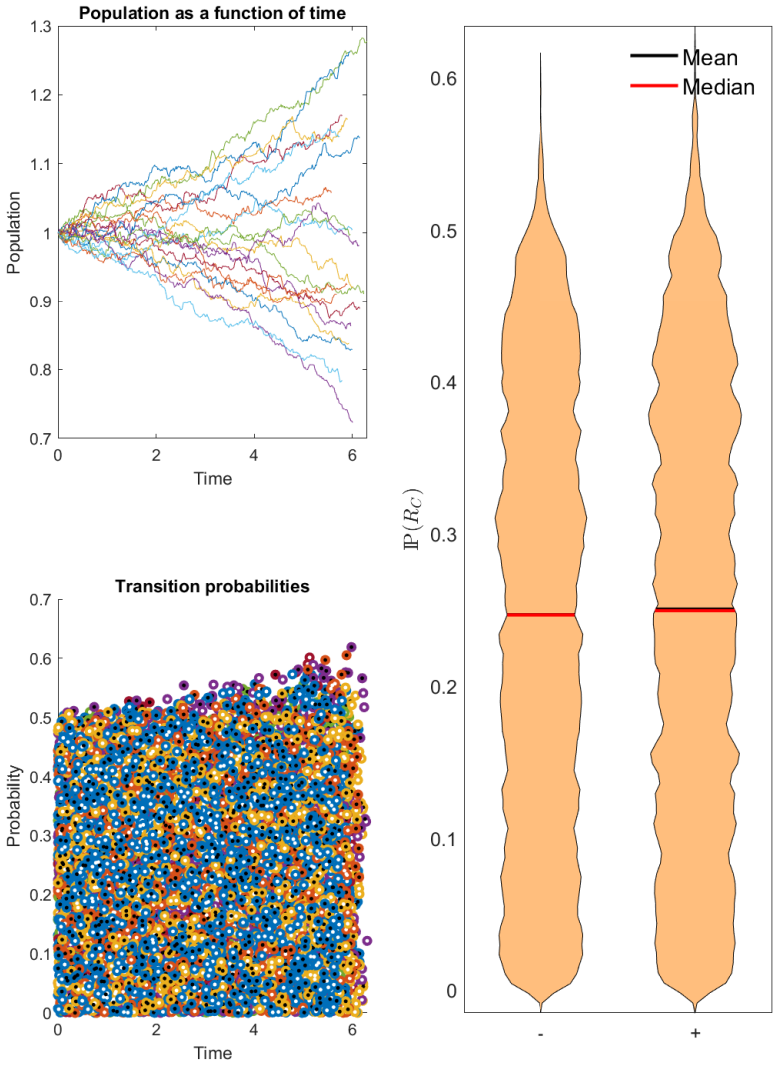


Figure 3.2: The top depicts a numerical implementation of the iterative scheme of the population. An ensemble of 20 different simulations are shown, each colored differently, with the same initial condition $x_0 = 1.00$. Each simulation was iterated for 600 steps, observing 599 transitions. The associated probabilities are shown below. The color of the data point (bottom) corresponds to the time series data (top). The white centered points correspond to a prediction that resulted in no-change. Likewise, a black-centered point denotes that a regime change event did occur. A violin plot [17] (right) shows the probabilities obtained, partitioned by those that were followed by a regime change event (denoted +), and those that were not followed by a regime change event (-). Here, $\tau = 0.01$ and r_1 is uniformly distributed on $(0, 0.25)$. The p-value for the 2-sample Kolmogorov-Smirnov test computed by Matlab is 0.2089.

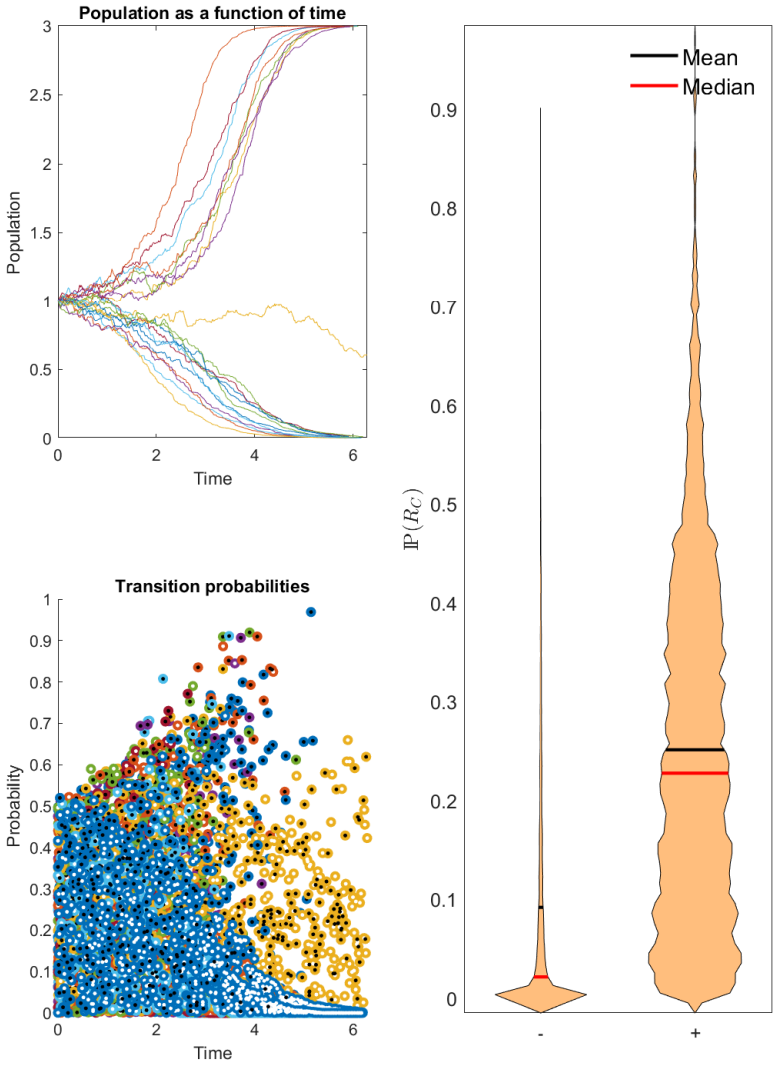


Figure 3.3: The top depicts a numerical implementation of the iterative scheme of the population. An ensemble of 20 different simulations are shown, each colored differently, with the same initial condition $x_0 = 1.01$. Of the 20, 11 resulted in an extinction event, 8 converged to the stable equilibrium, and one continues to exhibit transient behavior after 600 iterations. Each simulation was iterated for 600 steps, observing 599 transitions. The associated probabilities are shown below. The color of the data point (bottom) corresponds to the time series data (top). The white centered points correspond to a prediction that resulted in no-change. Likewise, a black-centered point denotes that a regime change event did occur. A violin plot [17] (right) shows the probabilities obtained, partitioned by those that were followed by a regime change event (denoted +), and those that were not followed by a regime change event (-). Here, $\tau = 0.01$ and r_1 is uniformly distributed on $(0, 1)$. The p-value for the 2-sample Kolmogorov-Smirnov test computed by Matlab is 0, suggesting $p \lll 1$.

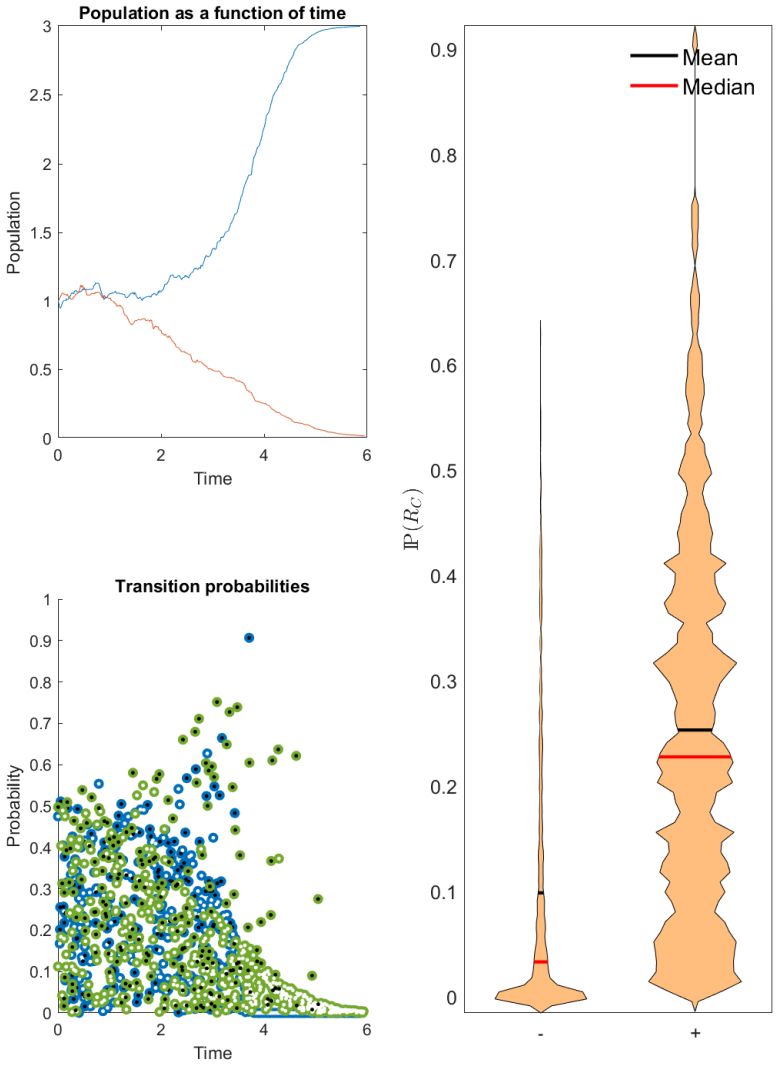
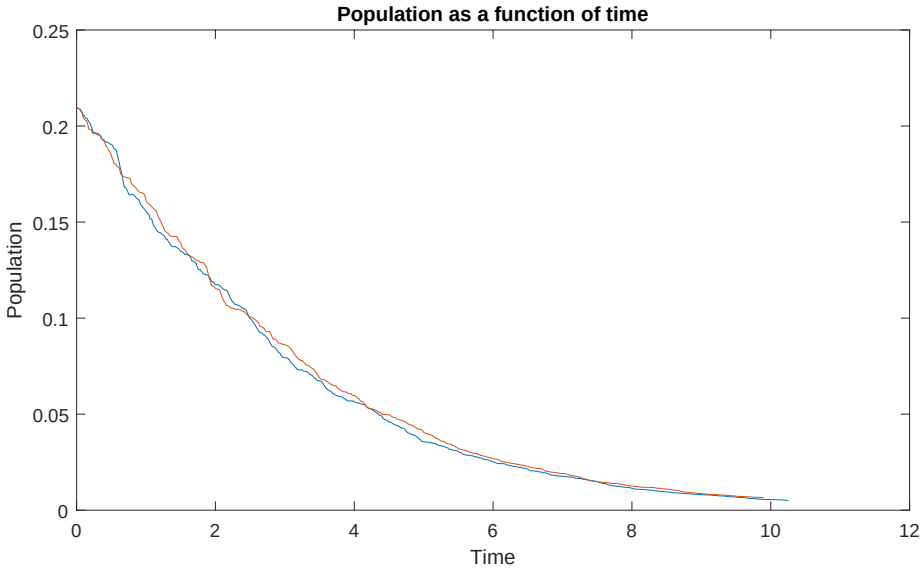


Figure 3.4: Two additional simulations for 600 iterations with the initial condition $x_0 = 1.01$. The blue set of points (bottom left) corresponds to the blue time series data (top left). The green set of points (bottom left) corresponds to the orange time series data (top left). The white centered points correspond to a prediction that resulted in no-change. Likewise, a black-centered point denotes that a regime change event did occur. Note that when the population is near the equilibrium, the proportion of high probability transitions that correctly predict transitions dominates the data. This holds for both the extinction and existence equilibrium. A violin plot [17] (Right) shows the probabilities obtained, partitioned by those that were followed by a regime change event (denoted +), and those that were not followed by a regime change event (-). Here, $\tau = 0.01$ and r_1 is uniformly distributed on $(0, 1)$.



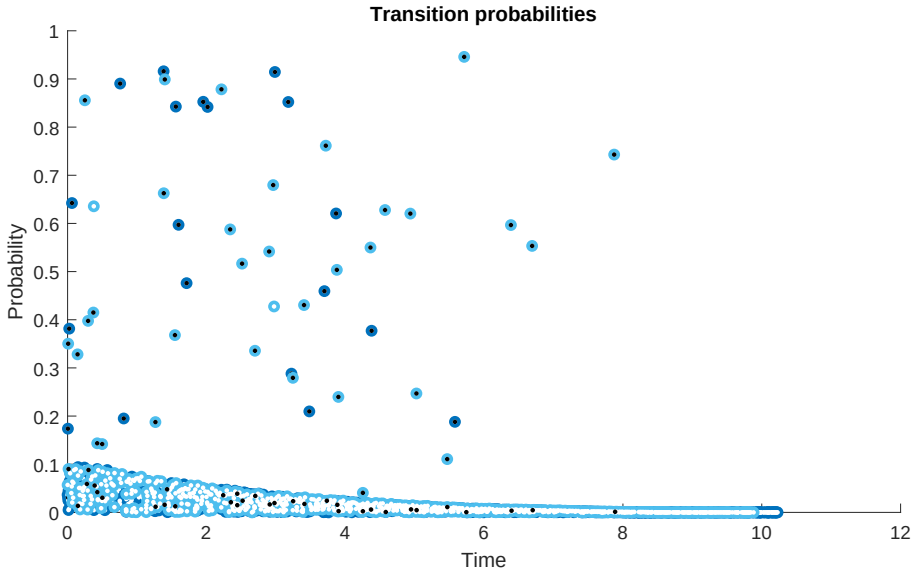


Figure 3.5: Two simulations for 1000 iterations with the initial condition $x_0 = 0.51$. Only 2 probabilities above 0.1 did not result in a change. Overall, 95% of probabilities over 30% correctly predicted a regime change event occuring. Additionally, over 96% of probabilities below 30% correctly predict no change in ecological regime. The 30% threshold is arbitrarily selected a priori. The density of points exceeds what can be plotted in the histogram in the bottom region of the scatter plot. Here, $\tau = 0.01$ and r_1 is uniformly distributed on $(0, 0.25)$.

without knowledge of the construction.

4 Method of stochastic parameters

This section formally introduces the method of stochastic parameters (MSP) that we have demonstrated in the section 3.1, develops the theory behind the technique, and introduce several new directions of study and applications.

4.1 Assumptions

We consider functions $\dot{\mathbf{x}} = f(\mathbf{x})$ such that $f \in C^{\infty}(\mathbb{R}^n_+)_l$, where $C^{\infty}_l(X)$ is the space of infinitely-differentiable Lipschitz continuous functions $f : Y \to X$ over any closed $Y \subset X$. While this is a strong condition, most differential equations used to describe ecological models can be easily shown to satisfy this condition. By the Picard-Lindelöf theorem equipped with a contraction map and the usual norms, there exist unique functions that are solutions to any differential equation characterized above with an initial condition $\mathbf{x}_0 \in \mathbb{R}^n_+$.

4.2 Derivation

We will motivate the construction of the MSP by considering three events, characterized by the number of parameter space transitions and length of time. We will first consider a parameter space transition (a 'jump') at a fixed time and known position. We then consider a single jump at a time sampled from an exponential distribution. We finally consider the case of multiple jumps, the time step between them given by an exponential random variable.

4.2.1 Case 1

4.2.1.1 Motivation

Consider the following question. Given an initial population state $x_0 \in \mathbb{R}^n_+$ in the region of attraction $Z_{x_k^\star}$ and parameter state $\Theta_0(\omega)$, what is the probability that selecting a new parameter triple $\Theta_1(\omega)$ such that under the new parameters, $x_0 \notin Z_{x_k^\star}$, $x_0 \in Z_{x_j^\star}$ for $j \neq k$.

We can provide an equivalent characterization of this question within an ecological context. Given an initial population state $\mathbf{x}_0 \in \mathbb{R}^n_+$ in a given ecological regime $\mathfrak{A}$ of an ecological system with the dynamics described by $\dot{\mathbf{x}} = f(\mathbf{x})$ and an initial parameter state $\mathbf{y}_0$ drawn from distribution Θ_0, what is the probability that drawing a new parameter state $\mathbf{y}_1$ transitions out of $\mathfrak{A}$, such that $(\mathbf{x}_0, \mathbf{y}_1) \notin \mathfrak{A}$, if the parameter state is drawn randomly from the parameter distribution?

4.2.1.2 Method

To do so, we must construct the set $S \subset \mathbb{R}^n$ such that $\mathbf{x}_0|\mathbf{y}_1 \notin [\mathfrak{A}]_{Er}$. This is rather straightforward with classical techniques in probability theory. For brevity, denote a regime change event at time t as R_{c_t}.

$$P(R_{c_t}) = P(\mathbf{y}_1 \in S) = \int_S \cdots \int r_\Theta(s)\mathrm{d}s \tag{4.1}$$

following equation 2.16.

4.2.2 Case 2

4.2.2.1 Motivation

Consider a variation on case 1, in which time that the parameter change occurs at some time $t \sim T$ which is exponentially distributed. The initial states $\mathbf{x}_0$ and $\mathbf{y}_0$ are known, as well as the dynamical system (equation 2.4) that describes the changes in the population.

4.2.2.2 Method

As the time at which the parameter change occurs is not known, we expand our approach and introduce our first theorem. This requires us to introduce a brief lemma.

Lemma 4.2.2.1. *For a continuous random variable X with continuous density function r_X,*

$$P(x < X < x + \mathrm{d}x) = r_X(x)\mathrm{d}x$$

Proof. Let X be a continuous random variable with continuous density function r_X. Then

$$P(x < X \leq x+\mathrm{d}x) = \lim_{h\to 0} P(x < X \leq x+h) = \int_x^{x+h} r_X(x)\mathrm{d}x \approx \lim_{h\to 0}(x+h)r_X(x) = r_X(x)\mathrm{d}x$$

□

Theorem 4.2.2.2. *Let $f : \mathbb{R}_+^n \to \mathbb{R}_+^n$ be a dynamical system under the prior assumptions, with a known ecological state $\mathbf{x}_i|\mathbf{y}_i \in [\mathfrak{A}]_{Er}$. Then the probability of $\mathbf{x}_i|\mathbf{y}_{i+1} \notin [\mathfrak{A}]_{Er}$ occurring over the interval $[t_i, t_{i+1})$ is given by*

$$\mathbb{P}(R_C \in [t_i, t_{i+1}]) = \frac{1}{\tau}\int_{t_i}^{t_{i+1}} \left(e^{\frac{(t-t_i)}{\tau}} \int_S \cdots \int r_\Theta(s)\mathrm{d}s \right) \mathrm{d}t \tag{4.2}$$

where R_C denotes the time that the regime change occurred $\tau > 0$ and the integral over the region S is defined in section 4.2.1.

Proof. Let the exponential random variable T have parameter $\frac{1}{\tau}$. Additionally, define R_{C_t} as a random variable denoting that a regime change occurred at time t and define B_E as an indicator variable denoting if the parameter change was big enough to cause a regime change. Then the probability of a regime change can be derived from the construct

$$\mathbb{P}(R_C \in [t_i, t_{i+1}]) = \int_{t_i}^{t_{i+1}} P(R_{C_t})P(B_E) \tag{4.3}$$

By lemma 4.2.2.1,

$$\mathbb{P}(R_C \in [t_i, t_{i+1}]) = \int_{t_i}^{t_{i+1}} P(t \leq T - t_i \leq t + \mathrm{d}t) P(B_E) \tag{4.4}$$

Then,

$$\mathbb{P}(R_C \in [t_i, t_{i+1}]) = \int_{t_i}^{t_{i+1}} \left((r_T(t - t_i)\, \mathrm{d}t) \int_S \cdots \int r_\Theta(s) \mathrm{d}s \right) \tag{4.5}$$

Finally,

$$\mathbb{P}(R_C \in [t_i, t_{i+1}]) = \int_{t_i}^{t_{i+1}} \left(e^{\frac{t-t_i}{\tau}} \int_S \cdots \int r_\Theta(s) \mathrm{d}s \right) \mathrm{d}t \tag{4.6}$$

□

4.2.3 Case 3

4.2.3.1 Motivation

In practice, we may be interested in the behavior of a system where at least one parameter change occurs in the interval of interest. Once a parameter change does occur, we cannot extend the integral described in theorem 4.2.2.2. Rather, once the parameter change event does occur, we can no longer predict the probability of the transition event occurring as it has already occurred. Instead, we may describe the occurrence of a sequence of parameter changes over a given interval.

4.2.3.2 Method

Definition 4.2.3.1. *Let U_n be an Erlang distribution which defines the time until n parameter changes occur. Thus,*

$$U_n = \sum_{k=1}^{n} T(\tau) = T(\tau) + T(\tau) + \cdots T(\tau) = \Gamma(\tau^{-1}, n) \tag{4.7}$$

where $T(\tau)$ is an exponential distribution with parameter τ, then $\mathrm{E}(U_n) = n\tau$ *and* $\mathrm{Var}(U_n) = n\tau^2$.

The Erlang distribution is considered a special case of the Gamma distribution, where the shape parameter n is a positive integer. Then we can construct the sequence of regime change probabilities

$$ {}^{n}X = \{X_i\}_{0<i\leq n},\ X_i = P(R_c) : t \in [t_{i-1}, t_i),\ (t_{i-1} - t_i) \sim T(\tau) \tag{4.8} $$

The total time that ${}^{n}X$ describes is given by U_n.

4.3 Computation of terms

This approach does not rely on the construction of Lyapunov functions to describe the regions of stability. Instead, the computational difficulty of this technique rests in the construction of equation 4.1. The general procedure is as follows for an initial state $\mathbf{x}_0|\theta_0$:

1. Determine the set of equilibrium points $\{x^\star \in \mathbb{R}^n : x^\star \in ker(f)\}$.
2. Consider just one construct $Z_{x^\star}$ such that $x^\star \in Z_{x^\star}$.
3. Construct a system of inequalities on the parameters Θ given $\mathbf{x}_0$.
4. Restrict the parameter space $\mathbb{R}^m$ by applying the system of inequalities. Declare this subset of parameter space $S(\mathbf{x})$.
5. Construct S^c. Then compute

$$ F(t) = \int_S \cdots \int r_\Theta(s|t)\mathrm{d}s = 1 - \int_{S^c} \cdots \int r_\Theta(s|t)\mathrm{d}s \tag{4.9} $$

as a function of time. These probability density functions r_Θ are conditioned on the time parameter t as the set S is a function of the position, which implicitly is a function of the time.

6. Draw $\Delta t \sim T$, update $t_i = t_{i-1} + \Delta t$. Integrate equation 4.2 to compute the i^{th} element of the sequence 4.8.

7. Repeat steps 1 - 6 to generate the sequence constructed in (4.8).

Where $Z_{x^\star}$ is defined in definition 2.1.5.6, S_B can be considered the subset of population space ($\mathbb{R}_+$) that does not belong to the same region of attraction as x_0.

4.4 Changing parameter distributions

In many cases, representing the parameter distribution Θ_n as a sequence of i.i.d. random variables may be unrealistic or be overly simplistic. Parameters may change over time while the functional forms used to construct the model given by equation 2.4 may be robust. Seasonal trends may have small influences on parameters, while evolutionary processes may be at play for large timescales which alter the distribution of parameters. Both conditions severely complicate classical ODE analysis of the model by introducing nonlinear or non-autonomous terms into the model. If the observed or predicted effect of these changes is small, estimation of parameters to reconstruct these models may be subject to increased uncertainty. However, by applying the periodic effects *to the parameter distributions instead*, and then sampling from them rather than explicitly including these model features, the complexity of the model analysis can be preserved. Simulation can be used to determine the variation in end behavior.

4.4.1 Always stable models and critical parameter identification

Some models do not include multiple stable equilibrium, thus only one regime is described by the model. The simulation portion of this technique can still be used to evaluate the stability of these models, however we must define a new question of interest. Instead, we can ask

1. Is the expected value of the population under the assumption of stochastic param-

eters equal to the constant-parameter model formulation? If so, does this limiting population average utilize mean parameters?

2. Do specific parameters not involved in the equilibrium position (e.g. scaling parameters) impact the expected value of the population? Do they alter the variance?

3. Given a bounded set S that containing the equilibrium, what is the probability that the population exits this bounded region?

Questions 1 and 2 can be answered directly through a statistical analysis of the time series of the population generated by simulation, followed by analysis step. The first question is analogous to the dominated convergence theorem for expectations. The third question is explored in section 4.2.

4.4.2 Seasonal variation

Seasonal variation can often be captured by a sine function. Consider

$$r(t) = r_c - r_w sin(2\pi t) \tag{4.10}$$

when $|r_w| \ll |r_c|$, we can approximate $r(t) \approx r_c$. We demonstrate the utility of this technique with a simple example. Consider the classic Lotka-Volterra model

$$\dot{x} = r_1 x - axy \tag{4.11}$$

$$\dot{y} = bxy - r_2 y \tag{4.12}$$

This system has an extinction equilibrium at $(0, 0)$ and a coexistence equilibrium at $\left(\frac{r_2}{b}, \frac{r_1}{a}\right)$. This conclusion is easily reached through a steady state analysis, and is excluded due to it's simplicity. Constructing this model where r_1 and r_2 are seasonally influenced gives the system of equations

$$\dot{x} = (r_1 - r_a \sin(2\pi t))x - axy \tag{4.13}$$

$$\dot{y} = bxy - (r_2 - r_b \sin(2\pi t))y \tag{4.14}$$

Where $r_a \ll r_1$ and $r_b \ll r_2$. No steady state exists for this model for all $t > 0$ as this is not an autonomous differential equation. A simplification to drop time-dependent terms allows for the incorporation of more complex parameters without significantly increasing model complexity.

5 Embedded Markov Chains models

In this chapter, we will connect and formalize the idea we have developed and provide an alternative method for simulation of populations that does not require the usage of numerical techniques to simulate the differential equation. Essential corollaries, theorems, and lemmas are proven with some generality to demonstrate the generality of this approach and provide a standard approach for further generalizations. Further, this section draws from global notions of stability and random dynamical systems. Many physical systems do permit a global characterization due to the possibility of explosion. However many ecological systems can be described by well-posed models which lack the capability of explosions found in the context of physical systems.

5.1 General approach

A primary technical challenge in the construction of probabilistic models is the development of good transition operators, either as stochastic differential equations, Markov Chains, or a general stochastic process. In sections 3 and 4, we have computed the change in the population as forward action of the differential equation or associated dynamical system. The significant drawback of this approach is that it computationally expensive, requiring hundreds to tens of thousands of numerical solutions to differential equations to be obtained. Rather, if we could identify the specific flow and the time step, we could determine symbolically a probability distribution that describes the next population at the next time point. Fortunately, the mathematical construction of our system permits this approach as we have already defined or assumed distributions for every parameter. Because parameter distributions are defined, we can construct a bijective map from the space of parameters into

the space of maps that satisfy an initial condition. By noting that the time step is known (even if randomly distributed), we can determine the next position if we know the map. This pair of observations allows us to randomly select a sequence of maps to be followed for randomly selected intervals of time. By combining both, we can randomly select a next position of the system.

Such a strategy can be furthered by invoking the memoryless property of the sequences of random variables describing the parameters and the dependence only on initial condition property of solutions to differential equations. Once at a population state, the probability of attaining a specific new state is entirely determined by the initial position and the distributions for each parameter. As a result, the sequence of population positions (population states) satisfies a Markov property. Further, if we can well-characterize the transition operator between states, we can well characterize a Markov chain. This is the transition operator we will develop in the remainder of this section.

5.2 Overview

First, we introduce formal definitions for specialized mathematical structures not yet used. We begin by providing a formal definition of the mathematical structure described in the previous chapter.

Definition 5.2.0.1 (Stochastic Parameters System (SP-system))**.** *The tuple* $(X, f, \{\Theta_k\}, \bar{\varsigma}, \tau, x_0)$ *is a SP-system where*

1. $X \subset \mathbb{R}_+^n$ *is the set of possible population states where* n *is the number of species in the model,*

2. $f : X \to X$ *is a well defined uniformly continuous map on* X *with a set of parameters* θ*,*

3. $\bar{\varsigma}$ *is the set of all solution flows (denoted as* φ*) of the differential equation described by* f*,*

4. $\{\Theta_k\}_{k\in\mathbb{N}_0}$ *is an infinite sequence of independent variables* θ_k*, which completely de-*

scribes the model parameters contained in the map f,

5. *τ is a strictly positive real number that is the single parameter of an exponential distribution ($T(\tau)$)*

6. *$x_0 \in X$ is an initial position of the system.*

Remark 5.2.0.2. *We say that an SP-system is well posed (definition 2.1.1.1) if the continuous map $f : X \to X$ is also well posed.*

We next define a specific class of Markov chain structures. This definition of a Markov chain is one of many found in literature and is not the most general definition. Rather, this definition captures a specific set of properties that will be most applicable.

Definition 5.2.0.3 (Discrete time continuous state Markov Chain)**.** *A discrete time continuous state Markov chain is a tuple (X,κ, $\mathbb{T}$,$\{Y_t\}$, ν) where*

1. *X is an infinite set called the state space*

2. *$\kappa : X \times 2^X \to [0, 1]$ is the transition kernel that describes*

3. *T is a discrete index set which is further indexed by $\mathbb{N}$,*

4. *$\{Y_t\}$ is a sequence of random variables indexed by $\mathbb{T}$.*

5. *ν is an initial state of the Markov chain.*

Additionally, the sequence of random variables satisfies the Markov property:

$$P(Y_{t_n} = x_n | Y_{t_{n-1}} = x_{n-1}) = P(Y_{t_n} = x | Y_{t_{n-1}} = x_{n-1}, Y_{t_{n-2}} = x_{n-2}, \ldots, Y_{t_1} = x_1) \quad (5.1)$$

where x_n is a sequence of observed values in X.

Rather than define Φ, it is often easier to construct the transition kernel $\kappa : X \times 2^X \to [0, 1]$

Remark 5.2.0.4. *The index set $\mathbb{T}$ is indexed by $\mathbb{N}$ to ensure that $\mathbb{T}$ is discrete and to emphasize that while t_n may not be uniformly interspersed, we may construct Y_n from Y_t.*

This formulation is essential for the case $\mathbb{T} \neq \mathbb{N}$ which is rarely studied within the context of Markov chains.

Note that while refer to Φ as a function, the dependence on the initial condition allows for the construction of a family of transition operators (dependent on the initial condition), each of which is defined a specific initial condition$x \in X$. In this chapter, we will show that a discrete time continuous state Markov chain on an integer index can be constructed from an SP-system. We will proceed by example.

5.3 Example 2

In this section, we show that the logistic differential equation (definition 5.3.0.1) can generate an SP-system, and then construct a markov chain. The logistic equation is a commonly used model for population growth due to the algebraic simplicity of the model and the number of parameters (see [24] section 2.8 for a full discussion and references). First, however, we will state and briefly prove several classical results about the logistic differential equation that would otherwise suggest that the logistic map is not an interesting object of study with this strategy.

Definition 5.3.0.1 (Logistic differential equation)**.** *The logistic differential equation $f : \mathbb{R}_+ \to \mathbb{R}_+$ is defined as*

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x) = f(x|r,k) = rx\left(1 - \frac{x}{k}\right)$$

where r and k are strictly positive real valued-constants. Note that this is sometimes called the Velhurst equation, in honor of Pierre Francois Velhurst [45].

Remark 5.3.0.2. *Classically, the logistic differential equation is defined where $f : \mathbb{R} \to \mathbb{R}$. We restrict the domain and codomain to non-negative values to emphasize the biologically significant events.*

Theorem 5.3.0.3. *The logistic model contains one stable equilibrium $x^\star = k$, the region of attraction Z_k is $(0, \infty)$.*

Proof. We first show that $x^\star = k$ is the only stable equilibrium. Let

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x|r,k) = rx\left(1 - \frac{x}{k}\right)$$

At equilibrium, $\frac{\mathrm{d}x}{\mathrm{d}t}|_{x=x^\star} = f(x^\star) = 0$ then

$$0 = rx^\star\left(1 - \frac{x^\star}{k}\right)$$

As this is a polynomial, either $rx^\star = 0$ or $0 = 1 - \frac{x^\star}{k}$. Then $x^\star = 0$ or $x^\star = k$. Then $x^\star \in \{0, k\}$ is the set of equilibrium. Next, we perform a linear stability analysis. As

$$f'(x) = r - 2\frac{rx}{k} = r\left(1 - \frac{2x}{k}\right)$$

then $f'(0) = r > 0$ and $f'(k) = -r < 0$, so the only stable equilibrium is $x^\star = k$. Next, recall the definition of a region of attraction (2.1.5.6). To show that the region of attraction for $x^\star = k$ is $(0, \infty)$, we will show that any initial condition $x_0 \in (0, \infty)$ trends towards k. We outline the next several steps, omitting the details of convergence for brevity. Note that such a result can also be attained by inspection of the solution flow of the system. Every $x_0 \in (k, \infty)$ satisfies $f'(x_0) < 0$, so $\lim_{t\to\infty} f(x) = f(x^\star) = 0$ implies $\lim_{t\to\infty} x(t) = k$, where $x(t_0) = x_0$. Likewise, every $x_0 \in (0, k)$ satisfies $f'(x_0) > 0$, so $\lim_{t\to\infty} f(x) = f(x^\star) = 0$ implies $\lim_{t\to\infty} x(t) = k$. Thus any initial position $x_0 \in (0, \infty)$ converges to k in the limit. □

The solution flow operator for the logistic differential equation $\varphi : \mathcal{T}_{t_0} \times \mathbb{R}_+ \to \mathbb{R}_+$is given by

$$\varphi(t - t_0, x|r, k, 0) = \varphi(x, t|r, k, t_0) = \frac{kxe^{rt}}{(k - x)e^{rt_0} + xe^{rt}} \tag{5.2}$$

where $x \in [0, \infty)$, $t \geq t_0 \geq 0$, and r, k are defined as above. Notice that the solution flow operator is conditioned on t_0, as well as r and k. This is a relaxation of the initial condition part of the definition, such that $\varphi(x, t_0) = x$, rather than formally requirement that $\varphi(x, 0) = x$, as our flow is defined over time index $[t_0, \infty)$ which may not include all inverse elements.

Corollary 5.3.0.4. *The set of all solution flows to the logistic function* $\{\varphi\}$ *satisfies*$\{\varphi\} \subset$

$C(\mathbb{R}_+)$.

Proof. This follows from theorem 5.3.0.3. If $x \in [0, k]$, then $0 \leq \varphi(t, x) \leq k$. Otherwise, $x > k$, and $f(x) < 0$ for all $t > t_0$, so $\varphi(t, x) \leq x$. Then $\varphi(t, x) \leq \max(\{\varphi(t_0, x), k\})$. Then $\varphi(t, x)$ is bounded. □

To proceed, we require k and r to be realizations of random variables. To do so with generality,we construct sequences of i.i.d. random variables $K = \{K_n\}_{n\in\mathbb{N}_0}$ and $R = \{R_n\}_{n\in\mathbb{N}_0}$, where these random variables are defined as

$$K_n : \Omega_K \to \mathbb{R}_+, \quad r_n : \Omega_r \to \mathbb{R}_+, n \in \mathbb{N}_0 \tag{5.3}$$

where r_{K_n} and r_{R_n} are the associated probability density functions for K_n and R_n respectively. As K and R are i.i.d., we abuse notation and write

$$r_R(r) = r_{R_n}(r), r_R(r) = r_{K_n}(r), \forall n \in \mathbb{N}_0 \tag{5.4}$$

For brevity, we construct the sequence of random vectors Θ_n as

$$\Theta_n : \Omega_K \times \Omega_r \to \mathbb{R}^2_+ \qquad r_\Theta(K, r) = \begin{bmatrix} r_K(k) \\ r_r(r) \end{bmatrix}, \qquad \theta \sim \Theta_n \tag{5.5}$$

Now we return to our flows. Define the space of all flows through an initial condition (x_0, t_0) as

$$\varsigma^{t_0}_{x_0} = \left\{ \varphi(t, x) \in C(\mathbb{R}_+) : \frac{\mathrm{d}\varphi(t, x_0)}{\mathrm{d}t} = f(x_0), \varphi(t_0, x_0) = x_0 \right\} \tag{5.6}$$

where $f(x)$ is defined in definition 5.3.0.1. This is the space of all continuous solution flows that intersect the space-time coordinate (x_0, t_0). By theorem 5.3.0.3, every solution flow is bounded. As this is a subspace, it inherits the subspace metric and subspace topology from $C(\mathcal{T})$ (see definition 2.1.3.1). This is in fact a metric space under the supremum norm, where $d_\varsigma : \varsigma^t_x \times \varsigma^t_x \to \mathbb{R}_+$, for any $\varrho, \psi \in \varsigma^t_x$, $d(\varrho, \psi) = \sup_{t\in\mathcal{T}} |\varphi(t, x) - \psi(t, x)|$.

Remark 5.3.0.5. *Biologically, $\varsigma^{t_0}_{x_0}$ is the space of all possible flows that arrive at the state x_0 at time t_0, and every possible 'route' forwards from the state x_0 at t_0.*

Lemma 5.3.0.6 (Uniqueness and existence of flows on parameters)**.** *If k and r specified, then there exists a unique $\varphi \in \varsigma_{x_0}^{t_0}$ whose parameters are k and r respectively.*

Proof. This follows from the existence/uniqueness criterion for solutions of differential equations, as by specifying r and k, we reduce $\dot{x} = f(x)$ to a specific differential equation which has a unique solution. □

Corollary 5.3.0.7. *For every $t_0 \in \mathcal{T}$ and $x_0 \in \mathbb{R}_+$, there exists a map $M_{(t_0,x_0)} : \mathbb{R}_+^2 \to \varsigma_{x_0}^{t_0}$, $M_{(t_0,x_0)} : \Theta_n \mapsto \varphi(t, x|t_0, \Theta_n)$.*

Proof. The proof of this corollary immediately follows from lemma 5.3.0.6. □

To summarize, we have constructed the random variable $\Theta_n : \Omega_0 \to \mathbb{R}_+^2$ and $M_{(t_0,x_0)} : \mathbb{R}_+^2 \to \varsigma_{x_0}^{t_0}$. For fixed (x_0, t_0), we can compose these to obtain $M_{t_0,x_0}(\Theta(\omega))$, which is a function. We can generalize this to obtain the random function

$$F_{x_0}^{t_0} : \Omega \to \varsigma_{x_0}^{t_0} \tag{5.7}$$

for $t_0 \in \mathcal{T}$ and $x_0 \in \mathbb{R}_+$. We can further generalize by constructing the set of all possible flows. Let

$$\bar{\varsigma} = \bigcup_{x_0 \in \mathbb{R}_+, t_0 \in \mathcal{T}} \left(\varsigma_{x_0}^{t_0}\right) \tag{5.8}$$

Remark 5.3.0.8. *The set $\bar{\varsigma}$ is still a metric space with the subspace metric inherited from $C(\mathbb{R}_+)$.*

Then we can define the F that contains flows globally as

$$F : \Omega \times \mathcal{T}_{t_0} \times \mathbb{R}_+ \to \bar{\varsigma}, (\omega, t_n, x) \mapsto \varphi(\cdot, x, |\Theta(\omega), t_n) \tag{5.9}$$

While we state that φ is conditioned on $\Theta(\omega)$ this is in reference to the flow function being conditioned on $\Theta(\omega)$, rather than the image of (ω, t_n, x) being conditioned on $\Theta(\omega)$. This F is sufficient to generate φ.

Proposition 5.3.0.9. *The map $F : \Omega \times \mathcal{T}_{t_0} \times \mathbb{R}_+ \to \bar{\varsigma}$ defines a random dynamical system.*

The proof of this proposition follows from the definition of a random dynamical system. The cocycle properties of $\varphi(\cdot, \omega, \cdot) : \mathbb{T} \times \mathbb{R}_+ \to \mathbb{R}_+$ follow from the prior fact that $\varphi(\cdot, \cdot|\Theta) : \mathbb{T} \times \mathbb{R}_+ \to \mathbb{R}_+$ is a already dynamical system.

Next, we utilize the exponential random variable T with parameter τ. Formally,

$$T : \Omega_T \to \mathbb{R}_+, r_T(t|t_0, \tau) = \tau^{-1} e^{-(t-t_0)\tau^{-1}}, t \in \mathcal{T}_{t_0} \tag{5.10}$$

One may notice that from $\varsigma_{x_0}^{t_0}$, we may randomly select a flow and some time step $\Delta t_1 = t_1 - t_0$ to arrive at $\varsigma_{\varphi(t_1, x_0|t_0)}^{t_1}$. This observation leads to our next theorem.

Theorem 5.3.0.10. *The generalized 1-step transition map $\Phi(\omega, t_0, x_0) : \Omega_T \times \varsigma_{x_0}^{t_0} \to \mathbb{R}_+$ defines all possible transitions $(x_0, t_0) \mapsto (\varphi(t_1, x_0|t_0), t_1)$ for the stochastic process $\{X_t\}_{t \in \mathbb{T}}$. If this mapping exists, then there also exists an analogous transition operator for the stochastic kernel $\kappa : \mathbb{R}_+ \times 2^{(\mathbb{R}_+)} \to [0, 1]$. For the logistic differential equation, the probability kernel κ is defined as*

$$\kappa(x, C) = \iiint_{\Upsilon_C} f_Y(x_n, r, t) \mathrm{d}(x_{n+1}) \mathrm{d}x \mathrm{d}r \mathrm{d}t \tag{5.11}$$

where

$$\Upsilon_C = \{(x, r, t) \in \mathbb{R}_+ \times \mathbb{R}_+ \times \mathcal{T} : x \in C, r \in \mathbb{R}_+, t > t_n \in \mathcal{T}\} \tag{5.12}$$

and f_Y is the joint density of the transformed variables if $x_n > 0$.

The following proof of this theorem is in some ways not rigorous as we use intuitive facts where possible. While we attempt to implement a broad technique for existence, we do rely on several properties demonstrated within the proof of theorem 5.3.0.3. We motivate the proof with the following observation.

Let $Im(f)$ denote the image of the map f within it's codomain. The event $x_{n+1} \in C$ occurs when both of the following occur:

1. the random value $T(\omega)$ satisfies $x_{n+1} = \varphi(t_n + T(\omega), x_n|t_n)$
2. there exists $\varphi \in \varsigma_{x_0}^{t_0}$ such that $x_{n+1} = \varphi(t_n + T(\omega), x_n|t_n) \in Im(\varphi)$,

Proof. Let $x \in \mathbb{R}_+ = Z$, and let C be some event such that $C \subset 2^{(\mathbb{R}_+)} = \sigma(X)$. κ can be loosely thought of as *measuring the probability* of transitioning from state x to state $y \in C$. Formally,

$$\kappa(x, C) = \mathbb{P}(X_{n+1} = x_{t_{(n+1)}} \in C | x_{t_n} = X_n)$$

To proceed, we require the parameterized functional forms of all solutions and the density function of the random vector Θ_n.

$$\mathbb{P}(X_{n+1} = x_{t_{(n+1)}} \in C | x_{t_n} = X_n) = \mathbb{P}\left(\left(\varphi(t_{(n+1)}, x_n | t_n, \Theta_n)\right) \in C | x_n \right)$$

Then the transition kernel can be constructed from the density functions. Our goal to construct a multivariate distribution conditioned on x_n. As a consequence of the existence of the map Φ Define $Y_1 = \varphi(t_1, r, K | x_0, t_0)$ as a new random variable. Let $|\Theta_n| = k$. We then expand to form an $k+1$ system of variables to transform with. Let

$$y_1 = h(t_{(n+1)}, r, k | x_n) = \frac{kxe^{rt_{(n+1)}}}{(k-x)e^{rt_n} + xe^{rt_{(n+1)}}}$$

where $y_1 = h(t_{(n+1)}, r, k | x_n)$ exists for every (t_n, x_{n+1}). We can remove the explicit dependence on t_n by substituting $\Delta t = t_{n+1} - t_n$ and simplifying. We write this function as g_1.

$$y_1 = g_1(\Delta t, r, k | x_n) = \frac{kx_n e^{r\Delta t}}{k + x_n\left(e^{r\Delta t} - 1\right)} \tag{5.13}$$

Now the new position $y_1 = x_{n+1} \sim Y_1$ can be entirely described as a function of random variables, conditioned on a single position value. To perform a change of variables to obtain the distribution of Y_1, we extend the system by constructing the transformed random variables: $y_2 \sim Y_2 = R$ $(r \sim R)$, $y_3 \sim Y_3 = T$ $(\Delta t \sim T)$ (note that $Y_n : n \geq 2$ are formed by identity transformations). This new system is invertible. As T, R, K are independent, let

$$f_X(x_1, x_2, x_3) = r_K(x_1) r_R(x_2) r_T(x_3) \tag{5.14}$$

Let g_i denote the transform between K, R, T and Y_1, Y_2, and Y_3 respectively. As g_2 and g_3

are identity transforms, the inverses g_2^{-1} and g_3^{-1} exist and are well defined. We select g_1 to map between K and Y_1 as the inverse g_1^{-1} is well defined for K. Then

$$g_1^{-1}(y_1, y_2, y_3) = \frac{x_n e^{y_2 t_n} - x_n e^{y_2 y_3}}{e^{y_2 t_n} - x_n y_1^{-1} e^{y_2 y_3}} \tag{5.15a}$$

$$g_2^{-1}(y_1, y_2, y_3) = y_2 = r \tag{5.15b}$$

$$g_3^{-1}(y_1, y_2, y_3) = y_3 = t \tag{5.15c}$$

where $y_1^{-1} = \frac{1}{y_1}$. We can then construct the Jacobian matrix for the transformation $J(y_1, y_2, y_3)$ as

$$J(y_1, y_2, y_3) = \begin{vmatrix} \frac{e^{y_2 y_3}(-1+e^{y_2 y_3})x_n^2}{(y_1 - e^{y_2 y_3} x_n)^2} & \frac{e^{y_2 y_3} x_n (x_n - y_1) y_1 y_3}{(y_1 - e^{y_2 y_3} x_n)^2} & \frac{e^{y_2 y_3} x_n (x_n - y_1) y_1 y_2}{(y_1 - e^{y_2 y_3} x_n)^2} \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{vmatrix} \tag{5.16}$$

$$J(y_1, y_2, y_3) = \left| \frac{e^{y_2 y_3} \left(e^{y_2 y_3} - 1\right) x_n^2}{\left(y_1 - e^{y_2 y_3} x_n\right)^2} \right| \tag{5.17}$$

From this, it is not clear that the denominator is always nonzero. To demonstrate that J is well defined, we back-substitute a substituted definition for y_1 to obtain

$$J(y_1, y_2, y_3) = \left| \frac{e^{-t_{(n+1)} y_2} \left(x_n e^{t_{(n+1)} y_2} + e^{t_n y_2} \left(y_3 - x_n\right)\right)^2}{x_n^2 \left(e^{t_{(n+1)} y_2} - e^{t_n y_2}\right)} \right| \tag{5.18}$$

From this, it is clear that the J is well defined if and only if $x_n \neq 0$. The denominator is strictly positive if $t_{(n+1)} > t_n$ and $x_n > 0$. Both of these requirements are fulfilled as $\Delta t_n = t_{(n+1)} - t_n > 0$ and the assumption that $x_n > 0$. Upon inspection of J, it should also clear that the numerator is also strictly as it can be expressed as the product of a square and an exponential, when $x_n > 0$.

Let f_Y denote the joint probability with respect to the transformed (Y_i) variables. Then

$$f_Y(y_1, y_2, y_3) = f_X(g_1^{-1}(y_1, y_2, y_3), g_2^{-1}(y_1, y_2, y_3), g_3^{-1}(y_1, y_2, y_3)) J(y_1, y_2, y_3) \tag{5.19}$$

Then by equation (5.14) and equations (5.15a), we obtain

$$f_Y(y_1,y_2,y_3) = r_K\left(\frac{x_n e^{y_2 t_n} - x_n e^{y_2 y_3}}{e^{y_2 t_n} - x_n y_1^{-1} e^{y_2 y_3}}\right) r_R(y_2) r_T(y_3) \cdot \frac{e^{-t_{(n+1)}y_2}\left(x_n e^{t_{(n+1)}y_2} + e^{t_n y_2}\left(y_3 - x_n\right)\right)^2}{x_n^2\left(e^{t_{(n+1)}y_2} - e^{t_n y_2}\right)}$$

This longer form is preferred as it has no explicit dependency on y_1. As y_2 and y_3 are invariant under this transformation, r_T is defined in equation (5.10), as $x_{n+1} = y_1$,

$$\begin{aligned} f_Y(x_{n+1}, r_1, t_{(n+1)} | x_n, t_n) =& r_K\left(\frac{x_n e^{r_1 t_n} - x_n e^{r_1 t_{(n+1)}}}{e^{r_1 t_n} - x_n x_{n+1}^{-1} e^{r_1 t_{(n+1)}}}\right) \\ & \cdot r_R(r_1)\tau e^{\tau(t_{(n+1)} - t_n)} \\ & \cdot \frac{e^{-t_{(n+1)}r_1}\left(x_n e^{t_{(n+1)}r_1} + e^{t_n r_1}\left(t_{(n+1)} - x_n\right)\right)^2}{x_n^2\left(e^{t_{(n+1)}r_1} - e^{t_n r_1}\right)} \end{aligned} \tag{5.20}$$

where $\tau > 0$, $t_{(n+1)} > t_n$, r_K and r_R are probability density functions. We can the define a region of integration Υ_C as

$$\Upsilon_C = \{(x,r,t) \in \mathbb{R}_+ \times \mathbb{R}_+ \times \mathcal{T} : x \in C, r \in \mathbb{R}_+, t > t_n \in \mathcal{T}\} \tag{5.21}$$

The subscript C attached to Υ_C denotes the explicit dependence of the set on C, Note that this requires r_R to be defined over all positive real values. If this is not the case, extend R by setting $r_R(t) = 0$ for $t \notin$ support(R). Then

$$\kappa(x_n, C) = \iiint_{\Upsilon} f_Y(x_n, r, t)\mathrm{d}(x_{n+1})\mathrm{d}x\mathrm{d}r\mathrm{d}t \tag{5.22}$$

where r, t are dummy variables.

□

5.4 Main Results

We require an additional definition that was implicitly used in the prior section.

Definition 5.4.0.1 (Invertible SP-system)**.** *An SP-system* $(\mathbb{R}_+, f, \{\Theta_k\}, \bar{\varsigma}, \tau, x_0)$ *is said to*

be invertible if for every flow φ, there exists some set of indices $i \in I$ such that that the system $\vec{y}_I = \varphi(t, \Theta_n(\omega)|t_0)$, and y_j is the j^{th} element of Θ_n for all $j \notin I, 0 < j \leq m+1$, where m is the length of the random vector of parameters Θ_n, the system $\vec{y}$ is a continuous invertible system of equations.

Remark 5.4.0.2. *While we have defined the time step random variable T as an exponential distribution, the following theorem does not depend on the type of random variable chosen for T.*

Theorem 5.4.0.3 (Relation between SP-system and random dynamical system)**.** *Let $(X, f, \{\Theta_k\}_{k\in\mathbb{N}_0}, \{\varphi\}, \tau, x_0)$ be a SP-system. Then there exists a corresponding random dynamical system $(\Omega, \mathcal{F}, P, (\theta(t))_{t\in\mathbb{T}})$, where each map is obtained by*

$$F : \Omega \times \mathcal{T}_{t_0} \times \mathbb{R}_+ \to \bar{\varsigma} \tag{5.23}$$

which is analogous to a dynamical system if and only if all of the following

1. *there exists a bijection between $\mathbb{T}$, $\mathcal{T}_{t_0}$, and $\mathbb{N}$,*
2. *$\Omega = \Omega_T \times \Omega_\Theta$,*

The argument presented in the prior section can be generalized into the following theorem.

Theorem 5.4.0.4. *Let $(X, f, \{\Theta_k\}_{k\in\mathbb{N}_0}, \{\varphi\}, \tau, x_0)$ be an invertible SP-system that satisfies the following conditions*

1. *$X \subset \mathbb{R}^n_+$ be a connected set such that $X \supset Im(f)$ over $\mathbb{R}^n_+$, upon which $f : X \to X$ is well defined and uniformly continuous,*
2. *The set $\bar{\varsigma} \subset C(X)$, that is every solution flow of f is continuous with respect to the time index $\mathcal{T}$ and is bounded over all $t \in \mathcal{T}$,*

then there exists a probability kernel $\kappa : X \times 2^X \to [0, 1]$ for all $x_n \in X$.

Remark 5.4.0.5. *Several generalizations of this theorem can easily be obtained by further relaxing structural requirements. The most significant relaxation is the removal of the i.i.d.*

requirement on Θ. As observed biological processes are often highly autocorrelated, the construction of a Markov chain of order $n > 1$ may be fruitful. The general strategy for the existence of such object does not change, however the associated algebraic manipulations and solutions may be significantly complicated to hinder the direct computational strategy used.

6 Discussion

This thesis has outlined two different approaches towards investigating and modeling biological systems through the usage of an SP-system. The SP-system is a newly defined mathematical object within the context of biological modeling, but we have shown that these define a class of random dynamical systems. The approach to the extinction prediction problem allows for the usage of the rich and well developed theory of Markov chains and random dynamical systems theory. Secondly, incorporating stochasticity at the parameter level provides a new technique to overcome a primary technical challenge in stochastic dynamics: the construction of the Markov (transition) kernel. In doing so, we reduce the problem to one of integration, rather than construction. This presents new challenges in developing integration strategies for these broad classes of integrands. However we have meaningfully shifted the problem into a different domain, which allows for different and new approaches. It also has opened the problem to advances in numerical analysis and numerical simulation.

We have also investigated the analysis of SP-systems to generate sequences of transition probabilities. The example presented proceeds with generality where possible. We have examined numerical simulations using uniform random variables, however this approach can easily be generalized by any disjoint distributions. This example can be further generalized by allowing the random variable that describes the larger parameter (a) to be drawn from any distribution with strictly positive values. This distribution can be linearly shifted such that it satisfies the bounds. However these describe fundamentally real systems, suggesting that there are practical upper and lower bounds on allowed parameter values from the physical system. Most biological parameters are strictly positive (see [30, 29, 4] for a brief

overview).

This approach can be generalized to larger systems of significantly higher algebraic complexity. This presents additional challenges in determining the region of attraction. While we have not explored strictly numerical techniques for this problem in detail, this thesis outlines a road map that can be followed to construct a numerical implementation that can be applied to an arbitrary system of equations.

6.1 General Applications

This techniques developed in this thesis demonstrate the utility of the SP-system for biological and ecological systems analysis. We have demonstrated that the SP-system characterization can lead to insightful statistical questions which posit direct ecological questions. We have also demonstrated that a Markov chain can be extracted from an SP-system. A direct application of this Markov chain is the hitting time problem for an epsilon bound around the origin. A slew of general techniques are well established for this problem at both the undergraduate and graduate level and are omitted here for brevity. While we have constructed parameters as stationary stochastic processes, we could apply a parameter evolution to them to determine the behavior of the system under rapid parameter evolution. Additionally, seasonal behavior can be modeled into the parameters by applying a periodic shift to the distribution parameters. The shape and/or mean parameters of many distributions are optimal candidates for this modification.

6.2 Important parameter identification

Identifying biologically significant parameters is sufficiently important to warrant further discussion. We first proceed by example, examining the results of example 1, then discuss further approaches and computational experiments.

First, notice that the growth parameter r_1 does not appear in the algebraic description of any region of attraction. Thus when $r_1 > 0$, any r_1 is allowed. This suggests that the parameter r_1 is not an essential parameter for determining end behavior. Additionally, note

that the parameter that defines the unstable equilibrium is a result of the inequality $a < b$. If we reversed the inequality, it follows from equation (3.5) that b would be the unstable equilibrium. Further, if a and b are not known to obey a strict ordering, then $\min(a, b)$ defines the unstable equilibrium, and $\max(a, b)$ defines the stable equilibrium. In this case, both a and b are biologically significant. The major complication of this case is an expansion in the algebraic representations with the addition of several min and max operations at most steps, the strategy executed does not change. However, both parameters are now significant, as modifications of the ecological system that impact the lesser of these two parameters also impacts the biological system. Impacts on the ecological system that decrease the larger parameter value do not alter the overall stability of the ecological system until the support of the random variable describing the upper parameter intersects the support of the random variable describing the lower random variable. A similar argument can be constructed from the previous approach but by increasing the support for the distribution that describes the lower parameter value as well.

While this approach may appear similar to bifurcation theory, is different than bifurcation theory as it constructed around the support of the random variables and does not require equilibrium to change stability. The latter is an essential component of bifurcation theory.

The above analysis relies on being able to perform a stability analysis. This is not always readily available. Multiple routes for numerical experimentation are available. A first approach is a modification on the classic parameter sweep. Hold all variables constant except for one and consider that parameter as a random variable. The approach can be used with multiple parameters as random variables additionally. Decreasing the number of parameters that are represented as random variables decreases the number of random number draws necessary per iterative step, decreasing the time to compute each step. This can be performed when the random variable has a support over $\mathbb{R}_+$ or a closed and bounded subset of $\mathbb{R}_+$. Weibull, Gamma, beta, log-normal, and uniform distributions are all potential candidates for this distribution depending on what properties the parameter is proposed to have. Simulations allow for the detection of additional behavior not predicted by the deterministic model and allow for the study of the impacts of single-parameter variations. If

a parameter must remain within a small interval for the model to be stable, then by sampling that parameter from a distribution wider than the small interval, the probability of drawing many (an overwhelming majority) of the parameter values from inside the small interval is very small. Then it is most likely that the parameter values obtained will be outside of the interval. This reduces the number of cases that need to be checked significantly. Classically, a parameter sweep requires potentially considering hundreds, thousands, or tens of thousands of parameter values, depending on an a priori estimate of the size of such interval.

6.3 Future directions

Throughout this work we have mentioned where there still exist gaps in computation, understanding, and proof. We have described immediate next steps that are beyond the scope of this work. Any of these steps may provide additional insight into biological systems. A general computational implementation of this technique is essential for its application toward higher (> 2) dimensional systems. There are additional challenges for this, primarily the complexity of computing regions of attraction in the presence of saddle equilibria which are characterized by stable and unstable manifolds. Often these manifolds partition regions of stability, but an explicit computation of these manifolds is generally unreachable. In 2-dimensional systems, there are binary search algorithms available to identify a point on the manifold which can be used as the basis for a numerical approximation of the manifold. Unfortunately, sampling 3-dimensional or higher dimensional space using a search algorithm is not guaranteed to obtain a point on the manifold. A more sophisticated technique to find this manifold and compute the stability bound is one potential route forward. Alternatively, we may decide that testing each point in the population space by forward numerical simulation to identify which region of attraction a point it is in is a sufficient approximation of the true regions of attraction. Then when we want to determine where a position is, we require a classification algorithm to accurately classify which region of attraction the specified point is in.

Many more results are likely accessible by the application of ergodic theorems to under-

standing the behavior of these systems. The applicability of ergodic theory to these systems remains under-explored. Additionally, under what additional conditions and assumptions do the dominated convergence theorem hold (or a new analog of this theorem) or Fatou's lemma? Additionally, the transition operator between random flows of a random dynamical system is a levy process on the space of random flows [9]. The biological and theoretical implications of this remark are not yet explored or characterized.

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