



MONTCLAIR STATE
UNIVERSITY

Montclair State University
**Montclair State University Digital
Commons**

Theses, Dissertations and Culminating Projects

5-2020

Control of Secondary Extinctions in Stochastic Food Webs

Dunia M. Fernandez
Montclair State University

Follow this and additional works at: <https://digitalcommons.montclair.edu/etd>



Part of the [Applied Mathematics Commons](#)

Recommended Citation

Fernandez, Dunia M., "Control of Secondary Extinctions in Stochastic Food Webs" (2020). *Theses, Dissertations and Culminating Projects*. 480.
<https://digitalcommons.montclair.edu/etd/480>

This Thesis is brought to you for free and open access by Montclair State University Digital Commons. It has been accepted for inclusion in Theses, Dissertations and Culminating Projects by an authorized administrator of Montclair State University Digital Commons. For more information, please contact digitalcommons@montclair.edu.

Abstract

Studies on both model-based and empirical food webs have shown that perturbations to an ecological community can cause a species to go extinct, often resulting in the loss of additional species in a cascade of secondary extinctions. These effects can seriously debilitate a food web and threaten the existence of an ecosystem. Here, we consider niche model-based food webs with internal noise and investigate the effects of a control on a secondary extinction cascade triggered by a noise-induced extinction. We show that the forced removal of a nonbasal species immediately after a primary extinction can extend the mean time to extinction of individual nonbasal species as well as that of the complete extinction cascade. An analysis of numerical and statistical results illustrates the effectiveness of a control in delaying the mean time to extinction for endangered species in stochastic food webs.

MONTCLAIR STATE UNIVERSITY

Control of Secondary Extinctions in Stochastic Food Webs

by

Dunia M. Fernandez

A Master's Thesis Submitted to the Faculty of

Montclair State University

In Partial Fulfillment of the Requirements

For the Degree of

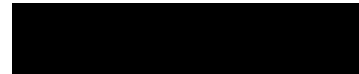
Master of Science

May 2020

College of Science and Mathematics

Department of Applied
Mathematics and Statistics

Thesis Committee:



Dr. Eric Forgoston
Thesis Sponsor



Dr. Lora Billings
Committee Member



Dr. David Trubatch
Committee Member

CONTROL OF SECONDARY EXTINCTIONS IN
STOCHASTIC FOOD WEBS

A THESIS

Submitted in partial fulfillment of the requirements

For the degree of Master of Science

by

DUNIA M. FERNANDEZ

Montclair State University

Montclair, NJ

2020

Acknowledgements

I would like to thank my advisor, Dr. Eric Forgoston, for the invaluable guidance and support he's provided me with during my time working with him. His dedication, valuable insights, and encouragement have meant so much and made all the difference.

I would also like to thank my committee members, Dr. Lora Billings and Dr. David Trubatch, for their input to this work and their support throughout my graduate studies.

Finally, thank you to my family and friends. Their constant love and support has uplifted me and motivated me to get to this point.

This work was supported by the National Science Foundation (DMS-1853610 and CNS-1625636).

Contents

1	Introduction	4
2	Generating Model-Based Food Webs	5
2.1	The Niche Model	6
2.2	Competitive Lotka-Volterra Equations	7
2.2.1	Deterministically Stable Food Webs	8
2.3	Deterministic versus Stochastic Models	9
3	Stochastic Modeling	10
3.1	General Theory and Master Equation	10
3.2	The Individual-Based Stochastic Predator-Prey Model	11
3.2.1	Gillespie Algorithm	11
4	Control of Secondary Extinction Cascades	12
4.1	Deterministic Control	12
4.2	Stochastic Control	13
5	Controlled Stochastic Cascade Results	13
6	Summary and Remarks	15
7	Bibliography	21

List of Figures

1	Diagram of the niche model (as presented by Williams and Martinez). In this example, inverted triangles represent species, and species j , standing in its niche position n_j , is the only prey of species i	6
2	Realization of a niche model-based food web of 50 species.	7
3	Persisting food web complete with a top predator (blue), nonbasal species (red), and basal species (green).	8
4	(a) Introducing random noise to the system triggers a cascade of extinctions. The initial loss of 41 causes 19, 49, 21, 27 and then 45 to go extinct. (b) In the deterministic system, the primary removal of 41 causes only 45 to go extinct.	14

List of Tables

1	Stochastic predator-prey population model events and associated transition rates.	10
2	Results for 1000 stochastic realizations of the food web dynamics. Table shows the 23 different types of extinction cascades that occurred along with the relative frequency and mean time to extinction (MTE) for each. The MTE for each individual nonbasal species is also given.	16
3	Results for the same 1000 noise realizations presented in Table 2 after implementing various controls (forced secondary extinctions). The entries in the rightmost section show relative change in MTE (%) for all nonbasal species (excluding the primary extinction) and the entire nonbasal cascade.	17
4	Results for every extinction cascade (blue) triggered by the primary extinction of 19 (red) with the implementation of a control (yellow). MTE for the entire cascade before the control (denoted MTE) and after the control (denoted MTE*) are given, as well as the relative change in MTE. A dashed entry indicates the corresponding cascade pattern did not occur in the initial 100 realizations without control.	18
5	Results for every extinction cascade (blue) triggered by the primary extinction of 41 (red) with the implementation of a control (yellow). MTE for the entire cascade before the control (denoted MTE) and after the control (denoted MTE*) are given, as well as the relative change in MTE. A dashed entry indicates the corresponding cascade pattern did not occur in the initial 100 realizations without control.	19
6	Results for every extinction cascade (blue) triggered by the primary extinction of 49 (red) with the implementation of a control (yellow). MTE for the entire cascade before the control (denoted MTE) and after the control (denoted MTE*) are given, as well as the relative change in MTE. A dashed entry indicates the corresponding cascade pattern did not occur in the initial 100 realizations without control.	20

1 Introduction

For years, one of the main focuses of biological and ecological research has been to better understand the complex living communities that make up the living world. Numerous studies have been done, at various scales, in order to accurately capture and quantify the characteristics and behaviors of different ecological communities [1–3]. In particular, food webs are of great interest to ecologists. These systems are comprised of a number of species along with all the observed interaction links and rates [4, 5]. The interconnected network of effects that species have on one another’s populations is what ecologists aim to encapsulate in what is called a community matrix [6]. These matrices provide much insight when studying community structure, stability, and resilience. The question of how these large and complex ecological systems function, persist, and respond to perturbations remains at the center of many modern scientific projects.

It is expected that in a perfectly stable, non-noisy, and undisturbed environment, a theoretical ecological community will thrive and persist, following the laws of its prescribed dynamics, forever [7]. However, this is not the case for actual systems found in the real world. It is well known that noise can significantly impact the behavior of biological systems [8, 9]. Stochasticity can arise in these systems in many different ways, both internally and externally. In particular, noise can present itself in ecological communities as a result of environmental factors, inter- and intraspecific competition and interactions, or demography [8, 10]. Different radical events like climate change, habitat destruction, disease, invasion, and many others often cause species extinctions within large ecosystems [11–18]. The initial loss of one species in a food web often triggers a cascade of secondary extinctions, thereby threatening the overall stability and survival of the ecosystem in question [19, 20]. Despite the inherent robustness of these systems, the extinction of one species can propagate through the network over time as the system evolves to a new equilibrium, potentially having long-term devastating effects on the community. The consequences of a single extinction event are usually unpredictable given the great structural and mechanical complexity exhibited in ecological communities [19, 20]. Such uncertainty poses sizable challenges to ecosystem management and conservation efforts.

Some studies have been done on the analysis of secondary extinction cascades in both deterministic and stochastic settings [19], and some have successfully attempted to implement controls on strictly deterministic food webs [20]. However, no work has been done to implement and study the success of a control method on a secondary extinction cascade triggered by a primary noise-induced extinction. Although population extinction events are considered rare, it is necessary to study how food webs, under the influence of noise, respond to species loss and mitigation efforts. Here, we consider dynamic, synthetic food webs with internal noise that are evolved over time until a natural extinction occurs and a cascade of secondary extinctions is observed. We then investigate the effects of forcing the removal of a species immediately after the primary extinction occurs in order to extend the mean time to extinction of the rest of the species in the cascade as well as the mean time to extinction for the entire cascade.

To investigate the consequences of stochastic primary extinctions and analyze the effects of different intervention efforts, we generate synthetic food webs and define the population dynamics of the systems. It is known that the structure of natural food webs is not arbitrary. In fact, a number of models exist that describe food web structure with varying degrees of success (cascade [21], niche [22], and nested hierarchy [23] to name just a few). The accuracy of these models is based on how well the structure of the resulting model food webs compares to the structure of empirical food webs, i.e. the resulting food webs have a realistic number of interaction links, they exhibit a hierarchical structure with different trophic levels, etc. In our studies, we consider synthetic food webs generated following the niche model framework. Some of the advantages of using the niche model are that it requires few initial constraints and that it allows for certain ecological mechanisms like looping and cannibalism to be present in the webs [22]. The population dynamics of the food webs are described by the competitive Lotka-Volterra predator-prey model [24–27] which accounts for species birth/death, self-regulation, and interactions with other species.

In this work, we present a novel investigation of stochastic extinction and secondary extinction cascades in food webs. We hope that the findings here illustrate the importance of considering stochastic dynamics and noise-induced extinctions in the field of ecology and beyond as it pertains to control and conservation.

2 Generating Model-Based Food Webs

In a real ecological community, both community dynamics and trophic structure are important. Therefore, it is necessary to consider structural and dynamical models that offer to explain these properties when attempting to study ecological systems from a mathematical perspective. The process of modeling and analyzing food web characteristics and behavior begins with generating synthetic networks with structures that closely resemble those observed from natural food webs. This means that the model-based food webs contain both basal and nonbasal species, which are non-consumers and consumers, respectively; they exhibit a realistic balance of basal, intermediate, and top-level predators, distributed into different trophic levels; and the interactions and mechanisms present are ecologically sound. Then, it is necessary to determine the population dynamics of the food webs. The deterministic community dynamics are modeled using differential equations that capture gain-loss processes like growth and death, as well as species gain and loss from predation. The following sections will discuss how the static network structure of a synthetic food web is generated following the niche model as well as how the competitive Lotka-Volterra model is used to make qualitative predictions about the long-term behavior of an ecological system. The need for deterministic and stochastic models, as well as the advantages and disadvantages of both, will also be discussed.

2.1 The Niche Model

Our initial synthetic food webs are constructed according to the rules of the niche model. In order to generate the network structure, we first determine the number of species in the food web S and the empirical directed connectance C , defined as the estimated fraction of all possible directed interaction (predation) links realized in the food web simulations. For any food web without restrictions, the total number of possible links is S^2 . In all of our simulations, the initial construction of the food web using the niche model uses $S = 50$ and $C = 0.2$. This choice of C is within the range of connectance observed for real food webs, and a starting community size of 50 ensures that the resulting persisting webs (discussed in Section 2.2.1) have 10-15 species. Every species in the network is then assigned a *niche value*, n_i , drawn uniformly on the interval $[0, 1]$. These values serve to hierarchically position all species on a one-dimensional axis from 0 to 1.

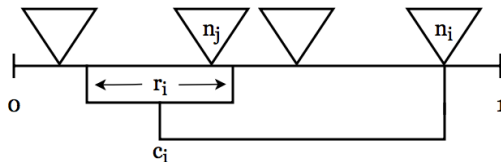


Figure 1: Diagram of the niche model (as presented by Williams and Martinez [22]). In this example, inverted triangles represent species, and species j , standing in its niche position n_j , is the only prey of species i .

All species i prey on all species j whose positions on the niche axis, n_j , fall inside of i 's feeding range. We denote the width of this range r_i and compute $r_i = xn_i$, where $x \in [0, 1]$ is randomly drawn from a beta distribution with an expected value equal to $2C$; in our simulations $E[X] = 0.4$. We chose $\alpha = 1$ and $\beta = 1.5$ to be the shape parameter values of the beta distribution in order to obtain the desired expected value. To guarantee that the number of basal species in the web is greater than or equal to unity, $r_i = 0$ is assigned to the species with the smallest niche value. The location of every feeding region is then determined by a center value, c_i , drawn uniformly from the interval $[r_i/2, n_i]$; this choice of interval allows for certain ecological interactions like cannibalism and looping to be present in our food webs though it is far more likely that a species will consume others lower in the niche hierarchy. Figure 1 shows a general example of a niche model diagram.

In order to simplify the process of generating interaction rates for the predator-prey equations (discussed later in Section 2.2), we chose to eliminate instances of mutual predation (species i and j prey upon each other) from our networks. The direction of predation that remains is randomly selected: two random numbers are drawn uniformly from $(0, 1)$; the direction corresponding to the largest random number is kept, the other is removed.

The food webs that result from following the niche model framework are entirely static. This means that the model does not consider the dynamical aspects of each

node or those of the network as a whole. Consequently, the resulting initial food webs are inherently unstable. In order to obtain stable and persisting networks, we must apply predator-prey dynamics; in this particular case, the competitive Lotka-Volterra model dynamics. Figure 2 presents an example of one niche model food web realization.

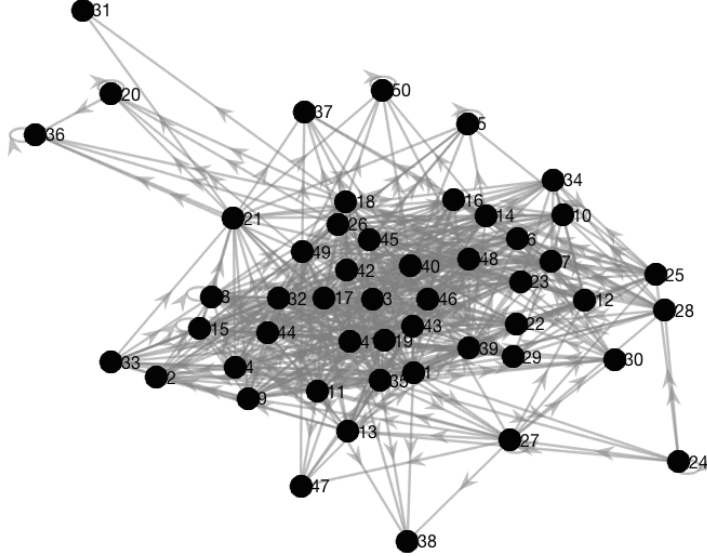


Figure 2: Realization of a niche model-based food web of 50 species.

2.2 Competitive Lotka-Volterra Equations

The population dynamics of our food webs are modeled by the competitive Lotka-Volterra equations. This model captures the population dynamics of species competing for common resources and is widely used to describe the dynamics of predator-prey systems. The equations are expressed as:

$$\frac{dX_i}{dt} = X_i \left(b_i + \sum_{j=1}^S a_{ij} X_j \right), \quad \text{for } i = 1, \dots, S. \quad (1)$$

For a system of S species, the population densities (number of individuals per unit of area) of all species in the community are denoted by the state vector $\mathbf{X} = (X_1, \dots, X_S)$, where each density X_i is drawn uniformly on $(0, 1)$. The first term on the right-hand side of (1) accounts for natural growth (death) if i is basal (nonbasal); here, b_i represents the positive birth rate for basal species and negative death rate for all nonbasal species, and it is drawn uniformly on $(0, 1)$ when i is basal, and $(-1, 0)$ otherwise. In the summation in (1), the self-regulating (intraspecific competition, cannibalism, etc.) term is accounted for when $i = j$ and the self-regulation rate a_{ii} is a uniformly selected value in $(-1, 0)$. Similarly, all interactions (gain from predation

and loss from being preyed upon) with other species in the system are considered and the predator-prey interaction rates are denoted a_{ij} , $i \neq j$. The values of these rates are determined according to the following constraints; if j feeds on i , then a_{ij} is randomly selected from a uniform distribution in the interval $(-1, 0)$ and $a_{ji} = -ea_{ij}$, where e is the efficiency parameter, a measure of the amount of preys required to produce a predator. In our simulations we define $e = 0.1$. If species i and species j do not share any direct link between them, then $a_{ij} = a_{ji} = 0$. The matrix $A = a(ij)$ represents all of the interactions and feeding relations present in the food web.

2.2.1 Deterministically Stable Food Webs

As mentioned previously, the large (50 species) food webs that result from the niche model without mutual predation are dynamically unstable. In order to obtain smaller but deterministically stable webs, we apply the competitive Lotka-Volterra dynamics to the niche model network and evolve the system over a period of time (our simulations evolve the system until time $t = 1000$). Many of the species will die off and the resulting small stable food webs will have anywhere from 10-15 species.

In our deterministic simulations, we consider a population density minimum threshold of 10^{-3} . Populations that fall below the threshold immediately go extinct. We let the vector of densities $\mathbf{X}^* = (X_1^*, \dots, X_{S^*}^*)$ denote the equilibrium state of the smaller webs where S^* is the number of species remaining in the stable system. These densities will be used for the initial conditions in the deterministic and stochastic simulations discussed later in this thesis. Figure 3 shows the stable food web of 12 species that results from applying the competitive Lotka-Volterra dynamics onto the 50-species network shown in Figure 2.

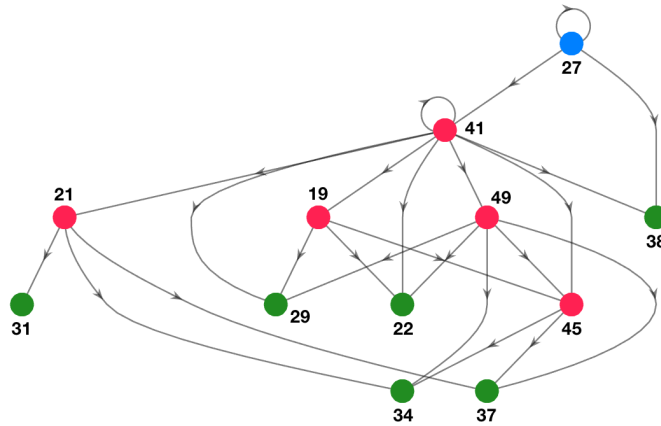


Figure 3: Persisting food web complete with a top predator (blue), nonbasal species (red), and basal species (green).

2.3 Deterministic versus Stochastic Models

To mathematically model the dynamics of an ecological community, there are two broad approaches that one can consider. The traditional approach, and the one used by most ecologists and mathematicians over many years, is a deterministic approach. A deterministic predator-prey model, specifically the competitive Lotka-Volterra model, is given by a finite set of first-order nonlinear differential equations whose solution determines the exact state of the community over time. However, food webs existing in the real world are constantly influenced by noise. Hence, there is a need for a different approach which is a stochastic approach. For internal noise, which is inherent in the food web itself and is caused by the random interactions between individuals and random natural birth and death events, the stochastic model consists of a very large (possibly infinite) set of differential equations, known as the master equation, that gives the probability of the system having a particular number of individuals for each species at any given time [8].

In the deterministic model, a large finite population is comprised of different compartments, each one representing a species group in the food web. The population size or density in each species compartment changes over time, deterministically, according to the birth/death and interaction rates and choice of initial conditions. Because there is no randomness accounted for in the deterministic model, for any prescribed set of parameter values and initial conditions, the solution will be the same every time the equations are solved. If the initial conditions of the system are close enough to a non-extinct equilibrium state, then the community will persist. In other words, in a deterministic setting, all of the species present at the start will coexist in the long term as long as no species is removed.

Due to the stability of the coexisting equilibrium state, in the deterministic approach there is no chance for a species to go extinct. However, species extinctions are often observed in real-life ecosystems, and in order to capture these extinction events mathematically, we must consider a stochastic model that takes into account the randomness and noise in the ecological system. The internal noise, which is captured in the stochastic model, often times can lead to a large and rare fluctuation that causes a certain species to go extinct. These types of extinctions are commonly referred to as noise-induced or natural extinctions [8].

Stochastic models involve random processes, and therefore the outcomes are unpredictable. In this approach, a single set of parameters and initial conditions will lead to a wide range of different outcomes upon observing a number of realizations of the system. In order to properly study the effects of stochasticity on food web modeling, it is necessary to consider a statistical framework for analyzing the results of the stochastic model. A statistic of particular interest in these stochastic food web models is the mean time to extinction (MTE) of a species. In the results presented here, the MTE is found by averaging the extinction times of a species over a number of noise realizations.

3 Stochastic Modeling

It is possible to perform a theoretical analysis for the simplest stochastic problems in order to obtain a solution. Often times, however, stochastic models are far too complex and it becomes impossible to derive an analytical solution. To overcome this, we must turn to numerical simulations of the stochastic systems in order to perform a statistical analysis and gain insight to the system’s underlying behavior. The following sections detail a brief presentation of the theoretical framework along with the numerical simulation algorithm and studies, which make up the bulk of this work.

3.1 General Theory and Master Equation

In order to study the effects of internal noise on a population, it is necessary to consider a stochastic model. Given that the transitions between states are short and uncorrelated, then we can describe the probability evolution of the system, which is a Markov process, by a master equation.

The time evolution of $\rho(X, t)$, the probability of the system taking on a particular state X at a given time t , is expressed as:

$$\frac{d\rho(X, t)}{dt} = \sum_r [W(X - r; r)\rho(X - r, t) - W(X; r)\rho(X, t)], \quad (2)$$

where $W(X; r)$ is the transition rate associated with the event of transitioning from state X to $X + r$, with r a positive or negative integer. In our model, X indicates the number of individuals present for a certain species at a particular time, and all of the transitions are single-step transitions. Hence, the increment r only takes on the values of ± 1 .

The stochastic model we consider fully characterizes the competitive Lotka-Volterra model that accounts for random noise. The model captures interactions between the species as stochastic transitions that occur at specified transition rates. Each of these transitions represents a random event (birth, predation, self-regulation, etc.) that can occur in the population. Table 1 quantifies the possible transition events and associated rates.

Event	$\mathbf{W(X;r)}$
Birth/death	$W(X_i; \pm 1) = \pm b_i X_i$
Self-regulation	$W(X_i; -1) = a_{ii} X_i^2$
Prey death from predation	$W(X_i; -1) = a_{ij} X_iX_j$
Predator growth from predation	$W(X_j; +1) = -ea_{ij}X_iX_j = a_{ji}X_iX_j$

Table 1: Stochastic predator-prey population model events and associated transition rates.

3.2 The Individual-Based Stochastic Predator-Prey Model

In taking a stochastic approach to modeling food web dynamics, we deal with a finite population that occupies a finite area which we will denote by Ω . The number of individuals in each species compartment at any time is given by the state vector $\hat{\mathbf{X}} = (\hat{X}_1, \dots, \hat{X}_{S^*})$. The simulation of a single stochastic realization starts with the stable food web community at equilibrium. In other words, the initial conditions of the system is taken to be the floor value of $\Omega \mathbf{X}^*$, where \mathbf{X}^* is the vector of steady state population densities in the deterministic setting.

In our simulations, $\Omega = 10^3$ (unit of area). For the stochastic model, the interaction rates in matrix A must be scaled accordingly so that the interaction rates of the food web community contained in a finite area are defined by the scaled matrix $\hat{A} = A/\Omega$.

The stochastic realizations of the community dynamics are simulated until a primary extinction is observed along with any resulting secondary extinctions. In our work, the primary extinction occurs naturally as opposed to as a result of intervention (forced removal). Given that the starting food web is persistent in a strictly deterministic setting (all species are expected to coexist for an indefinite amount of time), we know that the primary extinction is entirely noise-induced. Any extinctions observed after the first extinction are either noise-induced rare events or direct results of the deterministic predator-prey dynamics. However, the distinction is not clear.

It is important to note that in these simulations, a species is considered effectively extinct when only a single individual is left in its group, i.e. $\hat{X}_i = 1$. This decision is made based on the notion that a single individual cannot reproduce on its own. The numerical simulations are performed using the Gillespie algorithm described in the following section.

3.2.1 Gillespie Algorithm

To generate a solution of a stochastic equation where the noise is internal to the system we use the Gillespie algorithm or Gillespie's stochastic simulation algorithm (SSA) [28]. The algorithm is a type of Monte Carlo method that was originally proposed by Kendall [29] for simulating birth-death processes and was popularized by Gillespie [28] as a useful method for simulating chemical reactions based on molecular collisions. The results of a Gillespie simulation is a stochastic trajectory that represents an exact sample from the probability function that solves the master equation. Therefore the method can be used to simulate population dynamics where molecular collisions are replaced by individual events and interactions including birth, death, and infection [8].

Let $\mathbf{X} = (X_1, \dots, X_n)^T$ denote the state variables of a system, where X_i provides the number of individuals in state X_i at time t . The first step of the algorithm is to initialize the number of individuals in the population compartments \mathbf{X}_0 . For a given state \mathbf{X} of the system, one calculates the transition rates (birth rate, death rate, contact rate, etc.) denoted as $e_i(\mathbf{X})$ for $i = 1 \dots l$, where l is the number of

transitions. Thus the sum of all transition rates is given by $e_0 = \sum_{i=1}^l e_i(\mathbf{X})$.

Random numbers are generated to determine both the next event to occur as well as the time at which the next event will occur. One simulates the time τ until the next transition by drawing from an exponential distribution with mean $1/e_0$. This is equivalent to drawing a random number r_1 uniformly on $(0, 1)$ and computing $\tau = (1/e_0) \ln(1/r_1)$. During each random time step exactly one event occurs. The probability of any particular event taking place is equal to its own transition rate divided by the sum of all transition rates $e_i(\mathbf{X})/e_0$. A second random number r_2 is drawn uniformly on $(0, 1)$, and it is used to determine the transition event that occurs. If $0 < r_2 < e_1(\mathbf{X})/e_0$, then the first transition occurs; if $e_1(\mathbf{X})/e_0 < r_2 < (e_1(\mathbf{X}) + e_2(\mathbf{X}))/e_0$, then the second transition occurs, and so on. Lastly, both the time step and the number of individuals in each compartment are updated, and the process is iterated until the disease goes extinct or until the simulation time has been exceeded.

4 Control of Secondary Extinction Cascades

It is common to see species extinctions in real food webs, and these sorts of perturbations are mathematically interesting because they often lead to unexpected community responses. Often times, the loss of a single species in a food web will cause a secondary extinction cascade. Here, we consider a cascade to be the group of species that has gone extinct following the very first extinction in the community, and the cascade is ordered according to the extinction times. This sort of response can significantly weaken an ecological community and threaten its existence. Therefore, we look for effective control mechanisms that can save otherwise threatened species downstream the cascade.

Previous studies done by others have shown that it is possible to lessen the severity of secondary extinction cascades in deterministic food webs. There are a number of compensatory perturbations we can consider: immediate removal, mortality rate increase, or growth suppression of a target species. Here, we only consider a control that removes an entire species population.

Note that in this work, we focus on studying control mechanisms in a stochastic food web. This is a novel approach that requires a statistical analysis to be discussed later. In the stochastic setting, primary extinctions are noise-induced, not forced, and a control is implemented in effort to extend the mean time to extinction of individual nonbasal species as well as the mean time to extinction of the entire cascade. This is based on the idea that in a stochastic environment, all species in a system will go extinct if you wait long enough.

4.1 Deterministic Control

We've discussed previously that in the deterministic setting, no species in a persistent food web will go extinct on its own. So, in order to see what the effects of a primary

extinction will be on the rest of the food web, we must force the removal of a species in the web. Potential species candidates for the forced primary extinction are those that eventually go extinct in the secondary cascade. Some removals will trigger a cascade of secondary extinctions; others will only cause the remaining species to go to a new non-extinct equilibrium state.

The process of identifying an effective deterministic control goes as follows: (i) force a nonbasal species to go extinct; (ii) identify the species that vanish in the secondary extinction cascade; (iii) test the impact of removing a species that eventually goes extinct in the non-controlled secondary extinction cascade immediately after the primary extinction. A control is successful if the total number of species lost after implementing the control (including the control species) is less than the number of species that go extinct without a control.

4.2 Stochastic Control

In the case of stochastic food webs, the primary extinctions we consider are noise-induced. Therefore, the random processes that occur in the system are simulated, employing the Gillespie algorithm, until a natural extinction occurs. It is likely, that the first extinction will be followed by a series of secondary extinctions that are either noise-induced or a result of the dynamics. In our food webs, a complete cascade of extinctions can be captured in a simulation of 8×10^6 iterations. The remaining basal species are persisting about a steady state at the end of the computations.

Figure 4 shows the results of the same primary extinction in both the stochastic and deterministic setting. In the inset of Figure 4a, we see species 41 goes extinct just before time $t = 20$, and it is followed by the five other nonbasal species going extinct after some time. To evaluate the effect of noise on the cascade size and pattern of a web, we switch to the deterministic setting, where we take the primary noise-induced extinction in the stochastic simulation and force it to go extinct at the same time in the deterministic case. For this example, we see that by forcing 41 to go extinct in the deterministic web, only 45 goes extinct afterwards.

In order to identify the existence of an effective stochastic control, we do the following: (i) simulate the stochastic food web until a noise-induced primary extinction occurs; (ii) identify the species that go extinct in the secondary extinction cascade and record the extinction times; (iii) test the impact of removing a species that eventually goes extinct in the non-controlled secondary extinction cascade immediately (at the next time step) after the primary extinction. In the context of this problem, an effective stochastic control extends the mean time to extinction of every nonbasal species and the complete secondary cascade.

5 Controlled Stochastic Cascade Results

In order to further understand how these types of systems behave under the influence of noise and see the effects of noise on extinction events and patterns, we consider 1000 stochastic realizations of the food web dynamics of our example network (see

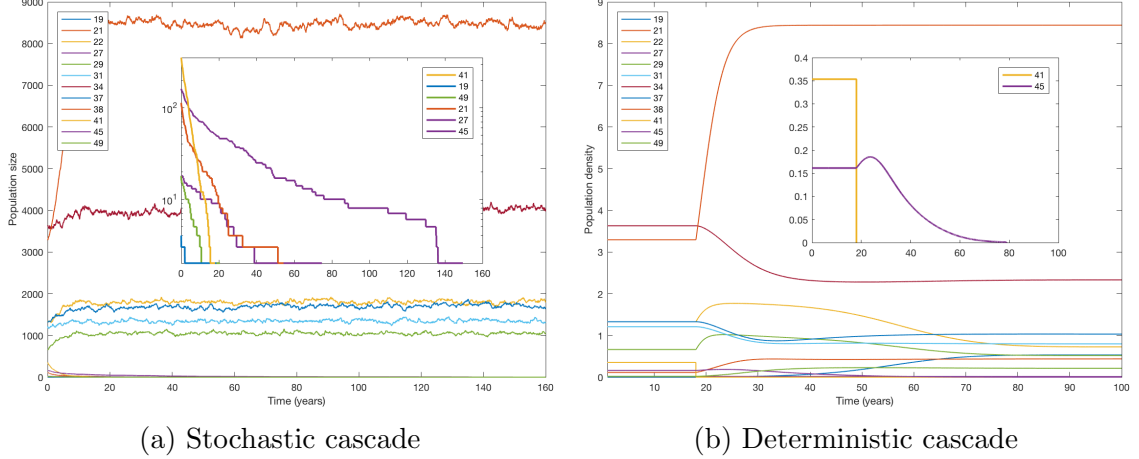


Figure 4: (a) Introducing random noise to the system triggers a cascade of extinctions. The initial loss of 41 causes 19, 49, 21, 27 and then 45 to go extinct. (b) In the deterministic system, the primary removal of 41 causes only 45 to go extinct.

Figure 2 and Table 1). Provided in Table 2 are basic statistics like relative frequency of each extinction cascade, mean time to extinction (MTE) for the entire cascade, and MTE for each individual nonbasal species. The 1000 noise realizations resulted in 23 different extinction cascade patterns; note all patterns begin with the extinction of either species 19, 41, or 49.

We compute the relative frequency (number of occurrences divided by the number of realizations) for each cascade and express it as a percentage. We can see that cascades like type 7, 16, and 19 occurred significantly more often than the rest. The MTE entered in the fourth column is an average measure of the time it takes for all nonbasal extinctions to occur for a particular cascade type. This MTE is found by averaging the times of the final extinction in the cascade, i.e., $MTE = \frac{1}{k} \sum_{i=1}^k t_i^{finalExt}$, where k is the number of times the cascade occurred in the total number of realizations. Finally, we calculate the MTE for each individual nonbasal species in the web, independent of the cascade types, as $MTE = \frac{1}{N} \sum_{i=1}^N t_i^{ext}$, where N is the total number of realizations.

These statistical results serve as the foundation for the analysis done on the extinction cascades that result from the implementation of a control. Table 3 contains the results of using every nonbasal species other than the primary extinction as a control. The data is divided so that we first consider a particular primary extinction (red), and then determine the success of a control (yellow) in extending the MTE of all other nonbasal species in the web (blue) and the entire cascade (green). The MTE given in parentheses take into account only the realizations with the corresponding primary extinction. Each primary extinction, 19, 41, and 49, occurred 571, 19, and 410 times respectively. The entries listed under the rightmost section quantify the relative change in MTE for the nonbasal species corresponding to the entry's row after implementing the column species as a control. For example, when 19 is the primary extinction in the web, forcing 49 to go extinct significantly reduces the MTE

of 49 but, we see improvement in the MTE for all other nonbasal species; the MTE for 21, 27, 41, and 45 increase by 1.68%, 1.06%, 0.43%, and 0.73% respectively, and the MTE for the entire cascade is extended by 0.75%.

It is necessary to analyze the cascade patterns that result from implementing a forced secondary extinction. Because some of the nonbasal species are never the second species to “naturally” go extinct in the non-controlled realizations, it is expected that many of the cascade patterns that emerge with control are new. This means that while there is no known MTE for such type of cascade without control, it is possible to compare the resulting MTE of the cascade with control to the MTE found for other choices of control. Tables 4, 5, and 6 contain the relative frequency and MTE data for the extinction cascades (blue) generated by a particular primary extinction (red) and choice of forced secondary extinction (yellow).

6 Summary and Remarks

In this study, we have used the well-studied niche model as a framework to generate synthetic food webs that exhibit a realistic ecological structure. This model allowed us to capture different predator-prey interactions in our webs, as well as different ecological mechanisms like cannibalism, looping, etc. We introduced dynamics, prescribed by the widely used competitive Lotka-Volterra equations, to our model-based networks in order to deterministically predict the behavior of the food webs. Taken together, both models provide an explanation of structural and dynamical properties of food webs that are necessary to perform a mathematical analysis of response to perturbations such as extinction.

To better understand and study the response of food webs with internal noise, we considered a stochastic approach to food web modeling. In this setting, due to the high-dimensionality and complexity of the system, it was necessary to approach the problem from a numerical standpoint. In our stochastic simulations of the food web dynamics, we observed noise-induced extinctions that were followed by a complete secondary cascade of extinctions. A statistical analysis allowed us to determine the MTE for all nonbasal species and extinction cascades. In order to determine the effects of different controls on the stochastic extinction cascade, we computed a number of descriptive statistics including percent change in MTE for individuals as well as complete cascades.

Our proof of concept and analysis provides a foundation for the study of noise-induced extinction events and cascades in stochastic food webs. The results of our numerical exploration suggest that effective extinction delay controls do exist for stochastic extinction cascades in food webs. Our results also provide evidence that noise plays an important role in food web modeling and it can heavily influence the stability and behavior of model ecological systems. In the future, we will need to investigate whether or not there exists an optimal time to implement a species removal, and we will consider real food web data in order to draw comparisons between empirical and model-based food webs.

Type	Cascade	Relative Frequency	MTE	Species	MTE
1	19-41-21-49-27-45	0.1%	129.11	19	11.65
2	19-41-49-21-27-45	5.6%	137.86	21	43.52
3	19-41-49-21-45-27	0.4%	157.98	27	69.54
4	19-41-49-27-21-45	1.1%	142.06	41	20.09
5	19-49-21-41-27-45	0.6%	135.44	45	142.06
6	19-49-27-41-21-45	0.1%	131.12	49	12.19
7	19-49-41-21-27-45	41.5%	141.96		
8	19-49-41-21-45-27	1.9%	119.44		
9	19-49-41-27-21-45	5.8%	135.05		
10	41-19-49-21-27-45	0.8%	139.58		
11	41-19-49-27-21-45	0.1%	142.42		
12	41-49-19-21-27-45	0.6%	124.72		
13	41-49-19-27-21-45	0.2%	135.54		
14	41-49-21-19-27-45	0.2%	158.31		
15	49-19-21-41-27-45	0.1%	175.37		
16	49-19-41-21-27-45	22.8%	147.63		
17	49-19-41-21-45-27	0.9%	123.84		
18	49-19-41-27-21-45	3.9%	146.54		
19	49-41-19-21-27-45	11.5%	147.00		
20	49-41-19-21-45-27	0.2%	122.26		
21	49-41-19-27-21-45	1.3%	125.49		
22	49-41-21-19-27-45	0.2%	169.58		
23	49-41-27-19-21-45	0.1%	157.61		

Table 2: Results for 1000 stochastic realizations of the food web dynamics. Table shows the 23 different types of extinction cascades that occurred along with the relative frequency and mean time to extinction (MTE) for each. The MTE for each individual nonbasal species is also given.

		Control (Forced Secondary Extinction)				
Primary Extinction (MTE)	Nonbasal Species (MTE)	21	27	41	45	49
19 (6.98)	21 (43.09)	-83.80	-0.53	4.66	0.91	1.68
	27 (70.03)	-1.70	-90.03	-0.91	0.71	1.06
	41 (20.09)	0.68	2.95	-65.24	-0.54	0.43
	45 (139.47)	0.02	0.25	1.33	-94.99	0.73
	49 (13.63)	0.22	0.31	5.50	1.11	-48.79
	Nonbasal Cascade (140.11)	-0.25	-0.21	1.07	-49.04	0.75
		19	21	27	45	49
41 (17.49)	19 (23.86)	-26.69	4.07	-8.08	7.92	4.28
	21 (41.27)	-3.59	-59.58	0.90	10.31	9.41
	27 (67.80)	11.79	0.82	-74.21	6.05	6.84
	45 (136.58)	6.92	7.89	9.39	-87.20	3.26
	49 (20.49)	0.00	-0.02	-0.90	-0.03	-14.66
	Nonbasal Cascade (136.58)	8.08	8.90	9.39	-46.58	3.26
		19	21	27	41	45
49 (9.80)	19 (17.59)	-44.32	2.11	-0.76	0.33	0.75
	21 (44.12)	-1.26	-77.80	-0.79	1.39	-0.55
	27 (68.94)	2.88	2.79	-85.79	3.08	-0.65
	41 (20.21)	-0.10	0.02	1.56	-51.54	0.13
	45 (145.93)	-0.37	-0.50	-0.08	-0.82	-93.29
	Nonbasal Cascade (146.203)	-0.37	-0.45	-0.26	-0.54	-52.03

Table 3: Results for the same 1000 noise realizations presented in Table 2 after implementing various controls (forced secondary extinctions). The entries in the rightmost section show relative change in MTE (%) for all nonbasal species (excluding the primary extinction) and the entire nonbasal cascade.

Primary Extinction	Control (Forced Secondary Extinction)	Cascades	Relative Frequency (%)	MTE	MTE*	Relative Change in MTE (%)
19		19-21-41-49-27-45	12.08	-	137.53	-
		19-21-41-49-45-27	0.53	-	119.35	-
	21	19-21-49-27-41-45	0.18	-	124.28	-
		19-21-49-41-27-45	85.26	-	140.64	-
		19-21-49-41-45-27	1.93	-	121.85	-
		19-27-41-49-21-45	12.43	-	135.70	-
	27	19-27-49-21-41-45	0.70	-	127.46	-
		19-27-49-41-21-45	86.87	-	140.50	-
	41	19-41-27-49-21-45	0.18	-	163.41	-
		19-41-49-21-27-45	80.91	137.86	142.56	3.41
		19-41-49-21-45-27	2.80	157.98	109.38	-30.76
		19-41-49-27-21-45	16.11	142.06	142.25	0.13
	45	19-45-21-41-49-27	0.18	-	37.81	-
		19-45-41-21-49-27	0.35	-	71.27	-
		19-45-41-27-49-21	0.18	-	34.46	-
		19-45-41-49-21-27	11.91	-	72.05	-
		19-45-41-49-27-21	2.10	-	51.91	-
		19-45-49-21-41-27	0.18	-	99.99	-
		19-45-49-41-21-27	75.31	-	74.35	-
		19-45-49-41-27-21	9.81	-	52.85	-
49	19-49-21-41-27-45	0.18	135.44	153.87	13.61	
	19-49-27-41-21-45	0.18	131.12	130.34	-0.59	
	19-49-41-21-27-45	81.96	141.96	142.12	0.11	
	19-49-41-21-45-27	3.85	119.44	126.48	5.89	
	19-49-41-27-21-45	13.84	135.05	139.50	3.29	

Table 4: Results for every extinction cascade (blue) triggered by the primary extinction of 19 (red) with the implementation of a control (yellow). MTE for the entire cascade before the control (denoted MTE) and after the control (denoted MTE*) are given, as well as the relative change in MTE. A dashed entry indicates the corresponding cascade pattern did not occur in the initial 100 realizations without control.

Primary Extinction	Control (Forced Secondary Extinction)	Cascades	Relative Frequency (%)	MTE	MTE*	Relative Change in MTE (%)
41	19	41-19-49-21-27-45	78.95	139.58	141.88	1.64
		41-19-49-21-45-27	10.53	-	114.01	-
		41-19-49-27-21-45	10.53	142.42	224.33	57.52
	21	41-21-19-49-27-45	31.58	-	134.79	-
		41-21-49-19-27-45	63.16	-	153.46	-
		41-21-49-19-45-27	5.26	-	175.79	-
	27	41-27-19-49-21-45	26.32	-	151.93	-
		41-27-49-19-21-45	73.68	-	148.51	-
	45	41-45-19-49-21-27	42.11	-	75.83	-
		41-45-19-49-27-21	10.53	-	58.18	-
		41-45-49-19-21-27	36.84	-	79.67	-
		41-45-49-19-27-21	5.26	-	41.44	-
		41-45-49-21-19-27	5.26	-	64.32	-
	49	41-49-19-21-27-45	84.21	124.72	143.09	14.73
41-49-19-27-21-45		15.79	135.54	130.09	-4.02	

Table 5: Results for every extinction cascade (blue) triggered by the primary extinction of 41 (red) with the implementation of a control (yellow). MTE for the entire cascade before the control (denoted MTE) and after the control (denoted MTE*) are given, as well as the relative change in MTE. A dashed entry indicates the corresponding cascade pattern did not occur in the initial 100 realizations without control.

Primary Extinction	Control (Forced Secondary Extinction)	Cascades	Relative Frequency (%)	MTE	MTE*	Relative Change in MTE (%)
49	19	49-19-21-41-27-45	0.98	175.37	142.85	-18.54
		49-19-41-21-27-45	84.63	147.63	147.16	-0.32
		49-19-41-21-45-27	2.20	123.84	124.29	0.37
		49-19-41-27-21-45	12.20	146.54	139.31	-4.93
	21	49-21-19-41-27-45	66.83	-	144.46	-
		49-21-19-41-45-27	1.71	-	135.86	-
		49-21-41-19-27-45	30.73	-	148.90	-
		49-21-41-19-45-27	0.49	-	135.96	-
		49-21-41-27-19-45	0.24	-	108.49	-
	27	49-27-19-21-41-45	0.24	-	148.48	-
		49-27-19-41-21-45	70.49	-	145.36	-
		49-27-41-19-21-45	26.56	-	143.73	-
		49-27-41-21-19-45	2.68	-	178.16	-
	41	49-41-19-21-27-45	81.46	147.00	146.35	-0.44
		49-41-19-21-45-27	3.41	122.26	132.23	8.15
		49-41-19-27-21-45	12.20	125.49	145.27	15.77
		49-41-21-19-27-45	1.46	169.58	139.14	-17.95
		49-41-21-19-45-27	0.24	-	114.45	-
		49-41-21-27-19-45	0.49	-	145.40	-
		49-41-27-19-21-45	0.24	157.61	99.85	-36.65
	45	49-41-27-21-19-45	0.49	-	142.09	-
		49-45-19-21-41-27	0.49	-	65.11	-
		49-45-19-41-21-27	55.85	-	72.69	-
		49-45-19-41-27-21	10.00	-	54.28	-
		49-45-41-19-21-27	28.05	-	73.70	-
		49-45-41-19-27-21	4.39	-	51.12	-
	49-45-41-21-19-27	1.22	-	70.97	-	

Table 6: Results for every extinction cascade (blue) triggered by the primary extinction of 49 (red) with the implementation of a control (yellow). MTE for the entire cascade before the control (denoted MTE) and after the control (denoted MTE*) are given, as well as the relative change in MTE. A dashed entry indicates the corresponding cascade pattern did not occur in the initial 100 realizations without control.

7 Bibliography

References

- [1] P. Morin, Community Ecology. Wiley, 2 ed., 2011.
- [2] S. A. Levin, S. R. Carpenter, H. C. J. Godfray, A. P. Kinzig, M. Loreau, J. B. Losos, B. Walker, and D. S. Wilcove, The Princeton Guide to Ecology. Princeton University Press, 2009.
- [3] I. Svirezhev and D. Logofet, Stability of Biological Communities. Mir Publishers, 1983.
- [4] R. M. May, “How many species are there on Earth?,” Science, vol. 241, no. 4872, pp. 1441–1449, 1988.
- [5] J. E. Cohen, F. Briand, and C. M. Newman, Community food webs: data and theory, vol. 20 of Biomathematics. Springer Verlag, 1990.
- [6] P. C. de Ruiter, A.-M. Neutel, and J. C. Moore, “Energetics, patterns of interaction strengths, and stability in real ecosystems,” Science, vol. 269, no. 5228, pp. 1257–1260, 1995.
- [7] S. H. Strogatz, Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry and Engineering. Westview Press, 2nd ed., 2015.
- [8] E. Forgoston and R. O. Moore, “A primer on noise-induced transitions in applied dynamical systems,” SIAM Review, vol. 60, no. 4, p. 969–1009, 2018.
- [9] L. S. Tsimring, “Noise in biology,” Reports on Progress in Physics, vol. 77, no. 2, p. 026601, 2014.
- [10] G. Nieddu, L. Billings, and E. Forgoston, “Analysis and control of pre-extinction dynamics in stochastic populations,” Bulletin of Mathematical Biology, vol. 76, no. 12, pp. 3122–3137, 2014.
- [11] C. D. Thomas, A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips, and S. E. Williams, “Extinction risk from climate change,” Nature, vol. 427, no. 6970, pp. 145–148, 2004.
- [12] B. W. Brook, N. S. Sodhi, and P. K. Ng, “Catastrophic extinctions follow deforestation in Singapore,” Nature, vol. 424, no. 6947, pp. 420–423, 2003.
- [13] K. F. Smith, D. F. Sax, and K. D. Lafferty, “Evidence for the role of infectious disease in species extinction and endangerment,” Conservation Biology, vol. 20, no. 5, pp. 1349–1357, 2006.

- [14] D. Pimentel, L. Lach, R. Zuniga, and D. Morrison, “Environmental and economic costs of nonindigenous species in the United States,” BioScience, vol. 50, no. 1, pp. 53–65, 2000.
- [15] M. Assaf, A. Kamenev, and B. Meerson, “Population extinction risk in the aftermath of a catastrophic event,” Physical Review E, vol. 79, no. 1, p. 011127, 2009.
- [16] S. L. Pimm, G. J. Russell, J. L. Gittleman, and T. M. Brooks, “The future of biodiversity,” Science, vol. 269, no. 5222, pp. 347–350, 1995.
- [17] S. L. Pimm and P. Raven, “Extinction by numbers,” Nature, vol. 403, no. 6772, pp. 843–845, 2000.
- [18] O. E. Sala, F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, *et al.*, “Global biodiversity scenarios for the year 2100,” Science, vol. 287, no. 5459, pp. 1770–1774, 2000.
- [19] B. Ebenman, R. Law, and C. Borrvall, “Community viability analysis: The response of ecological communities to species loss,” Ecology, vol. 85, no. 9, p. 2591–2600, 2004.
- [20] S. Sahasrabudhe and A. E. Motter, “Rescuing ecosystems from extinction cascades through compensatory perturbations,” Nature Communications, vol. 2, no. 1, p. 170, 2011.
- [21] J. E. Cohen and C. M. Newman, “A stochastic theory of community food webs I. models and aggregated data,” Proceedings of the Royal Society of London. Series B. Biological sciences, vol. 224, no. 1237, pp. 421–448, 1985.
- [22] R. J. Williams and N. D. Martinez, “Simple rules yield complex food webs,” Nature, vol. 404, no. 6774, p. 180–183, 2000.
- [23] M.-F. Cattin, L.-F. Bersier, C. Banašek-Richter, R. Baltensperger, and J.-P. Gabriel, “Phylogenetic constraints and adaptation explain food-web structure,” Nature, vol. 427, no. 6977, pp. 835–839, 2004.
- [24] A. J. Lotka, “Elements of physical biology,” Science Progress in the Twentieth Century (1919-1933), vol. 21, no. 82, pp. 341–343, 1926.
- [25] A. J. Lotka, “Undamped oscillations derived from the law of mass action.,” Journal of the American Chemical Society, vol. 42, no. 8, pp. 1595–1599, 1920.
- [26] V. Volterra, “Variations and fluctuations of the number of individuals in animal species living together,” Animal Ecology, pp. 409–448, 1926.
- [27] J. D. Murray, Mathematical Biology: I. An Introduction, vol. 17. Springer Science & Business Media, 2007.

- [28] D. T. Gillespie, “Exact stochastic simulation of coupled chemical reactions,” The Journal of Physical Chemistry, vol. 81, no. 25, p. 2340–2361, 1977.
- [29] D. G. Kendall, “An artificial realization of a simple “birth-and-death” process,” Journal of the Royal Statistical Society. Series B (Methodological), vol. 12, no. 1, pp. 116–119, 1950.