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Extinction of Species Due to Deterministic and Stochastic Interactions in Food Webs

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Abstract

Previous research on the extinctions that occur in niche model food webs with deterministic and stochastic dynamics has shown that the structure of the food web can play an important role in extinction cascades. In this thesis, other types of synthetic food web models are considered, namely the cascade and generalized cascade models, and the extinction cascades of these food webs are compared with previous findings on the extinction cascades from the niche model. It was found that there are many similarities in the results for all three models, which prompted a closer analysis using food webs with deterministic dynamics. We developed a method to theoretically predict the survival or extinction of species in two- and three-species food webs, and compared the predictions with numerical results.

MONTCLAIR STATE UNIVERSITY

Extinction of Species Due to Deterministic and Stochastic
Interactions in Food Webs

by

Claire M. Burke

A Master's Thesis Submitted to the Faculty of

Montclair State University

In Partial Fulfillment of the Requirements

For the Degree of
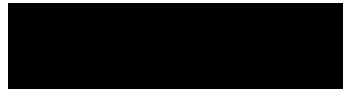
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Department of Applied
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EXTINCTION OF SPECIES DUE TO DETERMINISTIC AND STOCHASTIC INTERACTIONS IN FOOD WEBS

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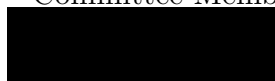
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1 Introduction

In real-life environments containing many species, there are interactions and dynamics between the species that are important to understand. These interactions and dynamics are complex, and have been an important part of biological and ecological research and studies. In particular, food webs provide structure to a group of species by organizing them according to their interactions [1]. In addition to empirical food webs found in nature, several methods to construct synthetic food webs have been developed over the years, each of which attempts to capture salient features of real food webs [2–7]. Furthermore, the dynamics that occur between species, such as births, predation, and competition, have been analyzed along with the topological structure. From these studies, it can be seen that the stability of a web depends greatly on both structure and dynamics, with possibilities of species surviving or becoming extinct based on these characteristics [8, 9].

However, the structure and dynamics alone is not enough to accurately predict how real life systems function. Specifically, when the food web models mentioned above are combined with deterministic Lotka-Volterra dynamics, the food webs will evolve in time and eventually will reach a steady state in which the species populations never vary [9]. This is obviously not true in the real world, since extinction of species does in fact occur [10].

The extinction of species is an important area of research, and studies have involved the extinction of real-world species and systems, as well as the extinction of species in theoretical food webs. Studies involving extinction in real-world systems include the effects of climate change and invasive species [11–14]. In research concerning theoretical food webs, studies have looked at stochastic perturbations and the effect that these perturbations have on biological systems [10, 15–17].

Another aspect of analyzing the extinction of species is the study of how extinctions can be prevented. Just as the control and prevention of extinction has been a focus in real-world systems [18], theoretical research has also been performed to better understand how one can prevent a secondary extinction cascade from occurring after a primary extinction [19–21]. Yet another area of interest involving extinction is the topological structure of the food web, and how the structure interacts with the deterministic and stochastic dynamics. Understanding the role of topology and dynamics is crucial to improving our knowledge of how food web extinctions occur. [22–24].

Although some research on food web extinctions has been performed, the vast majority of this work does not involve the effects of stochasticity [25]. Recently, Fernandez [26] considered food webs created using the niche model and studied the role of stochasticity on primary extinction, secondary extinction cascades, and how control can be used. However, this work only looked at food webs created from the niche model.

In this work, we consider other types of synthetic food webs and study the effect of noise on extinction. Although the different food web models all aim to emulate real food webs, the method for creating them, and the resulting topologies can be very different. It is therefore important to understand the differences in noise-induced extinction processes between these different types of food web models. In this thesis,

we consider two types of food web models that have not previously been analyzed with respect to stochastic-induced extinction processes, namely the cascade model and the generalized cascade model. The cascade model was chosen due to the difference in structure, since it does not allow for cannibalism or interactions between species on the same trophic level, while the niche model does. The generalized cascade model was chosen since it was proposed as an improvement for the cascade model. Also, with these improvements, the generalized cascade model is seen to more closely resemble the niche model, which makes the model interesting to compare with the niche model.

In order to investigate the effect of noise and compare the extinction cascades of each food web model with the niche model, we will first create food webs based on the structure dictated by the cascade and generalized cascade models. Once the food web is created, we add dynamics between the species. In this case, the Lotka-Volterra equations [27–30] will be used. This will create stable deterministic food web models of species, to which stochastic dynamics will be introduced, and we will investigate the effect that noise has on the food webs created by these different models. In addition, based on the results found, we will look at the fundamental structure of food web models governed by the Lotka-Volterra equations through studying the survival and extinctions of species in both two- and three-species food webs.

Through this work, it is hoped that there will be better understanding of the similarities and differences of the different proposed food web models as it relates to extinction processes. In addition, through analyzing small deterministic webs, it is hoped that the role that structure has on extinction or survival of species can be better understood.

2   Food Webs

One method used to study ecological systems and the unique roles that different types of species have in real-world environments is through the implementation of food webs. Food webs account for the structure that is an integral part of real-world systems of species. These webs order the species in a system based on the different characteristics attributed to those species. The species are broadly divided into two different types of groups, basal and non-basal. The species classified as basal species only have predators, since they do not eat any prey. These species are at the bottom level of the food web, and are usually producer-type species. In Fig. 1 the orange species are the basal species. The second group of species are the non-basal species. This group can be further separated into top and intermediate species, based on their trophic level. The top species have only prey, and no predators. This group of species is located at the top level of a food web, and is the blue colored species in Fig. 1. Finally, the intermediate species have both predators and prey, and are located in the middle levels of the food web. These are the green colored species in the figure. A food web is represented by a graph, where the species are the nodes, and the interactions between species are the directed edges. For example, if species j preys upon species i, there will be a directed edge going from node j to node i. In Fig. 1, there is an arrow pointing from species 51 to species 2, implying that species 51 preys on species
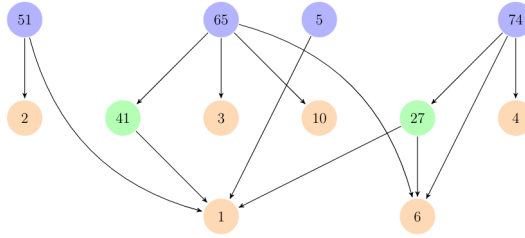
Figure 1: In this food web the orange species are the basal species, the green species are intermediate species, and the blue species are top species. The intermediate and top species are the nonbasal species.

2. These predator-prey relationships are determined according to different food web models that impose certain structures and assumptions in an attempt to capture the behavior of a real ecological system.

3 Food Web Models

Based on the important role of food webs in understanding real ecosystems, many attempts have been made to describe these webs and the interactions and behavior between species in various types of models. Each of these models generates a synthetic food web of species, using certain parameters and random distributions to choose the links between the species. The following sections describe three of these models: the cascade, generalized cascade, and niche models.

3.1 The Cascade Model

The cascade model is one of the first models capable of generating synthetic food webs that accurately resemble real food webs. The model provides a fair description of the numbers of top and basal species, but is rather poor at describing the number of basal-top links [31]. In the cascade model, the structure specifies the prey of each species in the food web. After the number of species, S, is determined, the species are ordered into a square matrix, with both the rows and columns numbered from species 1 to S. This ordering of the species is determined before the trophic links, or the predation interactions, are chosen. Next, the probability of the existence of a trophic link between two species is determined using a Bernoulli distribution. For elements above the main diagonal, the probability, p, of the existence of a trophic link is $p = c/S$. The variable, c, is a finite positive real number, and as mentioned previously, S, is the number of species. For elements on and below the diagonal, the probability of a trophic link existing is $p = 0$. This results in an upper triangular matrix, where $a_{i,j} = 0$ whenever $i \geq j$, with i being the row (or prey) and j being the

column (or predator). This implies that a species can only prey upon another species that has a value less than the current species and that cannibalism is not a possibility. Also, the interactions between species on the same trophic level is not allowed and the predator of a species can only be from the groups of species that have a higher value than the current species [2, 7]. For example, species 3 can possibly prey on species 1 or 2, and can only possibly be eaten by the species 4 to S. Figure 2a shows an example of a 75 species cascade food web.

3.2   The Niche Model

The niche model was created to improve upon the cascade model. In the niche model, a synthetic web is created by having each species assigned and ordered by a randomly drawn niche value. The species is then limited to consume all prey in a specified range of species. The center of this range must be less than the niche value of the predator species, which allows for up to half of the prey species to have niche values greater than or equal to the niche value of the predator species. This also enables species with similar niche values to often share the same predators. By determining the trophic links in this way, the niche model is able to provide a food web that more closely resembles real ecological systems. In fact, the niche model is able to capture key structural properties of the most complex and comprehensive food webs [4].

3.3   The Generalized Cascade Model

Another type of food web model, the generalized cascade model, was proposed to improve upon the cascade model by generating the same distributions of trophic connections as the niche model. Due to the highly structured rule for predator-prey relationships, the cascade model did not allow for cannibalism or for interactions within a trophic level, both of which are possible and do occur in real ecological systems. In order for these to occur, the criteria for determining trophic links was modified in the generalized cascade model. Unlike in the cascade model where the probability p of a link existing between two different species is the same for all species, in the generalized cascade model each species i has its own specific probability, p_i. This probability is chosen randomly from a Beta distribution, with mean $\mu = 2c$, where c is a finite positive real number. The trophic links between species are then chosen from a Bernoulli distribution, using the specified p_i for each species [3, 6]. As a result of these differences, the generalized cascade model creates a synthetic food web that is similar to the web generated by the niche model. Figure 2b shows an example of a 75 species generalized cascade food web.

4   The Lotka-Volterra Equations

While food web models are able to capture the structure of real systems, the synthetic food webs which are created do not account for the dynamic interactions between species. This is an important feature that is often neglected by researchers studying
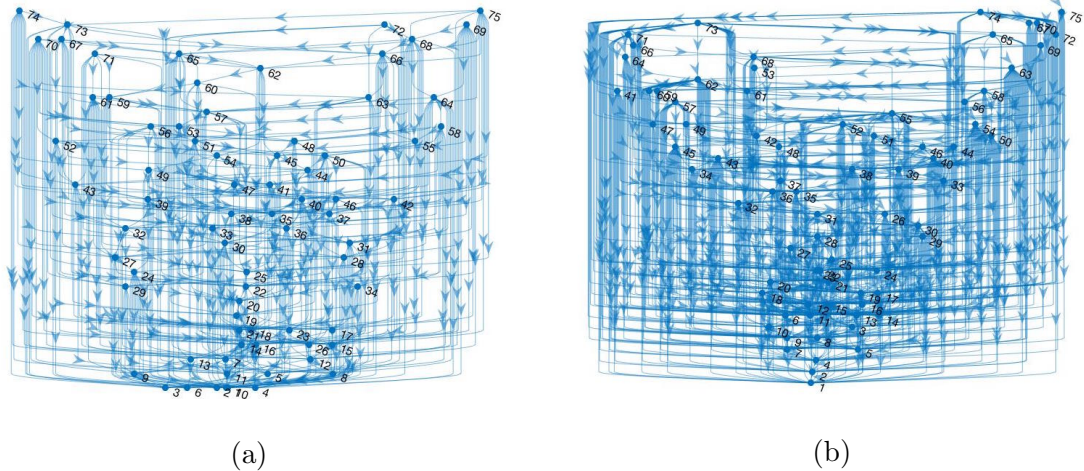
Figure 2: Food webs consisting of 75 species generated using (a) the cascade model, and (b) the generalized cascade model.

ecological food webs. We consider the competitive Lotka-Volterra equations, and apply these population dynamics to the food webs generated by the models discussed previously.

The Lotka-Volterra equations are nonlinear first-order differential equations given by

$$\frac{dX_i}{dt} = b_i X_i + \sum_{j=1}^{S} a_{i,j} X_i X_j, \qquad i = 1, 2, \ldots, S, \qquad (1)$$

where X_i is the population density of each species in the food web. The state vector, X includes all population densities so that $X = (X_1, X_2, \ldots X_S)$. The first term in the right-hand side of the equation is the natural growth or death of the species, where b_i is positive for basal species and is drawn uniformly from the interval (0,1), and negative for nonbasal species and drawn uniformly from (-1,0). In the second term, the summation defines the interactions between the species in the model. The self regulation term, where $i = j$, can include events such as cannibalism, and is denoted as $a_{i,i}$ and drawn uniformly from (-1,0). Interactions between species are denoted as $a_{i,j}$, with $i \neq j$. When species j preys on species i, the value $a_{i,j}$ is uniformly chosen from the interval (-1,0), and represents the loss in population density of the prey due to predation. The value $a_{j,i} = -e a_{i,j}$ is the predator population density growth from predation, and ranges from (0,0.1), given that the efficiency parameter $e = 0.1$. It is worth noting that the synthetic food webs without dynamics are inherently unstable, and when the Lotka-Volterra dynamics are applied, multiple species extinctions occur. Eventually, a smaller, stable food web persists, with each of the species surviving at a constant steady-state density.

Once the Lotka-Volterra population dynamics are applied to the food web models, the system is evolved through time, using the fourth-order Runge-Kutta scheme. Depending on which model is used and the number of initial species, the stable systems can range in size. For instance, consider a 75 species food web generated

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(a)

(b)
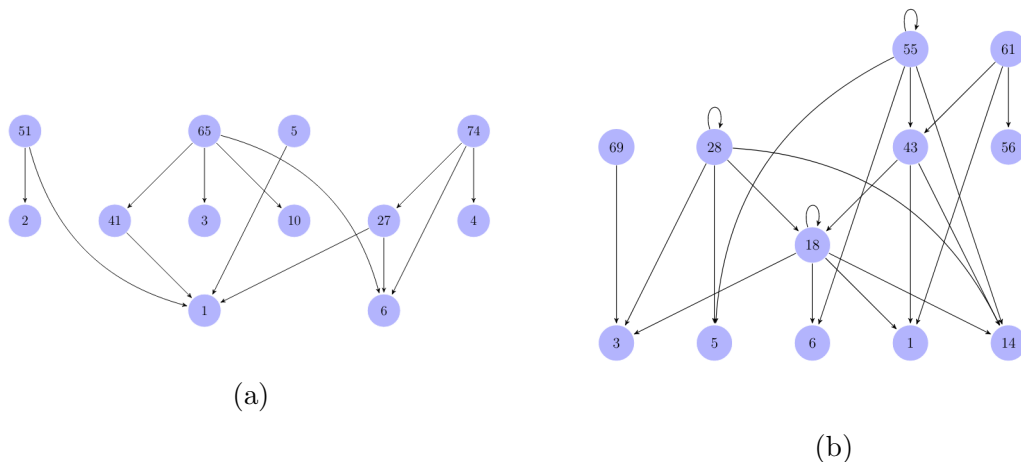
Figure 3: Example of stable food webs based on (a) the cascade model, and (b) the generalized cascade model. In both (a) and (b), the stable food webs contain 12 species (six basal and six nonbasal).

by the cascade model, as seen in Fig. 2a. Once the Lotka-Volterra dynamics were incorporated, the stable system that resulted from this initially larger web contained 12 species, six of which are basal species, and six of which are nonbasal species, as seen in Fig. 3a. Similarly, the generalized cascade food web shown in Fig. 2b decreased from 75 species to 12 species, six of which are basal species and six of which are nonbasal species, as seen in Fig. 3b.

These resulting webs are deterministically stable, and the remaining species will continue at their respective steady states and never become extinct. With a lack of extinction, these food webs will always be the same. When starting with the same initial food web, initial conditions, and birth/death/interaction rates then the evolution of the original food web will always lead to the same stable food web with each species at their respective steady state values.

In reality, however, this is unrealistic, since real ecological systems continuously experience random perturbations due to external and internal noise. Because noise can induce extinction of species, even from their deterministically stable state, we must include stochasticity to understand primary and subsequent extinctions.

5   Stochastic Dynamics

To better model real ecological systems, we consider internal, demographic stochasticity that arises from the random interactions between individuals of each species that comprise the food web [10]. The noise causes each species population to fluctuate around its deterministic steady state, and as a rare event, the noise will induce a large fluctuation that causes a species to go extinct. Different from the deterministically stable food web which never shows an extinction, the addition of noise will induce

a primary extinction. This primary extinction likely will lead to further secondary extinctions, and beyond this the noise may induce further extinctions. If one waits long enough, eventually the noise will lead to every species in the food web going extinct. Since these noise-induced extinctions are random, the resulting order of species extinctions and the time at which the different species become extinct will vary for different stochastic realizations of the same food web with the same initial conditions and parameters.

The change of the population in time with internal noise can be described by the master equation

$$\frac{\partial \rho(X,t)}{\partial t} = \sum_r W_r(X-r)\rho(X-r,t) - W_r(X)\rho(X,t), \tag{2}$$

where X is the number of individuals at time t, W_r are the transition rates, and r is an integer increment [10]. In this case, the increment will increase the population by either +1 or -1 individuals depending on which event occurs. In the case of the Lotka-Volterra system, the events that can occur are as follows:

- Birth (basal): $\qquad\qquad\qquad\qquad W_{+1}(X_i) = b_i X_i$

- Death (nonbasal): $\qquad\qquad\qquad W_{-1}(X_i) = |-b_i|X_i$

- Self-regulation: $\qquad\qquad\qquad\quad W_{-1}(X_i) = |a_{i,i}|X_i X_i$

- Prey death from predation: $\qquad\quad W_{-1}(X_j) = |a_{i,j}|X_i X_j$

- Predator growth from predation: $\qquad W_{+1}(X_i) = -ea_{i,j}X_i X_j = a_{j,i}X_i X_j$

These stochastic systems are complex, and only the simplest of systems can be solved analytically. Therefore, we must numerically solve the stochastic system. We do this using the Gillespie algorithm which we now describe.

5.1 Gillespie Algorithm

We numerically handle the internal noise using the Stochastic Simulation Algorithm, also known as the Gillespie algorithm [32]. The Gillespie algorithm starts with an initial population amount for each species, S, present in the food web, measured in the amount of individuals of the species, and a known list of all possible events, with the corresponding probability that each event will occur, $prob(i)$, where i is an event. Then $P_0 = \sum_{n=1}^{N} prob(n)$ is the sum of these probabilities, where N is the number of events that can occur. In the algorithm, two random numbers, r_1 and r_2 are chosen uniformly from (0,1). Then the next random time step, τ is found using r_1 and P_0, with $\tau = \frac{1}{P_0}\ln\left(\frac{1}{r_1}\right)$. In order to determine which event will occur in the current random time step, an integer, μ, is determined using r_2 and P_0, and μ is the value for which $\sum_{v=1}^{\mu-1} P_v < r_2 P_0 \leq \sum_{v=1}^{\mu} P_v$. The chosen μ determines which event will occur. Then the populations of each species, the next time step, and the event probabilities will be updated [32, 33]. The process is repeated until a set time

limit has been reached or all of the species become extinct. The non-basal species that are part of the stable web will quickly become extinct, while the basal species will continue to fluctuate around their respective deterministic steady states, taking a much longer amount of time to become extinct.

6   Results

6.1   Stochastic Extinction Cascades

In order to find the extinction patterns for systems generated by the cascade and generalized cascade models, and to compare them with the niche model [26], the Gillespie algorithm must be applied to both systems. We find 1000 stochastic realizations for each of the systems generated by the cascade and generalized cascade models, and statistically compare the extinction results. Specifically, the results from all 1000 realizations allow us to determine the different types of extinction cascades, as well as the relative frequency of each type of secondary extinction cascade. The mean time to extinction (MTE) for each extinction cascade was also calculated by averaging together the time the last species in each cascade went extinct.

Cascade Model			
Type	Cascade	Relative Frequency	Mean Extinction Time
1	5 41 74 51 27 65	15.1%	188.3993
2	5 41 74 51 65 27	1.2%	166.397
3	5 74 41 51 27 65	5.6%	187.6068
4	5 74 41 51 65 27	1.1%	161.3095
5	41 5 74 51 27 65	31.8%	184.4922
6	41 5 74 51 65 27	3.2%	165.0961
7	41 74 5 51 27 65	23.2%	184.9006
8	41 74 5 51 65 27	2.4%	163.8622
9	74 5 41 51 27 65	5%	186.4148
10	74 5 41 51 65 27	1.2%	167.8189
11	74 41 5 51 27 65	9.1%	186.9049
12	74 41 5 51 65 27	1.1%	164.3298

Table 1: Results from 1000 realizations of a cascade model food web with stochastic dynamics. The table displays the 12 different types of extinction cascades along with the relative frequency and mean time to extinction for each cascade.

In order to compare the three models, the systems generated by the cascade and generalized cascade models were chosen to have a similar make up to the niche model system analyzed in [26]. As a result, the stable deterministic food webs each have 12 species, with six basal and six nonbasal species. The mean time to extinction information for a food web generated by the cascade model is found in Table 1, while similar information can be found in Table 2 for a food web generated by the generalized cascade model.

As seen in the results in Table 1, there were 12 different types of extinction cascades for the stable food web generated using the specific cascade model shown in Fig. 3a. Similarly, Table 2 shows that 16 different types of extinction cascades were seen for the stable food web generated using the generalized cascade model shown in Fig. 3b. However, it is important to note that the number of extinction cascades that one sees depends on the topology of the food web; for example, another food web created using the cascade model resulted in 84 different types of extinction cascades.

Generalized Cascade Model			
Type	Cascade	Relative Frequency	Mean Extinction Time
1	55 18 28 61 69 43	0.5%	720.2165
2	55 18 61 28 43 69	1.8%	832.9115
3	55 18 61 28 69 43	5.3%	708.6423
4	55 18 61 69 28 43	0.1%	436.5253
5	55 28 18 61 69 43	0.5%	728.6705
6	55 28 61 18 43 69	0.1%	779.1873
7	55 28 61 18 69 43	0.5%	662.0258
8	55 61 18 28 43 69	13.6%	696.2781
9	55 61 18 28 69 43	55.5%	689.4483
10	55 61 18 69 28 43	0.7%	590.1712
11	55 61 28 18 43 69	4.4%	645.5312
12	55 61 28 18 69 43	16.5%	677.3436
13	55 61 28 69 18 43	0.1%	555.1232
14	55 61 69 18 28 43	0.1%	478.0537
15	61 55 18 28 69 43	0.2%	442.0687
16	61 55 18 69 28 43	0.1%	545.2125

Table 2: Results from 1000 realizations of a generalized cascade model food web with stochastic dynamics. The table displays the 16 different types of extinction cascades along with the relative frequency and mean time to extinction for each cascade.

Although the amount of extinction cascades changed, there were similarities found when comparing the extinction cascades from the cascade and generalized cascade food webs with the ones from the niche model presented in [26]. For all three types of food webs, there were certain extinction cascades that occurred far more frequently than the rest of the cascades. In the niche model (see [26]), cascade 7 occurred 41.5% of the time, and cascades 16 and 19 occurred 22.8% and 11.5% of the time. The rest of the extinction cascades occurred around 5% or less of the time. For the cascade model, cascade type 5 occurred with the highest frequency, 31.8%, and 7 and 1 occurred at 23.2% and 15.1%, respectively. The other cascades occurred from 1.1% to 9.1%, with most cascades occurring less than 5%. Finally for the generalized cascade model, the three highest occurring cascades were 9, 12, and 8, with frequencies of 55.5%, 16.5%, and 13.6%, respectively, and the other cascades occurring much less frequently. In all three types of food webs, there was also a similarity for the MTE, where the MTE varied depending on the cascade (Table 3 and 4 respectively for the cascade and generalized cascade food webs, and [26] for the niche food web.)

In addition to the MTE for the extinction cascades, the MTE for each specific species was also calculated, by averaging the time of extinction for each species from the total amount of realizations (Tables 3 and 4 respectively for the cascade and generalized cascade food webs). The results also match with the niche model (see [26]) and intuitively make sense, with the species that most often start the cascade or become extinct quickly having lower MTE and the species that become extinct last or later in the cascade having a higher MTE.

Species	Mean Extinction Time
5	13.8705
27	123.6445
41	12.1713
51	42.6107
65	181.2134
74	14.7140

Table 3: Results from 1000 realizations of a cascade model food web with stochastic dynamics. The table displays the mean time to extinction for each species based on the extinction cascades in Table 1.

The fact that these similarities exist is an interesting result. Although the niche, cascade, and generalized cascade models are created differently and capture different ecological features, the resulting extinctions occur in a similar way. As a result, we have begun an investigation to explain this behavior. Since these food webs were created by randomly generating a network, randomly generating the rates and initial conditions associated with the deterministic dynamics, and then studying how random noise affected the systems, we began our study by considering food webs of 12-15

Species	Mean Extinction Time
18	73.13876
28	94.2527
43	652.43576
55	18.47
61	49.24989
69	422.589

Table 4: Results from 1000 realizations of a generalized cascade model food web with stochastic dynamics. The table displays the mean time to extinction for each species based on the extinction cascades in Table 2.

species, but fixed certain parameters to remove some of the random aspects. However, even these scenarios were far too complicated to provide insight. We therefore started with the most basic food web, a two species food web with cascade topology, and examined what extinctions could occur when deterministic Lotka-Volterra dynamics were added. The goal is to use this information to better understand three species food web extinctions (cascade and generalized cascade) and eventually understand the deterministic extinctions that occur for larger food webs. This information would then enable understanding of stochastic-induced extinction events.

6.2   Two Species Food Webs with Deterministic Dynamics

In order to better understand the structure of food webs and the interactions between species, the smallest food web possible for two species was analyzed. This analysis was done by finding the steady states and then finding the eigenvalues of the linearized system (i.e. stability analysis for the steady states). This information was used to predict the extinction outcomes of the food web with deterministic dynamics. In this case, species 2 preys on species 1, which implies that species 1 is the basal species and species 2 is the nonbasal species. The corresponding Lotka-Volterra equations are

$$\frac{dx_1}{dt} = ax_1 - bx_1^2 - a_{1,2}x_1x_2, \tag{3}$$

$$\frac{dx_2}{dt} = -cx_2 - dx_2^2 + ea_{1,2}x_1x_2. \tag{4}$$

There are four possible solutions or outcomes to these equations:

- Both species become extinct.

- The basal species survives while the nonbasal becomes extinct.

- The nonbasal species "survives" (but with a non-biological negative population), while the basal species becomes extinct.

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- Both species survive and coexist.

However, clearly the third option cannot occur in this application, since biologically a species cannot have a negative population (although, mathematically this is a valid steady state). Therefore, there are only three possible outcomes that can occur: both species become extinct, both species survive and coexist, or the basal species survives while the nonbasal species becomes extinct.

For the steady state scenario where both species become extinct, the eigenvalues are a and $-c$. Since one eigenvalue is positive and one is negative, this implies a saddle point at $(0,0)$. For the scenario where the basal species survives and the nonbasal species becomes extinct, the first eigenvalue, $-a$, is always negative. However the second eigenvalue is $-c + \frac{aea_{12}}{b}$ and can either be positive or negative, depending on the parameters in the Lotka-Volterra equations. This implies that the steady state $(\frac{a}{b}, 0)$ can be either a saddle point or a sink. Finally, for the scenario where both species coexist, $(\frac{ad+ca_{12}}{bd+ea_{12}^2}, \frac{aea_{12}-bc}{bd+ea_{12}^2})$, the eigenvalues are:

$$\lambda_1 = -\frac{1}{2(bd + a_{12}^2 e)}(bd(a - c) + a_{12}(bc + ade)+$$

$$\sqrt{4(a_{12}c + ad)(bc - aa_{12}e)(bd + a_{12}^2 e) + (b(a - c)d + a_{12}(bc + ade))^2})$$

$$\lambda_2 = -\frac{1}{2(bd + a_{12}^2 e)}(bd(a - c) + a_{12}(bc + ade)-$$

$$\sqrt{4(a_{12}c + ad)(bc - aa_{12}e)(bd + a_{12}^2 e) + (b(a - c)d + a_{12}(bc + ade))^2})$$

If we set $q = bd(a - c) + a_{12}(bc + ade)$, the eigenvalues will be:

$$\lambda_1 = -\frac{1}{2(bd + a_{12}^2 e)}(q + \sqrt{4(a_{12}c + ad)(bc - aa_{12}e)(bd + a_{12}^2 e) + q^2})$$

$$\lambda_2 = -\frac{1}{2(bd + a_{12}^2 e)}(q - \sqrt{4(a_{12}c + ad)(bc - aa_{12}e)(bd + a_{12}^2 e) + q^2})$$

In the piece under the square root, if $bc - aea_{12} < 0$, both eigenvalues will be negative, which implies a stable node. On the other hand, when $bc - aea_{12} > 0$, one eigenvalue will be positive and one will be negative, which implies a saddle point. The complete phase plane is shown in Fig. 4.

Furthermore, for two species food webs the condition $aea_{12} - bc > 0$ is enough to predict the outcome of the deterministic system with Lotka-Volterra dynamics. This was numerically confirmed by considering numerous iterations with different values for the parameters a, b, c, d, and a_{12}, and different values for the initial population densities for both species, with the values chosen uniformly from $(0,1)$. The efficiency parameter e was kept at the same value, 0.1. If the condition $aea_{12} - bc > 0$ is met, the nontrivial solution is biologically possible, and both species are predicted to survive. The theoretical prediction agrees with the numerical results of two species food webs meeting this condition. However, if $aea_{12} - bc < 0$, the nontrivial solution is not possible, and only the basal species is predicted to survive. Again, this agreed
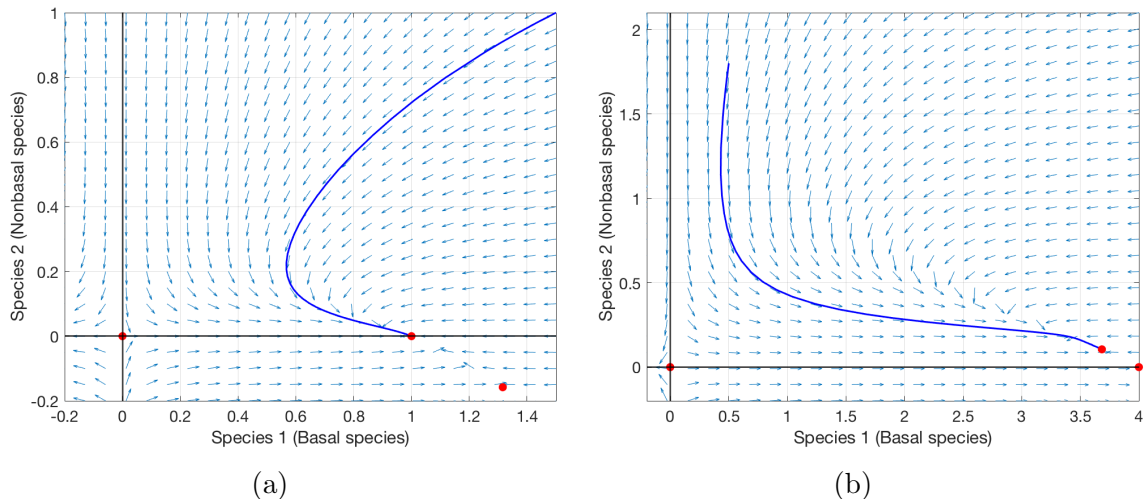
Figure 4: Phase planes for a two species food web with two different sets of parameter values. In (a) we have $aea_{12} - bc < 0$, and the stable steady state is the scenario where the nonbasal species becomes extinct and the basal species survives. In (b) we have $aea_{12} - bc > 0$, and the stable steady state is the scenario where both species survive and coexist.

with the numerical outcome of food webs that had $aea_{12} - bc < 0$. The numerical results are shown in Fig. 5, where the blue dots reflect systems where both species survive ($aea_{12} - bc > 0$), the red dots reflect systems where only the basal species survive ($aea_{12} - bc < 0$), and the line $aea_{12} = bc$ divides the two outcomes. The section resulting with both species surviving (blue dots) is much smaller due to the fact that the possible values for $aa_{12}e$ are much smaller than the possible values for bc, since $e = 0.1$. This implies that the $aa_{12}e$ term has values that lie in $(0, 0.1)$, and the bc term has values that lie in $(0, 1)$. Since the bc term range is much larger, there is more chance that this term will be larger, resulting in $aea_{12} - bc < 0$. The outcome where both species become extinct is not possible in this context, since one of the species must start with a zero population in order for the other species to become extinct, and the initial populations were always set to be nonzero. This condition $aea_{12} - bc > 0$ was able to accurately predict the outcome of all the food webs with the different parameter values and initial conditions for a two species model.

6.3 Expanding to Three Species Food Webs

The possibility of predicting the outcome of food web extinctions by considering its pairwise interactions was then expanded to food webs with three species. As with two species food webs, three species food webs were created. However, with three species, the webs can have different topologies. In particular, there are four different configurations of three species food webs, as shown in Fig. 6. Based on each of these food webs, the Lotka-Volterra equations for each topology were formulated and the steady states were computed, which varied according to the structure of the food
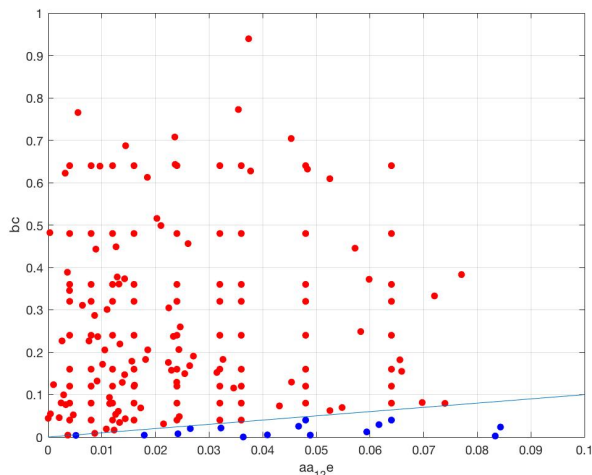
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Figure 5: Plot of condition $aea_{12} - bc$ for different sets of parameters for the system captured by Eqs. 3 and 4. The x-axis contains the values of aea_{12} term and the y-axis contains the value of the bc term. The red dots indicate $aea_{12} - bc < 0$, or that only the basal species (species 1) survives. The blue dots indicates $aea_{12} - bc > 0$, or that both species survive. The line $aea_{12} = bc$ divides the two sections.

web. Similarly to the two species food web, 100 iterations with different values for the parameters a, b, c, d, f, g, a_{12}, a_{13}, a_{23}, and different initial population densities for the species were completed for each type of food web, with the values chosen randomly from a uniform distribution. All of the pairwise interactions between the species in a particular three species food web was then analyzed, using the same condition as in the two-species web for predicting the outcome. Based on the outcomes of all pairwise interactions, we predicted which species in the three species food web would go extinct. Although this method was successful for some three species food webs, overall the pairwise analysis was not enough to predict the three species extinction outcomes. For example, in one of the food webs shown in Fig. 6d, the pairwise analysis indicated that all three species would survive. However, only two out of the three species survived when the entire three species food web was considered.

Since the pairwise interaction analysis was not enough to predict the three species extinction outcomes, additional information about the interactions between species is needed. We therefore considered the three-way interactions in each food web. In order to do this, the condition that would make each steady state biologically possible was found. As in the condition $aa_{12}e - bc$ for the two species web, if the condition is greater than zero, the steady state is biologically possible. For example, the steady state for the case where species 1 and species 3 survive in the web in Fig. 6d is biologically possible if the condition $aa_{13}e - bf > 0$ is true. Using this information, the possible options of species that survived were narrowed down, with some being biologically possible, and others not.

However, the final extinction outcome was still unable to be clearly predicted, since in some cases there were multiple outcomes that were biologically possible. Since the
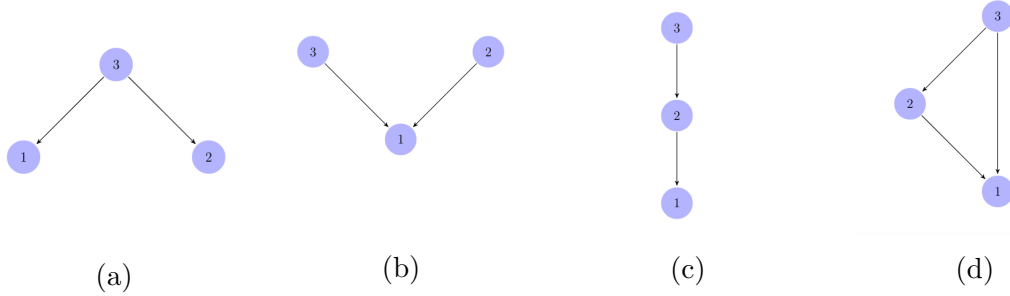
Figure 6: A food web with three species has one of these four different topologies. The four different configurations of three species were analyzed.

eigenvalues can be found for the three species food web, we again performed stability analysis of the steady states, and it was found that there was only one outcome where all three eigenvalues were stable. This stable steady state correctly predicts the extinction outcome for the three species food web. Numerics once again confirmed the theoretical predictions.

For example, for a food web with the structure shown in Fig. 6d, the corresponding Lotka-Volterra equations are:

$$\frac{dx_1}{dt} = ax_1 - bx_1^2 - a_{1,2}x_1x_2 - a_{1,3}x_1x_3 \tag{5}$$

$$\frac{dx_2}{dt} = -cx_2 - dx_2^2 + ea_{1,2}x_1x_2 - a_{2,3}x_2x_3 \tag{6}$$

$$\frac{dx_3}{dt} = -fx_1 - gx_1^2 + ea_{1,3}x_1x_3 + ea_{2,3}x_2x_3 \tag{7}$$

The three-way interaction analysis found that the cases where only species 1 survives, only species 1 and 2 survive, and only species 1 and 3 survive are the biologically possible outcomes. This rules out the outcome where all three species survive, but still leaves three possible outcomes (the case where all species become extinct cannot occur in this context because of similar reasoning as for the two species web). By calculating the eigenvalues, it is seen that only one scenario has all stable eigenvalues, namely where species 1 and species 3 survive. This therefore results in the prediction that species 1 and species 3 survive while species 2 becomes extinct. This matches with the actual outcome, where the population density steady states of the species are as follows: species 1 reaches a density of 7.73, species 2 approaches 0, and species 3 reaches a density of 0.56. Using the three-way interactions to narrow down the biologically possible cases, then calculating the eigenvalues of these cases and finding the stable option was able to accurately predict the outcome of three-species food webs.

7   Summary and Remarks

Through this study, the cascade model and the generalized cascade model have been used as the framework for creating food webs. When combined with the deterministic

dynamics of the Lotka-Volterra equations that are characteristic of species interactions, the end result are small and deterministically stable food webs. Incorporation of noise into these deterministically stable food webs induces primary extinctions which in turn cause secondary extinction cascades. Using statistical analysis, the extinction cascades and the mean time to extinctions for the extinction cascades and for each of the specific species were found for each type of food web model. Comparison of these two models with data from the niche model revealed more similarities than differences. For all three food web models, a few extinction cascades occurred the most, while the majority of extinction cascades only occurred a small amount of the time. Also, the MTE of each species corresponded to its place in the extinction casade: species that tended to become extinct quickly had low MTE and species that went extinct later in the extinction cascades had larger MTE.

Due to these similarities, attention was then focused on small deterministic webs in order to study the structure of food webs and how it relates to extinction events. For two species webs where one species preys upon the other, the survival or extinction of the species could be accurately predicted by analyzing the pairwise interactions with the condition $aea_{12} - bc$. For $aea_{12} - bc > 0$, the predicted outcome was the survival of both species, but for $aea_{12} - bc > 0$ only the basal species was predicted to survive, and these predictions for both conditions matched with numerical results. For three species webs, the pairwise interactions could not predict the three species food web extinction events, and both the conditions that made the three way interactions biologically possible as well as the stability of the eigenvalues were needed to accurately predict the survival or extinctions of species. Predictions based on both criteria for the three species food webs also matched with numerical results.

These findings from the extinction cascades suggest that stochastic food webs generated from different food web models will have similar extinction cascades and MTE characteristics. In addition, the findings from analyzing small deterministic webs suggest that the outcome of survival or extinctions of food webs with a small amount of species can be accurately predicted from using the information learned from the stability analysis. This opens up a number of questions for prediction of extinction in larger food webs. In the future, it will have to be investigated whether some of the methods used in the two and three species webs can also be used to predict the outcome of larger webs, or if this approach can be used as a basis to find new methods so that the outcome of survival or extinction for species in larger webs can be accurately predicted.

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