Understanding the Effects of Functional Responses in Ecological Dynamical Systems

by

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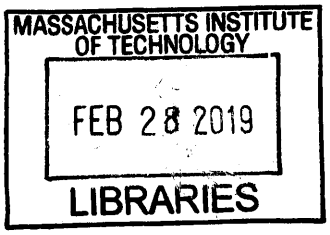

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Abstract

The main purpose of incorporating functional responses into ecological models has been to add more realism and to help us to mechanistically explain the dynamics of species abundances in nature. Yet, their effects have not been widely understood, especially in multispecies systems. That is, it remains unclear whether the perceived benefits of adding functional responses are simply mathematical artefacts or not. For example, while functional responses have been useful to model the dynamics of 2-species systems, still some functional responses have been criticized for producing unrealistic results. Moreover, it has been unclear the extent to which adding functional responses in multispecies systems can allow the dynamics to reach any type of behavior, contrary to the limits that nature may impose. Thus, it is necessary to fully understand the effect of functional responses on ecological models as it is directly linked to their explanatory power of ecological dynamics.

In this Masters thesis, we examine the effect of functional responses in 2-species and multispecies models (or systems). In particular, we examine the number of interior fixed points that are added into dynamical models by introducing functional responses. This number is linked to the capacity of a model to fit data and to the model's sensitivity to perturbation in its parameters. Note that classic ecological models without functional responses have only one interior fixed point regardless of the dimension of the system. We introduce, for the first time, a methodology to count the number of interior fixed points present in a dynamical system with functional responses. In particular, for 2-species models, we uncouple the 2-variable isocline equations (after some manipulations) into two separate single variable equations and examine them. For multispecies models, we compute the mixed volume (number of interior fixed points) of the system's isocline equations (after some manipulation). We show that incorporating functional responses into 2-species models feeds the system with one or two extra interior fixed points. Importantly, this number increases exponentially in multispecies systems. Hence, we conclude that the explanatory power of multispecies models with functional responses is drastically reduced if model parameters are not ecologically restricted. We believe this work sheds new lights on the applicability of functional responses and opens a new dialogue of what constitutes a realistic model.

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Chapter 1

Introduction

1.1 Motivations and Overview

One of the main interests of ecologists has been understanding how species interact with one another, and whether it is possible that they can coexist under certain environmental conditions [2]. Observing and modelling changes in species' abundances over time has been one of the main attempts in understanding ecological patterns. Indeed, some existing models have helped us to understand and predict ecological processes despite treating species as particles (whose behaviors exhibit a degree of randomness) and neglecting the fact that species have the capability of learning and adapting to different environments [3]. Lotka-Volterra (LV) models [4, 5], which are considered a pillar in the field of ecology, have helped us unlocking some population dynamics puzzles, such as the existence of periodic patterns in species's abundances [6]. Despite their predictive capacity, LV models are still approximations that do not capture all the complexities of ecological dynamics [7]. Hence, in order to add realism in ecological modeling, phenomenological models (such as the LV model) have been modified to capture more of nature's complexities. One central modification to these models has been the incorporation of functional responses [1, 6].

Functional responses, which in a nutshell, are the number of prey attacked, killed, and consumed per predator, enter the equations of ecological models as an attempt to add more realism or mechanistic understanding into them. In fact, functional responses naturally appear in predator-prey models, of which LV models are a sub-class [1]. Previous studies have shown that models that include functional responses have been successful in reproduc-

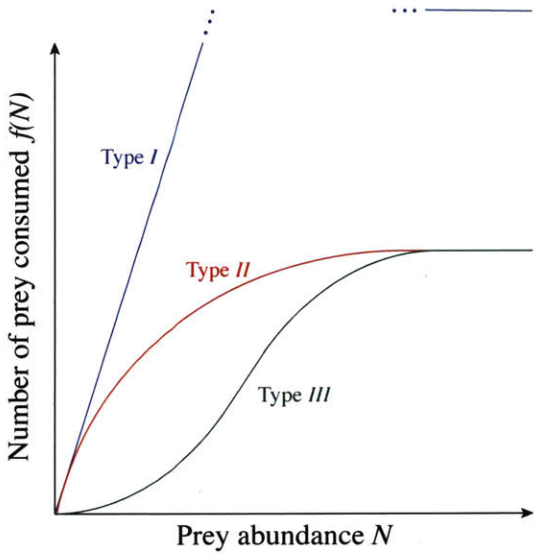

Figure 1-1: The diagram illustrates Howling functional responses of type I, II and III. The blue line is the linear functional response (type I), while the red and the green curves correspond to Howling responses of type II and III, respectively.

ing some of the dynamics of many 2-species systems [8]. As a result, they have become a major part in the field of ecology and they are mentioned in almost every major theoretical textbook in the field. The implementation of the concept of functional responses, which originated in the late 1940's, is not unique and can take many mathematical forms. These responses incorporate two important quantities which are (i) the prey handling time (the time the predator requires to attack, consume, and digest the prey), and (ii) predator's attack rate or searching rate (the rate at which a predator searches for its prey) [9]. Howling in 1959 considered three types of functional responses that are most commonly used nowadays [8].

The three most commonly used functional responses are the linear, hyperbolic, and the sigmoid responses. These are also called Howling functional response of type I, II and III, respectively (see Fig. 1-1 for an illustration of these responses). In type I, the number of prey consumed (functional response) is a linear function of the prey abundance. For large prey abundances, the linear relationship becomes constant to accommodate the concept that "in unity there is strength". That is, the higher the density of the prey, the smaller the proportion of them killed. The derivation of this functional response centers around the statement that the total time to consume prey t equals the time to search for them t_s (i.e., the time to handle prey $t_h = 0$). Note that after some time t_s, predators swipe an

area $t_s a$ and capture $F(t) = t_s aN$ prey, where a is the predator's search rate and N is the prey abundance. Hence, the Howling response $f^I(N)$ of type I at low prey abundances is simply

$$f^I(N) = \frac{F(t)}{t} = \frac{F(t)}{t_s} = \frac{at_s N}{t_s} = aN. \tag{1.1}$$

This type of functional responses appears in nature with spiders and flies as an example [10]. The more flies there are, the more of them will appear in the spider's web. Now moving to the functional response of type II, the prey handling time is non-zero. That is, the total time to consume prey t equals the time to search for them t_s plus the time to handle them t_h. We know from earlier that $t_s = F(t)/(aN)$. By settling $t_h = F(t)h$, where h is the time to handle a single prey, then $f^{II}(N)$ can be written as

$$f^{II}(N) = \frac{F(t)}{t} = \frac{F(t)}{t_s + t_h} = \frac{at_s N}{t_s + at_s Nh} = \frac{aN}{1 + ahN}. \tag{1.2}$$

Howling response of type II appears in nature with small mammals and gypsy mouth pupae as an example [11]. In sparse populations of gypsy, most of the pupae are killed by the small mammals; however, that number levels off for high density of prey. Regarding Howling response of type III, unlike type II, it lacks rigor in justifying its mathematical formula. If we think of a as a function of N, i.e., $a(N) = kN$ for some constant k and substitute it in the expression of $f^{II}(N)$, we have:

$$f^{III}(N) = \frac{kN^2}{1 + khN^2} = \frac{\frac{1}{h}N^2}{\frac{1}{kh} + N^2} \equiv \frac{cN^2}{d^2 + N^2}, \tag{1.3}$$

where $c = 1/h$ is the maximum killing rate and $d^2 = 1/(kh)$ is just a constant. In addition to the Howling functional responses, the constant functional response $f(N) = c$ is often used as the three howling responses level off for high prey abundances. For 2 species, functional responses have been incorporated into many models, such as Volterra in 1931, Leslie's Logistic Predation model in 1948, Rosenzweig-MacArthur in 1963, Bazykin in 1974, May's logistic predation model in 1974, DeAngelis in 1975, Ludwig in 1978, Yodzis in 1989, Eberhardt in 1997 and the variable territory model in 2001 [5, 12–20]. For multispecies, recent work by Ong and Vandermeer [21] incorporates functional responses (type II and III) into a predator-pest-pathogen model. Nevertheless, very few work has been done integrating with functional responses into multispecies models. Moreover, there has been

little understanding about the effects of functional responses on these models. Some models have been praised for mimicking some experimental results which involve 2 species, while others have been criticized for being unrealistic (logistic predation models) [1, 8]. In other words, it still remains unclear whether the perceived benefits of adding functional responses are simply mathematical artefacts or not, especially in multispecies systems. Yet, it is necessary to fully understand the effect of functional responses on ecological models as it is directly linked to their explanatory power of ecological dynamics.

1.2 Thesis Outline

In this thesis, we start with Chapter 2 which examines the effects of functional responses in predator-prey (2-species) models. In chapter 2, we first state the general mathematical form of continuous time predator-prey models, list well-known predator-prey models along with a list of the most commonly used functional responses in the literature. Then, we examine the effect of functional responses in such models and illustrate that the number of interior fixed points provides a key property of their behavior. We show that this number is linked to the capacity of a model to fit data and to the model's sensitivity to perturbation in its parameters. Then, we propose a methodology to quantify the number of interior fixed points that are added into 2-species models by introducing functional responses. Next, we present our findings and discuss the trade-offs induced by functional responses plus their implications. In Chapter 3, we move to multispecies models, and we quantify the effects of functional responses in these multi-dimensional models. Specifically, we start Chapter 3 by extending the general form of the predator-prey model presented in Chapter 2 to the multispecies case. Then, we introduce a methodology to evaluate the number of interior fixed points that are added into multispecies models by introducing functional responses. Finally, we discuss our findings and the implications of functional responses in multispecies models.

Chapter 2

Effects of Functional Responses in Predator-Prey (2-Species) Models

2.1 The General Mathematical Form of Continuous Time Predator-Prey Models

In this section, we revise the conditions leading to the generalized continuous-time predator-prey (2-species) model that takes the following form [1, 6]:

$$\begin{cases} \dfrac{dN}{dt} = \underbrace{r_N(N,P)}_{\text{prey growth rate}} - \underbrace{d_N(N,P)}_{\text{prey decline rate}} \\ \dfrac{dP}{dt} = \underbrace{r_P(N,P)}_{\text{predator growth rate}} - \underbrace{d_P(N,P)}_{\text{predator decline rate}} \end{cases}, \tag{2.1}$$

where N and P are the abundances of the prey and predator, respectively. Note that one can interpret $d_N(N,P)$ as the total killing rate of prey by predators. This means that the prey mortality due to natural causes is not part of $d_N(N,P)$ in Model (2.1), but it can be expressed by setting a smaller prey growth rate. Because the predator functional response $f(N,P)$ is the number of prey killed per predator, then the prey decline rate can be expressed as

$$d_N(N,P) = f(N,P)P. \tag{2.2}$$

Table 2.1 lists many variations of commonly used predator-prey models that have been

studied in the literature. Importantly, all of them can be classified under the family of generalized Lotka-Volterra (GLV) models. This family assumes that (i) $r_N(N,P)$ is independent of P. That is, $r_N(N,P) \equiv r_N(N)$ and has the form $r_N(N) = r_0N(1-N/K)$, where r_0 is the growth rate of the prey in the absence of the predator and K is the prey carrying capacity. (ii) $d_P(N,P)$ is independent of N. That is, $d_P(N,P) \equiv d_P(P)$ and has the form $d_P(P) = d_0P$, where d_0 is the per capita death rate of the predator (by natural causes). (iii) $r_P(N,P)$ is proportional to $d_N(N,P)$. That is, $r_P(N,P) = \chi f(N,P)P - \delta(N)P^2$, where the proportionality constant χ represents the fraction of eaten prey that is converted into predators. Here, $\delta(N)$ sets a limit to predator size, which makes sense in models for which $f(N,P)$ is independent of P. To see why, note that

$$\begin{cases} \dfrac{dP}{dt} = \chi f(N)P - \delta(N)P^2 - d_0P = s_0(N)P(1 - \dfrac{P}{K'(N)}), \\ \text{where } s_0(N) = \chi f(N) - d_0 \text{ and } K'(N) = \dfrac{s_0(N)}{\delta(N)}. \end{cases} \tag{2.3}$$

In Model (2.3), $s_0(N)$ represents the effective growth rate of the predator and $K'(N)$ is the predator carrying capacity, which is independent of P. Therefore, a GLV predator-prey model has the form

$$\begin{cases} \dfrac{dN}{dt} = r_0N(1 - \dfrac{N}{K}) - f(N,P)P, \\ \dfrac{dP}{dt} = \chi f(N,P)P - \delta(N)P^2 - d_0P. \end{cases} \tag{2.4}$$

However, not every predator-prey model can be classified under the family of GLV models. Table 2.2 lists general continuous-time predator-prey models that have a similar form to Model (2.4), but use two different functional responses instead of one, as shown below

$$\begin{cases} \dfrac{dN}{dt} = r_0N(1 - \dfrac{N}{K}) - f_1(N,P)P, \\ \dfrac{dP}{dt} = \chi f_2(N,P)P - \delta(N)P^2 - d_0P. \end{cases} \tag{2.5}$$

In many of these other models, $f_2(N,P)$ can be expressed as a constant function c leading to $s_0(N) = \chi c - d_0$, where $s_0(N)$ is also a constant and $\delta(N) = s_0q/N$. Hence, we can now write $dP/dt = s_0P(1 - qP/N)$. However, the constant c is chosen so that $s_0 = 0$ and $P(t) = g/c = d_og/\chi$, which is a constant term for all t (see for example Ludwiq model).

Model	Equations	$f(N,P)$	$\delta(N)$
Volterra	$\frac{dN}{dt} = r_0 N(1-\frac{N}{K}) - aNP$ $\frac{dP}{dt} = \chi aNP - d_0 P$	aN	0
Rozenweig-MacArther	$\frac{dN}{dt} = r_0 N(1-\frac{N}{K}) - \frac{cNP}{d+N}$ $\frac{dP}{dt} = \chi\frac{cNP}{d+N} - d_0 P$	$\frac{cN}{d+N}$	0
Yodzis	$\frac{dN}{dt} = r_0 N(1-\frac{N}{K}) - \frac{cN^2P}{d^2+N^2}$ $\frac{dP}{dt} = \chi\frac{cN^2P}{d^2+N^2} - d_0 P$	$\frac{cN^2}{d^2+N^2}$	0
DeAngelis	$\frac{dN}{dt} = r_0 N(1-\frac{N}{K}) - \frac{cNP}{d+bP+N}$ $\frac{dP}{dt} = \chi\frac{cNP}{d+bP+N} - d_0 P$	$\frac{cN}{d+bP+N}$	0
Bazykin	$\frac{dN}{dt} = r_0 N(1-\frac{N}{K}) - \frac{cNP}{d+N}$ $\frac{dP}{dt} = \chi\frac{cNP}{d+N} - d_1 P^2 - d_0 P$	$\frac{cN}{d+N}$	d_1
Variable Territory	$\frac{dN}{dt} = r_0 N(1-\frac{N}{K}) - \frac{cNP}{d+N}$ $\frac{dP}{dt} = \chi\frac{cNP}{d+N} - \frac{s_0 q P^2}{N} - d_0 P$	$\frac{cN}{d+N}$	$\frac{s_0 q}{N}$

Table 2.1: This table lists continuous-time predator-prey models that are classified under the family of generalized Lotka-Volterra (GLV) models. In addition, the table lists the functional response utilized for each model along with predator size limiter $\delta(N)$. Here, $s_0 = \chi c - d_0$

Model	Equations	$f_1(N,P)$	$f_2(N,P)$	$\delta(N)$
Logistic Predation (Leslie)	$\frac{dN}{dt} = r_0N(1-\frac{N}{K}) - aNP$ $\frac{dP}{dt} = s_0P(1-\frac{qP}{N})$	aN	c	$\frac{s_0q}{N}$
Logistic Predation (May)	$\frac{dN}{dt} = r_0N(1-\frac{N}{K}) - \frac{cNP}{d+N}$ $\frac{dP}{dt} = s_0P(1-\frac{qP}{N})$	$\frac{cN}{d+N}$	c	$\frac{s_0q}{N}$
Eberhardt	$\frac{dN}{dt} = r_0N(1-\frac{N}{K}) - c_1P$ $\frac{dP}{dt} = s_0P(1-\frac{qP}{N})$	c_1	c	$\frac{s_0q}{N}$
Prey-Dependent Consumption	$\frac{dN}{dt} = r_0N(1-\frac{N}{K}) - aNP$ $\frac{dP}{dt} = \chi\frac{aNP}{1+ahN} - d_0P$	aN	$\frac{aN}{1+ahN}$	0
Generalist Predators	$\frac{dN}{dt} = r_0N(1-\frac{N}{K}) - \frac{Ng}{d+N}$ $\frac{dP}{dt} = 0$	$\frac{cN}{d+N}$	$c = \frac{d_0}{\chi}$	$\frac{s_0q}{N}$
Ludwig	$\frac{dN}{dt} = r_0N(1-\frac{N}{K}) - \frac{N^2g}{h^2+N^2}$ $\frac{dP}{dt} = 0$	$\frac{cN^2}{h^2+N^2}$	$c = \frac{d_0}{\chi}$	$\frac{s_0q}{N}$

Table 2.2: This table lists continuous-time predator-prey models that are not classified under the family of generalized Lotka-Volterra (GLV) models. In addition, the table lists the two functional response utilized for each model along with predator size limiter $\delta(N)$. Here, $s_0 = \chi c - d_0$

Name	$f(N,P)$
Constant	c
Linear	aN
Hyperbolic	$\frac{aN}{1+ahN}$
Sigmoid	$\frac{cN^2}{d^2+N^2}$
Sigmoid (mechanistic)	$\frac{bN^2}{1+gN+bhN^2}$
θ-sigmoid	$\frac{cN^\theta}{d^\theta+N^\theta}$
Predator interference (mechanistic)	$\frac{aN}{1+awP}$
Predator interference (phenom.)	$aNP^{-\theta}$
Beddington	$\frac{aN}{1+awP+ahN}$
Hyperbolic ratio dependent	$\frac{cN}{dP+N}$
Linear ratio dependent	$c\frac{N}{P}$

Table 2.3: The table mentions commonly used functional responses in predator-prey models. Here, N and P are the abundances of the prey and predator, respectively. c is the maximum killing rate, a is the predator searching rate, h is the handling time, w is the wasted time, b is the maximum searching rate, g is a parameter regulating how fast search rate saturates with prey density, d is the half-saturation constant and θ is an exponent. Table and caption are taken from Turchin et al. [1].

2.2 Functional Responses and their Effects on Predator-Prey Models

As noted earlier, predator-prey models incorporate some form of functional response $f(N,P)$ (see Tables 2.1 and 2.2). Table 2.3 lists a variety of these functional forms. For example, the most commonly used types are the constant, linear, hyperbolic, and the sigmoid forms [1, 6]. These common types are usually linked to the so-called Howling functional responses [8]. Recall that Howling type I is a linear response (which turns sharply to the constant function), while the hyperbolic and sigmoid responses are typically known as Howling type II and III, respectively. Less common functional responses include the θ-sigmoid, predator interference, beddington, hyperbolic ratio dependent, and the linear ratio dependent (see

Table 2.3). Yet, many functional responses are used without a formal mechanistic derivation [1]. Moreover, some models (see Table 2.1) use only one type of functional response, while others use more than one type (see Table 2.2). Hence, it is natural to ask how can the exact form of the functional response affect the dynamics of predator-prey systems. In line with this question, the main goal of this work is two fold: (1) To quantify the effect of functional responses in predator-prey models. (2) To examine how the exact form and number of functional responses affect the behaviour of a system.

Indeed, the main purpose of incorporating functional responses in ecological models has been linked to adding more realism and to helping us to better explain the dynamics of species abundances. Yet, their effects have not been widely understood, especially in multispecies systems. For example, functional responses in 2-species models have been used extensively and they have been mentioned in almost every major textbook of theoretical ecology [1, 2, 6]. However, some models that utilize functional responses have been criticized for not being realistic and producing ambiguous results. For instance, it has been shown that in some predator-prey models, when the predators are starving (at low attack rates) it is possible to observe an increase in predator abundances, which does not make sense ecologically [1]. This implies that with some functional responses it may be possible to arrive to any type of behavior. Thus, it remains necessary to fully understand the effect of functional responses on predator-prey models, and as a consequence, their explanatory power of ecological dynamics.

2.3 Quantifying the Effect of Functional Responses in Predator-Prey Models

To answer the questions raised in the previous section, we propose to link the behavior of a dynamical system with the properties and number of its fixed points (steady state abundances). Regarding the properties, the existence of a feasible fixed point for which both of its components are positive is a necessary condition for species coexistence and permanence (regardless of the initial condition of species abundances as these abundances will be bounded from above and below by positive constants as time goes to infinity, [22, 23]). It is useful to note that in 2-species dynamics, necessary and sufficient conditions

for permanence correspond to the existence of a feasible fixed point that is stable; however, without a feasible fixed point, the predator and/or the prey will go extinct. In addition, limit cycles cannot exist without a feasible fixed point [22, 24]. Hence, properties of fixed points are important in determining the dynamics of ecological models as their existence enriches their dynamics [25].

Additionally, the number of fixed points is also a central determinant of the dynamics of ecological systems. For example, functional responses are expected to facilitate the process of fitting empirical data into ecological models [8]. It is well known that coexistence in a 2-species LV model with mutualistic interactions will never occur without adding functional responses to it [6]. However, there is no clear understanding about why this happens. From a mathematical perspective, the LV model has only one interior fixed point [24], but functional responses may feed the system with extra fixed points. Therefore, with more fixed points and parameter tuning, a feasible fixed point (i.e., coexistence) can be attained easier compared to the original system which has one fixed point due to parameter restrictions (imposing mutualism). Hence, it becomes necessary to know the extent to which functional responses increase the number of fixed points in a system.

Because GLV models are a special case of Model (2.5) for which $f_1(N,P) = f_2(N,P) \equiv f(N,P)$, then we can examine and quantify the number of fixed points in the generalized Model (2.5). To study Model (2.5), we need to obtain the equations linking its fixed points. To do this, we first obtain the isocline equations of Model (2.5). Then, we perform a fraction addition between the terms in the isocline equations, where the denominator of each isocline equation is unified and a resultant numerator for each isocline equation is obtained. Next, we delete the denominators for both isocline equations from the expression given the two following reasons: (i) They are positive in the feasible domain for all positive N and P. That is their roots are always not in the feasible domain (no feasible poles). (ii) They do not affect the location of the fixed points. Finally, we separate analytically the coupled multivariate polynomial equations of the isocline equations numerators (which are both in terms of N and P) for further examination.

Following the methodology above for Model (2.5), the system isoclines are first obtained by setting the time derivative of the abundances of both the prey and predator to zero. This gives the following set of equations

$$\begin{cases} r_0 N^*(1 - \dfrac{N^*}{K}) - f_1(N^*, P^*)P^* = 0, \\ \chi f_2(N^*, P^*)P^* - \delta(N^*){P^*}^2 - d_0 P^* = 0, \end{cases} \tag{2.6}$$

where N^* and P^* are steady-state abundances. Note that in the second equation of (2.6), P^* is a common factor of all the terms. This implies that $P = 0$ is an isocline of the second equation. Because we are interested in species coexistence and the event of prey and/or predator extinction will be ignored, we can safely divide the equations by P^*. In addition, the functional responses $f_1(N^*, P^*)$ and $f_2(N^*, P^*)$ are quotient of two polynomials. Hence, we can write $f_i(N^*, P^*) = f_i^U(N^*, P^*)/f_i^D(N^*, P^*)$ for $i = 1, 2$ and $\delta(N^*) = \delta^U(N^*)/\delta^D(N^*)$. In this case, the isoclines of system (2.5) can be written as

$$\begin{cases} r_0 N^*(K - N^*) f_1^D(N^*, P^*) - K f_1^U(N^*, P^*)P^* = 0, \\ \chi f_2^U(N^*, P^*)\delta^D(N^*) - f_2^D(N^*, P^*)(\delta^U(N^*)P^* - d_0\delta^D(N^*)) = 0. \end{cases} \tag{2.7}$$

If $f_1^U(N^*, P^*) = N^* f_1'^U(N^*, P^*)$, then we can divide the first equation of Eqs.(2.7) by N^*. Depending on the form of $f_1^U(N^*, P^*)$, we call the equations in either (2.7) or (2.8), the isocline equations in standard form where there is no common factors shared by all terms.

$$\begin{cases} r_0 (K - N^*) f_1^D(N^*, P^*) - K f_1'^U(N^*, P^*)P^* = 0, \\ \chi f_2^U(N^*, P^*)\delta^D(N^*) - f_2^D(N^*, P^*)(\delta^U(N^*)P^* - d_0\delta^D(N^*)) = 0. \end{cases} \tag{2.8}$$

The coupled multivariate polynomial equations presented in Eqs.(2.7) or (2.8) in terms of N^* and P^* can be separated analytically into two uncoupled polynomials, one in terms of N^* only (i.e., without P^*) and the other is in terms of p^* only (i.e., without N^*). Therefore, the uncoupled form of Eqs.(2.7) will have the following form

$$\begin{cases} \displaystyle\sum_{k=0}^{\Theta} c_k {N^*}^k = 0, \\ \displaystyle\sum_{k=0}^{\Theta} d_k {P^*}^k = 0. \end{cases} \tag{2.9}$$

Upon reaching the form (2.9), the number of fixed points that the dynamical system (2.5) has is given simply by Θ—the degree of the uncoupled univariate polynomials. Note that we have excluded fixed points for which at least one species (the predator or prey) is

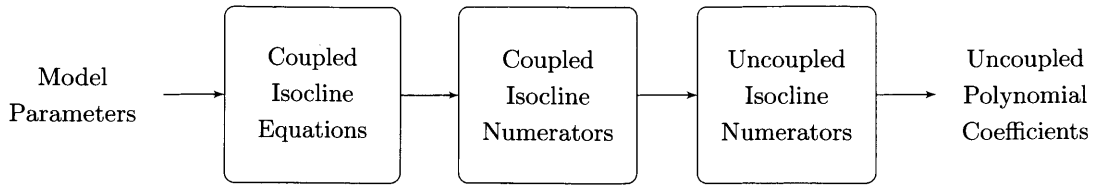

Figure 2-1: The figure summarizes the methodology illustrated in Section (2.3). First, the coupled isocline equations are obtained. Afterwards, fraction addition is performed to obtained coupled equations linking the isocline numerators. These equations are then uncoupled analytically. From this process, a model parameter, which appears only once in the coupled isocline equations, will show up in many locations and with higher orders in the uncoupled equations.

extinct. That is, if a species goes extinct, then it cannot be revived as predator-prey models do not allow revival of species. In this case, the dynamical model would reduce to a single population dynamics model, which are already well studied [1, 6]. Here, the c_k's and d_k's of Model (2.9) are functions of r_0, d_0, K, χ and any constants embedded in $f_1(N^*, P^*), f_2(N^*, P^*)$ and $\delta(N)$. Hence, to quantify the effect of functional responses on predator-prey models, we just need to obtain the polynomial structures that result from Eqn. (2.9) for the different models presented in Tables (2.4) and (2.5) and the polynomial structures that result from incorporating functional responses.

2.4 Trade-offs of Functional Responses and their Implications

As previously mentioned, functional responses are added into ecological models in order to add realism or a mechanistic understanding of ecological dynamics. Indeed, functional responses add fixed points and this can increase the capacity of a system to fit any type of data, especially without parameter restrictions. While this can be beneficial for prediction purposes, it is unclear whether this can also be beneficial for increasing our understanding of these systems. For example, this facilitation comes with a price. These models are more sensitive to perturbations in model parameters, as perturbing a single parameter in a coupled multivariate polynomial system has more severe consequences than in a single variable one [26]. Moreover, as we have already mentioned, these functional responses have also been criticized for producing ambiguous results. For instance, focusing on the Logistic Predation (Leslie) model, we can see from Table (2.5) the isolated form of the isocline equations, which are

Model	Isocline Equations in the Standard Form	Isocline Equations in the Uncoupled Form
Volterra	$r_0(K-N^*)-aKP^*=0$ $\chi aN^*-d_0=0$	$(-K\chi a^2)P^*+(K\chi r_0 a-d_0 r_0)=0,$ $(\chi a)N^*+(-d_0)=0$
MacArther	$r_0(K-N^*)(d+N^*)-cKP^*=0$ $\chi cN^*-d_0(d+N^*)=0$	$(Kc^3\chi^2-2Kc^2\chi d_0+Kcd_0^2)P^*+(-Kr_0c^2\chi^2 d+d_0r_0c\chi d^2+Kd_0r_0c\chi d)=0,$ $(c\chi-d_0)N^*+(-d_0d)=0$
Yodzis	$r_0(K-N^*)(d^2+N^{*2})-cKN^*P^*=0$ $\chi cN^{*2}-d_0(d^2+N^{*2})=0$	$(-K^2c^3\chi^2d^2d_0+2K^2c^2\chi d^2d_0^2-K^2cd^2d_0^3)P^{*2}+(-2Kr_0c^2\chi^2d^4d_0$ $+2Kr_0c\chi d^4d_0^2)P^*+(K^2c^2\chi^3d^4r_0^2-d_0K^2c\chi^2d^4r_0^2-d_0c\chi^2d^6r_0^2)=0,$ $(c\chi-d_0)N^{*2}+(-d_0d^2)=0$
DeAngelis	$r_0(K-N^*)(d+bP^*+N^*)-cKP^*=0$ $\chi cN^*-d_0(d+bP^*+N^*)=0$	$(-b^2c\chi d_0r_0)P^{*2}+(2Kc^2\chi d_0-Kcd_0^2-Kc^3\chi^2+Kbc^2\chi^2r_0-Kbc\chi d_0r_0$ $-2bc\chi dd_0r_0)P^*+(Kr_0c^2\chi^2d-d_0r_0c\chi d^2-Kd_0r_0c\chi d)=0,$ $(-bc\chi r_0)N^{*2}+(Kcd_0-Kc^2\chi+Kbc\chi r_0)N+(Kcdd_0)=0$
Bazykin	$r_0(K-N^*)(d+N^*)-cKP^*=0$ $\chi cN^*-(d+N^*)(d_1P^*-d_0)=0$	$(Kcd_1^2)P^{*3}+(-2K\chi d_1c^2-2Kd_0d_1c)P^{*2}+(Kc^3\chi^2+2Kc^2\chi d_0+d_1r_0c\chi d^2$ $+Kd_1r_0c\chi d+Kcd_0^2)P^*+(-Kr_0c^2\chi^2d-d_0r_0c\chi d^2-Kd_0r_0c\chi d)=0,$ $(d_1r_0)N^{*3}+(2dd_1r_0-Kd_1r_0)N^{*2}+(K\chi c^2+Kd_0c+d_1r_0d^2-2Kd_1r_0d)N^*$ $+(-Kd_1r_0d^2+Kcd_0d)=0$
V.Territory	$r_0(K-N^*)(d+N^*)-cKP^*=0$ $\chi cN^{*2}-(d+N^*)(s_0qP^*-d_0N^*)=0$	$(Kcq^2r_0s_0^2)P^{*3}+(K^2c^4\chi^2+2K^2c^3\chi d_0-qr_0s_0K^2c^2\chi+K^2c^2d_0^2$ $-qr_0s_0K^2cd_0+3dqr_0s_0Kc^2\chi+dqr_0s_0Kcd_0)P^{*2}+(-2K^2c^3\chi^2dr_0$ $-3K^2c^2\chi ddr_0-K^2cdd_0^2r_0-Kc^2\chi d^2d_0r_0-qs_0Kc\chi d^2r_0^2-qs_0c\chi d^3r_0^2)P^*$ $+(K^2c^2\chi^2d^2r_0^2+d_0K^2c\chi d^2r_0^2+d_0Kc\chi d^3r_0^2)=0,$ $(qr_0s_0)N^{*3}+(K\chi c^2+Kd_0c-Kqr_0s_0+2dqr_0s_0)N^{*2}+(d^2qr_0s_0$ $+Kcdd_0-2Kdqr_0s_0)N^*+(-Kd^2qr_0s_0)=0$

Table 2.4: This table lists the isocline equations of models that are classified under the family of generalized Lotka-Volterra (GLV) models in both the standard and the uncoupled forms. Here, $s_0=\chi c-d_0$

Model	Isocline Equations in the Standard Form	Isocline Equations in the Uncoupled Form
Logistic Predation (Leslie)	$r_0(K - N^*) - aKP^* = 0$ $N^* - qP^* = 0$	$(-Ka - qr_0)P^* + (Kr_0) = 0,$ $(-Ka - qr_0)N^* + (Kqr_0) = 0$
Logistic Predation (May)	$r_0(K - N^*)(d + N^*) - cKP^* = 0$ $N^* - qP^* = 0$	$(-q^2r_0)P^{*2} + (Kqr_0 - Kc - dqr_0)P^* + (Kdr_0) = 0,$ $(qr_0)N^{*2} + (Kc - Kqr_0 + dqr_0)N^* + (-Kdqr_0) = 0$
Eberhardt	$r_0N^*(K - N^*) - c_1KP^* = 0$ $N^* - qP^* = 0$	$(q^2r_0)P^* + (Kc_1 - Kqr_0) = 0,$ $(qr_0)N^* + (Kc_1 - Kqr_0) = 0$
Prey-Dependent Consumption	$r_0(K - N^*) - aKP^* = 0$ $\chi aN^* - d_0(1 + ahN^*) = 0$	$(Ka^2\chi - Ka^2d_0h)P^* + (d_0r_0 - Ka\chi r_0 + Kad_0hr_0) = 0,$ $(ad_0h - a\chi)N^* + (d_0) = 0$
Generalist Predators	$r_0(K - N^*)(d + N^*) - gK = 0$	$(-r_0)N^{*2} + (Kr_0 - dr_0)N^* + (-Kg + Kdr_0) = 0$
Ludwig	$r_0(K - N^*)(h^2 + N^{*2}) - gKN^* = 0$	$(-r_0)N^{*3} + (Kr_0)N^{*2} + (-r_0h^2 - Kg)N^* + (Kh^2r_0) = 0$

Table 2.5: This table lists the isocline equations of models that are not classified under the family of generalized Lotka-Volterra (GLV) models in both the standard and the uncoupled forms. Here, $s_0 = \chi c - d_0$

$$\begin{cases} (-Ka - qr_0)P^* + (Kr_0) = 0, \\ (-Ka - qr_0)N^* + (Kqr_0) = 0. \end{cases} \tag{2.10}$$

In this model, when the attack rate a is set to zero (that is, when the predators are starving), the system will still have one feasible fixed point. This means that the predator and the prey can still coexist, which does not make sense ecologically.

$$\begin{cases} P^* = \dfrac{Kr_0}{qr_0}, \\ N^* = \dfrac{Kqr_0}{qr_0}. \end{cases} \tag{2.11}$$

In general, from Tables (2.4) and (2.5), we can see that the isolated form of isocline equations ranges from linear to cubic polynomials for both N^* and P^*. That is, $\Theta = 1$, 2, or 3 in the given models. This confirms that functional responses do feed ecological models with more fixed points. But more importantly, this analysis motivates the hypothesis that Θ increases when (i) the order of the polynomial in the numerator of functional response increases; (ii) the order of the polynomial in the denominator of functional response increases; or (iii) the number of different functional responses that are incorporated in the system increases.

In addition, the larger Θ is, the more complex the analytical formulas of c_k's and the d_k's in Eqns.(2.9), which can be seen as well from the isolated form of the isocline equations in Tables (2.4) and (2.5). That is, the isolated form for Bazykin and Variable Territory models are more *complex* than the rest. Also, we can see from Tables (2.1) and (2.2) that model parameters are involved in many of the terms c_k's and the d_k's. For example, prey's carrying capacity K in DeAngelis, Bazykin and the Variable Territory models are involved in most of the terms in the isolated form of the isocline equations and a similar argument applies to many of the models' parameters. Hence, as Θ increases, then a small perturbation in the model parameters can induce changes in many values c_k's and d_k's, thus inducing a notable change in the location of roots of both N^* and P^*. This observation suggests that introducing functional responses can increase the sensitivity of ecological models to perturbations which worsens when Θ increases. We will study all the aforementioned effects on Θ in the upcoming chapter.

Chapter 3

Quantifying the Effects of Functional Responses in Multispecies Models

3.1 The Multispecies Predator-Prey Model

In this section, we consider the multispecies version of the GLV predator-prey model (2.4), which was discussed in the previous chapter. The multispecies model consists of n species and takes the following general form:

$$\frac{dN_i}{dt} = N_i r_i - \sum_{j \in A_i} N_j f_{i,j} + \sum_{j \in B_i} \chi_{j,i} N_i f_{j,i}, \quad i = 1, \ldots, n, \tag{3.1}$$

where the N's are the species abundances, the r's are the species' growth rates (or decline rates if they are negative), the f's are the functional responses, and the χ's are proportionality constants that represent fractions of the prey converted into predators. We recall that functional responses are the total rate of prey killed and consumed by predators. Hence, any pair of species i and j that are interacting in the system is a predator-prey one. In Model (3.1), the A_i's and B_i's are indices of the predators and the prey of species i respectively. These are subsets of the set $S = \{1, \ldots, n\}$, which indexes each of the n species that exist in the system. We define A_i and B_i as follows: if $j \in A_i$ then species j is the predator, while species i is the prey. Similarly, if $j \in B_i$ then species j is the prey, while species i is the predator. If the pair of species i and j is a predator-prey one, then $j \in A_i$ if and only if $i \in B_j$. We impose that A_i (predators of i) as well as B_i (prey of i)

are disjoint sets. That is, $A_i \cap B_i = \Phi$ for $i = 1, \ldots, n$, which is a reasonable assumption to make.

It is also important to note that prey can sometimes kill their predators; however, this effect can be reflected in other quantities in the model such as a smaller proportionality constant of prey converted into predators or a smaller effective attack rate of predators, or a lower effective growth rate of predators (or a higher mortality rate). Because of the way we have expressed functional responses in Model (3.1), both $f_{i,j}$ and $f_{j,i}$ cannot simultaneously coexist in the system. It can only exists one of them for which the first and second indices represent the prey and the predator, respectively. In Table (2.3), which lists commonly used functional responses in the literature, we can make the important observation that functional responses are functions that depend heavily on the prey and are multiples of the prey abundances, taking the following form:

$$f_{i,j} \equiv f_{i,j}[N_i] = c_{i,j} N_i \phi_{i,j}[N_i] \equiv c_{i,j} N_i \phi_{i,j}, \qquad i, j = 1, \ldots, n, \tag{3.2}$$

where the c's are constants which represent the predator searching rate or maximum killing rate depending on the used form of functional responses (see Table (2.3) for details) and the ϕ's are the remaining multiplicative part of the functional responses. The brackets $[N_i]$ are only a notion to indicate that functional responses depend heavily on the prey's abundance N_i, but they can depend on the predator's abundance as well.

Importantly, when the Expression (3.2) is substituted in Model (3.1), we get the following model:

$$\begin{cases} \dfrac{dN_i}{dt} = N_i(r_i - \displaystyle\sum_{j \in A_i} c_{i,j} N_j \phi_{i,j}[N_i] + \sum_{j \in B_i} \chi_{j,i} c_{j,i} N_j \phi_{j,i}[N_j]), \quad i = 1, \ldots, n \quad \text{or} \\ \dfrac{dN_i}{dt} = N_i(r_i + \displaystyle\sum_{j \in A_i} a_{i,j} N_j \phi_{i,j} + \sum_{j \in B_i} a_{i,j} N_j \phi_{j,i}), \qquad\qquad i = 1, \ldots, n, \end{cases} \tag{3.3}$$

where $a_{i,j} = -c_{i,j} < 0$ if index i represents the prey, while $a_{i,j} = \chi_{j,i} c_{j,i} > 0$ if index i represents the predator. From Model (3.3), it is easy to see from the second version that if (i) there are no sign restrictions on the a's, (ii) $A_i \cup B_i = S$ for $i = 1, \ldots, n$, and (iii) the ϕ's are all 1 (linear functional responses), then we get the LV model of the form

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^{n} a_{i,j}N_j), \quad i = 1, \ldots, n. \tag{3.4}$$

From Model (3.3), it is easy to derive the generalized version of the 2-species predator-prey model (2.5) that is not classified under the family of LV models that is shown below:

$$\begin{cases} \dfrac{dN_i}{dt} = N_i(r_i - \sum\limits_{j\in A_i} c_{i,j}N_j\phi_{i,j}[N_i] + \sum\limits_{j\in B_i} \chi_{j,i}c_{i,j}N_j\phi_{i,j}[N_j]), & i = 1, \ldots, n \quad \text{or} \\ \dfrac{dN_i}{dt} = N_i(r_i + \sum\limits_{j\in A_i} a_{i,j}N_j\phi_{i,j} + \sum\limits_{j\in B_i} a_{i,j}N_j\phi_{i,j}), & i = 1, \ldots, n. \end{cases} \tag{3.5}$$

Model (3.5) simply replaces $c_{j,i}\phi_{j,i} \equiv c_{j,i}\phi_{j,i}[N_j]$ in the second sum over the indices of B_i's with $c_{i,j}\phi_{i,j} \equiv c_{i,j}\phi_{i,j}[N_j]$, which is still heavily dependent on the prey's abundance N_j. Note that Model (3.5) loses the structural symmetry that GLV models (3.3) have. In addition, we note that the expression $a_{i,j} = \chi_{j,i}c_{i,j}$ changes compared to Model (3.3), where index i represents the predator. Although the second expression of Eqns.(3.5) is more neat, the first expression is more useful when it comes to carrying capacities. To limit the species abundance N_i to K_i (carrying capacity of species i), we simply modify the first expression of Eqns.(3.5) to limit the overall growth rate of species i as follows:

$$\begin{cases} \dfrac{dN_i}{dt} = N_i(\underbrace{(r_i + \sum\limits_{j\in B_i} \chi_{j,i}c_{i,j}N_j\phi_{i,j}[N_j])}_{\text{species' growth rate}}(1 - \dfrac{N_i}{K_i}) - \sum\limits_{j\in A_i} c_{i,j}N_j\phi_{i,j}[N_i]), \text{ if } r_i > 0 \\ \dfrac{dN_i}{dt} = N_i(r_i + \underbrace{(\sum\limits_{j\in B_i} \chi_{j,i}c_{i,j}N_j\phi_{i,j}[N_j])}_{\text{species' growth rate}}(1 - \dfrac{N_i}{K_i}) - \sum\limits_{j\in A_i} c_{i,j}N_j\phi_{i,j}[N_i]), \text{ if } r_i < 0, \end{cases} \tag{3.6}$$

where the overall growth and decline rates of species i are simply $r_i + \sum_{j\in B_i} \chi_{j,i}c_{i,j}N_j\phi_{i,j}[N_j]$ and $\sum_{j\in A_i} c_{i,j}N_j\phi_{i,j}[N_i]$, respectively if $r_i > 0$. However, if $r_i < 0$, then the overall growth and decline rates will be $\sum_{j\in B_i} \chi_{j,i}c_{i,j}N_j\phi_{i,j}[N_j]$ and $r_i + \sum_{j\in A_i} c_{i,j}N_j\phi_{i,j}[N_i]$, respectively. Note that r_i moves from the growth to the decline expression.

3.2 Evaluating the Effects of Functional Responses in Multispecies Models

As we have observed in Chapter 2, incorporating functional responses in 2-species predator-prey models feeds the system with more fixed points. Recall that the more fixed points a system has, the easier it is to fit ecological data to such a model without parameter restrictions. However, this benefit comes with a price, which is an increased sensitivity when model parameters are perturbed. For two species, the number of fixed points in a model varies between 1 and 3, but this number is expected to increase drastically when non-linear functional responses are added and the dimension of the model increases. Importantly, under the premise that nature is resilient to slight environmental perturbations [27], the increased benefit of fitting data to models will not necessarily increase our understanding in ecological models that incorporate functional responses. Hence, it is essential to study the number of fixed points of Models (3.3) or (3.5) in order to assess their data-fitting ability and sensitivity to environmental perturbations.

To address the point above, for simplicity we will assume a dense network of species interactions. That is, every pair of species $i, j \in S$ where $i \neq j$ is a predator-prey pair or equivalently $A_i \cup B_i = S$ for $i = 1, \ldots, n$. We embed the latter assumption in Model (3.5), which is the more general version of the multispecies GLV Model (3.3), and add the self-regulatory term $a_{i,i}N_i^2\phi_{i,i}$ in the expression of dN_i/dt (for a more generalized model), to obtain the following dynamical system:

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^{n} a_{i,j}N_j\phi_{i,j}), \qquad i = 1, \ldots, n. \tag{3.7}$$

Our objective in this chapter is to study the number of fixed points of Model (3.7) under different scenarios. To do this, we follow a similar procedure to the method described in Section 2.3. We first obtain the isocline equations of Model (3.7), where we assume that no species is extinct. Next, the common denominator between the added fractions in the isocline equations is acquired and the numerators are multiplied with the appropriate factors to get the common numerator in the resultant fraction. Because the common denominator is usually non-negative (no feasible poles), and the their presence neither affects the location of the fixed points nor their numbers, then they can be deleted from

the expression. Finally, we compute the number of fixed points in the resultant coupled multivariate polynomial equations of the isocline equations' numerators. Note that Models (3.3) and (3.5) do not allow species revival. Therefore, if a species i goes extinct, then after substituting $N_i = 0$ in the model, the dimension of the model reduces and the reduced model can be studied in terms of its non-zero fixed points. Similarly, for the dynamical model (3.7), the isocline equations are obtained by setting the time derivative for all species abundances to zero. This gives the following set of coupled equations:

$$r_i + \sum_{j=1}^{n} a_{i,j} N_j \phi_{i,j} = 0, \qquad i = 1, \ldots, n. \tag{3.8}$$

Note that in Model (3.8), the ϕ's are written as a quotient of two polynomials. That is, $\phi_{i,j} = \phi_{i,j}^U / \phi_{i,j}^D$, where $\phi_{i,j}^U$ and $\phi_{i,j}^D$ are polynomials. If we let $\Phi_{i,0} = \phi_{i,1}^D \phi_{i,2}^D \ldots \phi_{i,n}^D$ and define $\Phi_{i,j}$ to be $\Phi_{i,0}$ but with its term $\phi_{i,j}^D$ being replaced with $\phi_{i,j}^U$, then the previous system of equations can be expressed as follows:

$$r_i \Phi_{i,0} + \sum_{j=1}^{n} a_{i,j} N_j \Phi_{i,j} = 0, \qquad i = 1, \ldots, n. \tag{3.9}$$

Unlike the 2-species case, the coupled multivariate polynomial System (3.9) cannot be generally decoupled into n equations of a single variable. However, we are interested in computing the number of roots (Θ) from Eqns. (3.9).

To compute Θ, we simply need to pick arbitrary r's and a's in Eqns. (3.9), solve the multivariate polynomial system and count how many roots there are. This approach can be used because for arbitrary choices of r's and a's in Eqns. (3.9), Θ is independent of the r's and a's which is an extension to the fundamental theorem of algebra. Recall that solving a multivariate polynomial system is a very expensive task and that Θ can be computed faster without solving the system using the software packages such as DEMiCs or MixedVol-2.0 (see [28–30] for more information). Indeed, given a multivariate polynomial system as an input, the output of these packages give the number of the system's isolated roots. The idea behind the algorithm of the software package DEMiCs is centered around the dynamic enumeration method, proposed by Mizutani, Takeda and Kojima as well as the polyhedral homotopy continuation method which plays an important role in solving a system of coupled polynomial equations (see [28] for more details). We also use the package MixedVol-2.0, where a different enumeration technique is employed [29].

3.3 Assessing the Effects of Functional Responses in Multispecies Models

In this section, we assess the effects of functional responses in Model (3.3) by counting how many fixed points (Θ) do they feed the system with. Recall that a model's Θ is linked to its sensitivity to perturbations and its easiness to fit data to it. We use the classic LV Model (3.4) as the benchmark model to compare other models. Recall that the classic LV model has only 1 interior fixed point regardless of the dimension n of the system. This is because the isocline equations of the LV model are a system of n linear equations with n unknowns (species' abundances) as shown below:

$$r_i + \sum_{j=1}^{n} a_{i,j} N_j = 0, \quad i = 1, \ldots, n. \tag{3.10}$$

It is known that such systems have either zero, one, or infinitely many solutions. However, with a generic choice of the r's and the a's, obtaining two isocline planes that are parallel (0 solutions) or identical (infinitely many solutions) is unlikely. Not to mention that these special cases are ecologically unrealistic, and therefore can be omitted. To assess the effect of functional responses in Model (3.3), compared to the special case of the LV model for which all the ϕ's are 1 (linear functional responses), we consider the simplest extension for which all the ϕ's are 1 except for a few locations where the ϕ's are different. In those few locations, we consider the hyperbolic and the sigmoid functional responses (we also consider the θ-sigmoid functional response). Recall that the hyperbolic and sigmoid responses are commonly used functional responses after the linear response (they correspond to the Howling responses of type II and III, respectively). These functional responses are also special cases of the θ-sigmoid functional response, when θ is 1 and 2, respectively.

To assess the effects of functional responses in Model (3.3), we start with a model for which all the ϕ's are 1 except for $\phi_{1,2}$. Specifically, when $f_{1,2}$ is the hyperbolic response (i.e., $\phi_{1,2} = 1/(1 + cN_1)$ for some constant c), the isocline equations expressed in the form (3.9) take the following form:

$$\begin{cases} r_1 + \sum_{j=1}^{n} a'_{1,j} N_j + \sum_{\substack{j=1 \\ j \neq 2}}^{n} b'_{1,j} N_1 N_j = 0 \\ r_i + \sum_{j=1}^{n} a_{i,j} N_j = 0, \quad i = 2, \ldots, n, \end{cases} \tag{3.11}$$

where the a's and b's are constants. We confirm, using the software package MixedVol-2.0, that the number of fixed points for this system is 2 regardless of the dimension n of the system. Hence, adding a hyperbolic functional response in one of the system's locations feeds it with an extra fixed point.

Instead, if $f_{1,2}$ is the sigmoid response (i.e., $\phi_{1,2} = N_1/(d^2 + N_1^2)$ for some constant d) then the isocline equations of Model(3.3) expressed in the form (3.9) take the following form:

$$\begin{cases} r'_1 + \sum\limits_{\substack{j=1 \\ j\neq 2}}^{n} a'_{1,j} N_j + b'_{1,2} N_1 N_2 + \sum\limits_{\substack{j=1 \\ j\neq 2}}^{n} c'_{1,j} N_1^2 N_j = 0 \\ r_i + \sum\limits_{j=1}^{n} a_{i,j} N_j = 0, \quad i = 2, \ldots, n, \end{cases} \tag{3.12}$$

where again, the r'_1, a's, b's, and c's are constants. In this case, the number of fixed points becomes 3 regardless of n. From the intuition gained from the latter two examples, we expect that if $f_{1,2}$ is the θ-sigmoid functional response (which is the more generalized version of the hyperbolic and the sigmoid responses, i.e., $\phi_{1,2} = N_1^{\theta-1}/(d^\theta + N_1^\theta)$ for some constant d and an integer $\theta \geq 1$) then the number of fixed points becomes $\theta + 1$.

We can prove the statement above by starting again with the standard form of the isocline equations shown below:

$$\begin{cases} r'_1 + \sum\limits_{\substack{j=1 \\ j\neq 2}}^{n} a'_{1,j} N_j + b'_{1,2} N_1^{\theta-1} N_2 + \sum\limits_{\substack{j=1 \\ j\neq 2}}^{n} c'_{1,j} N_1^\theta N_j = 0 \\ r_i + \sum\limits_{j=1}^{n} a_{i,j} N_j = 0, \quad i = 2, \ldots, n. \end{cases} \tag{3.13}$$

Note that the last $n-1$ equations of Eqns.(3.13) are linear equations of $N_2, N_3, \ldots, N_n$ (the $r_i + a_{i,1} N_1$ terms for $i = 1, \ldots, n$ can be moved to the RHS of the equations). Upon solving the linear system, the solutions $N_2, N_3, \ldots, N_n$ to the last $n-1$ equations of Eqns.(3.13) are linear functions of N_1. Hence, the first multivariate polynomial will simply be

$$\begin{aligned} &r'_1 + \sum_{\substack{j=1 \\ j\neq 2}}^{n} a'_{1,j} N_j + b'_{1,2} N_1^{\theta-1} N_2 + \sum_{\substack{j=1 \\ j\neq 2}}^{n} c'_{1,j} N_1^\theta N_j \\ &= r'' + a'' N_1 + b'' N_1^\theta + c'' N_1^{\theta+1} = 0. \end{aligned} \tag{3.14}$$

The degree of Eqn.(3.14) is $1+\theta$, which is also the number of fixed points in the system as there are $1+\theta$ roots for N_1, while $N_2, N_3, \ldots, N_n$ are linear functions of N_1. That is, any particular value N_1 maps to a unique tuple $(N_2, N_3, \ldots, N_n)$. Then, to increase the complexity of the system, let us assume that $f_{1,j}$ is the $\theta_{1,j}$-sigmoid response for $j = 1, \ldots, n$. For simplicity, let us assume that the linear functional response is θ-sigmoid response when $\theta = 0$. As in the latter θ-sigmoid functional response, which was present in a single location in the system, the last $n-1$ equations of the isocline equations in standard form are linear equations of $N_2, N_3, \ldots, N_n$. Upon solving these equations, each of the variables $N_2, N_3, \ldots, N_n$ is a linear function of N_1, which is a consequence of solving a linear system. From the form present in Eqns.(3.9), the degree of the first polynomial of Model (3.3), which is also the number of fixed points Θ_1, is:

$$\begin{aligned}
\Theta_1 &= \max(\deg(\Phi_{1,0}[\underline{\mathbf{N}}]), \deg(N_1\Phi_{1,1}[\underline{\mathbf{N}}]), \ldots, \deg(N_n\Phi_{1,n}[\underline{\mathbf{N}}])) \\
&= \max(\deg(\Phi_{1,0}[N_1]), \deg(N_1\Phi_{1,1}[N_1]), \ldots, \deg(N_1\Phi_{1,n}[N_1])) \\
&= \max(\deg(\phi^D_{1,1}\phi^D_{1,2}\ldots\phi^D_{1,n}), \deg(N_1\phi^U_{1,1}\phi^D_{1,2}\ldots\phi^D_{1,n}), \ldots, \deg(N_1\phi^D_{1,1}\phi^D_{1,2}\ldots\phi^U_{1,n})) \\
&= \max(\sum_{j=1}^{n}\theta_{1,j}, 1+\deg(\phi^U_{1,1}) + \sum_{\substack{1\le j\le n \\ j\neq 1}}\theta_{1,j}, \ldots, 1+\deg(\phi^U_{1,n}) + \sum_{\substack{1\le j\le n \\ j\neq n}}\theta_{1,j}) \\
&= \max(0, 1+\deg(\phi^U_{1,1}) - \theta_{1,1}, \ldots, 1+\deg(\phi^U_{1,n}) - \theta_{1,n}) + \sum_{j=1}^{n}\theta_{1,j}.
\end{aligned}$$

Note that $\underline{\mathbf{N}}$ is the vector of species' abundances. Similarly, note that for the θ-sigmoid functional response $\deg(\phi^U_{1,j}) = \theta_{1,j} - 1$ if $\theta_{1,j} \geq 1$, while $\deg(\phi^U_{1,j}) = \theta_{1,j}$ if $\theta_{1,j} = 0$. Therefore, $\max(0, 1+\deg(\phi^U_{1,1}) - \theta_{1,1}, \ldots, 1+\deg(\phi^U_{1,n}) - \theta_{1,n})$ can either be 0 or 1. The value 0 occurs if no linear functional responses are used in the first row. That is, $\theta_{1,j} \geq 1$ for $j = 1, \ldots, n$ (only hyperbolic, sigmoid or θ-sigmoid functional responses are used in the first row). Instead, if there is a linear functional response in the first row, then an additional constant 1 is added to the sum of the θ's. Here the θ's associated with linear functional responses will be zero and the value of sum of the θ's will not be affected. Hence,

$$\Theta_1 = \begin{cases} \sum_{j=1}^{n}\theta_{1,j}, & \text{if } \theta_{1,j} \geq 1 \text{ for } j = 1, \ldots, n \\ 1 + \sum_{j=1}^{n}\theta_{1,j}, & \text{otherwise.} \end{cases} \tag{3.15}$$

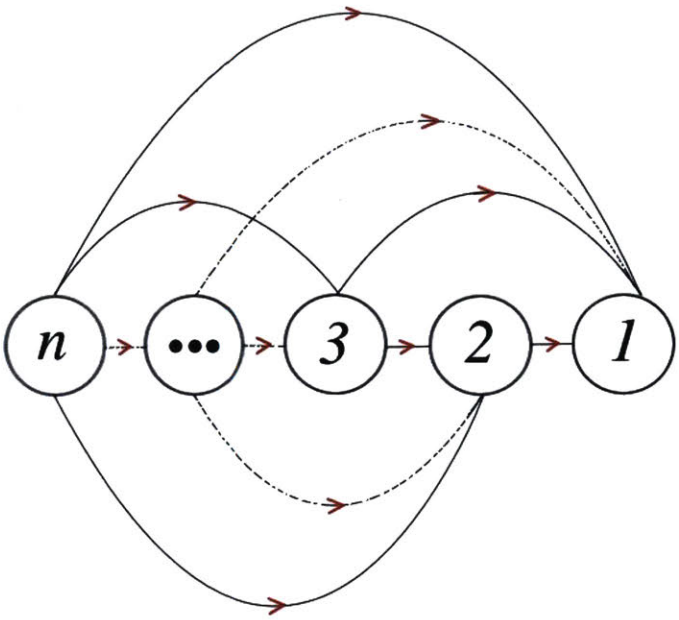

Figure 3-1: The diagram illustrates a community of n species for which species i is the predator of species $1, 2, \ldots, i-1$ and is the prey of species $i+1, i+2, \ldots, n$ for all i. The arrows in the diagram point from the predators to the prey. The dashed arrows are multiple arrows that connect to each of the species $4, 5, \ldots, n-1$, whose internal connections mimic the overall connectivity pattern shown in the figure.

Next, we move to an extreme case, when the hyperbolic response is utilized in almost all locations of Model (3.3). For an artificial example, let us assume that in an n species community, species i is the predator of species $1, 2, \ldots, i-1$ and is the prey of species $i+1, i+2, \ldots, n$ for all i. In particular, species 1 is the prey of all other species and is not a predator of any species, while species n is the predator of all other species and is not a prey of any species. The model is shown below and illustrated in Fig.(3-1).

$$\begin{cases} \dfrac{dN_1}{dt} = N_1(r_1 + a_{1,1}N_1 + a_{1,2}\dfrac{N_2}{1+c_{1,2}N_1} + a_{1,3}\dfrac{N_3}{1+c_{1,3}N_1} + \ldots + a_{1,n}\dfrac{N_n}{1+c_{1,n}N_1}) \\ \dfrac{dN_2}{dt} = N_2(r_2 + a_{2,1}\dfrac{N_1}{1+c_{1,2}N_1} + a_{2,2}N_2 + a_{2,3}\dfrac{N_3}{1+c_{2,3}N_2} + \ldots + a_{2,n}\dfrac{N_n}{1+c_{2,n}N_2}) \\ \dfrac{dN_3}{dt} = N_3(r_3 + a_{3,1}\dfrac{N_1}{1+c_{1,3}N_1} + a_{3,2}\dfrac{N_2}{1+c_{2,3}N_2} + a_{3,3}N_3 + \ldots + a_{3,n}\dfrac{N_n}{1+c_{3,n}N_3}) \\ \qquad\qquad \vdots \\ \dfrac{dN_n}{dt} = N_n(r_n + a_{n,1}\dfrac{N_1}{1+c_{1,n}N_1} + a_{n,2}\dfrac{N_2}{1+c_{2,n}N_2} + a_{n,3}\dfrac{N_3}{1+c_{3,n}N_3} + \ldots + a_{n,n}N_n). \end{cases} \tag{3.16}$$

Number of Species n	3	4	5	6	7	8	9
Number of fixed points Θ_H	13	73	501	4051	37,633	394353	4596553

Table 3.1: This table lists the number of fixed points Θ_H of Model (3.16) for hyperbolic functional responses as the dimension n of the model increases. It is clear that Θ_H increases drastically as n increases.

Note that when the isocline equations of Model (3.16) are expressed in the form of Eqns.(3.9), then $\Phi_{i,0} = 1/(\phi_{i,1}\phi_{i,2}\dots\phi_{i,n})$ for $i = 1,\dots,n$. Therefore, the formula of $\Phi_{i,j}$ is given by:

$$\begin{cases} \Phi_{i,j} = \Phi_{i,0}\phi_{i,j}, & i,j = 1,\dots,n \\ \Phi_{i,0} = \prod_{j=1}^{i-1}(1 + c_{j,i}N_j)\prod_{j=i+1}^{n}(1 + c_{i,j}N_i), & i = 1,\dots,n. \end{cases} \tag{3.17}$$

By integrating Eqns.(3.17) into the software package MixedVol-2.0, we calculate the number of fixed points of Model (3.16) for various systems (illustrated in Table (3.1))) and dimensions n. Results show clearly that Θ increases drastically with n. For example, with 3, 5, 7, and 9 species, the system has 13, 501, 37633, and 4.5 million fixed points, respectively. Note that engineering any possible conclusion is facilitated with so many fixed points in a system.

To further illustrate the effect of functional responses, let us repeat the process above and revisit Model (3.16) but this time utilizing the sigmoid functional response in all the locations where the hyperbolic one has been used. This model is shown below:

$$\begin{cases} \dfrac{dN_1}{dt} = N_1(r_1 + a_{1,1}N_1 + a_{1,2}N_2\dfrac{N_1}{d_{1,2}^2 + N_1^2} + a_{1,3}N_3\dfrac{N_1}{d_{1,3}^2 + N_1^2} + \dots + a_{1,n}N_n\dfrac{N_1}{d_{1,n}^2 + N_1^2}) \\ \dfrac{dN_2}{dt} = N_2(r_2 + a_{2,1}N_1\dfrac{N_1}{d_{1,2}^2 + N_1^2} + a_{2,2}N_2 + a_{2,3}N_3\dfrac{N_2}{d_{2,3}^2 + N_2^2} + \dots + a_{2,n}N_n\dfrac{N_2}{d_{2,n}^2 + N_2^2}) \\ \dfrac{dN_3}{dt} = N_3(r_3 + a_{3,1}N_1\dfrac{N_1}{d_{1,3}^2 + N_1^2} + a_{3,2}N_2\dfrac{N_2}{d_{2,3}^2 + N_2^2} + a_{3,3}N_3 + \dots + a_{3,n}N_n\dfrac{N_3}{d_{3,n}^2 + N_3^2}) \\ \qquad\qquad \vdots \\ \dfrac{dN_n}{dt} = N_n(r_n + a_{n,1}N_1\dfrac{N_1}{d_{1,n}^2 + N_1^2} + a_{n,2}N_2\dfrac{N_2}{d_{2,n}^2 + N_2^2} + a_{n,3}N_3\dfrac{N_3}{d_{3,n}^2 + N_3^2} + \dots + a_{n,n}N_n) \end{cases} \tag{3.18}$$

Number of Species n	3	4	5	6	7	8	9
Number of fixed points Θ_S	37	361	4,361	62,701	1,044,205	19,748,177	417,787,921

Table 3.2: This table lists the number of fixed points Θ_S of Model (3.18) for sigmoid functional responses as the dimension n of the model increases. It is clear that Θ_S increases drastically as n increases and in a much drastic form than the hyperbolic case.

Then, the formula of $\Phi_{i,j}$ for Model (3.18) can be written as:

$$\begin{cases} \Phi_{i,j} = \Phi_{i,0}\phi_{i,j}, & i,j = 1,\ldots,n \\ \Phi_{i,0} = \prod_{j=1}^{i-1}(d_{j,i}^2 + N_j^2) \prod_{j=i+1}^{n} (d_{i,j}^2 + N_i^2), & i = 1,\ldots,n. \end{cases} \tag{3.19}$$

Finally, integrating the formulas presented in Eqns. (3.19) into the software package MixedVol-2.0, we compute the number of fixed points of Model (3.18) for $n = 3,\ldots,9$. These numbers are illustrated in Table (3.2). Results show that for 3, 5, 7 and 9 species, Model (3.18) is fed with 37, >4 thousand, > 1 million, and > 417 million fixed points, respectively. Additionally, from Tables (3.1) and (3.2), we can see that

$$n^{0.5n} < \Theta_H < n^n < \Theta_S < n^{1.5n}. \tag{3.20}$$

Of course, if the θ'sigmoid functional responses are used, the increase in the number of interior fixed points will be more drastic. However, incorporating the hyperbolic and the sigmoid functional responses in ecological models increases their fixed points by a factor that depends on n^n, which is drastic compared to the classic LV model which has only 1 interior fixed point.

3.4 Functional Responses and their Implications in Multispecies Models

In the previous section, we have seen that the number of fixed points added by functional responses depends on: (i) How many places (times) functional responses are incorporated into the system. The more functional responses there are, the more fractions to add,

and the more terms added to the numerator of the resultant fraction under a common denominator. This fact can be seen clearly by Eqns. (3.15), which show that the number of fixed points that are fed by functional responses depends on the how many functional responses are there in the system. (ii) The types of functional responses. The higher the orders of the monomials in the numerators and denominators of functional responses, the more higher-order terms added to the numerator of the resultant fraction under a common denominator. This can be seen in Tables (3.1) and (3.2), which show that incorporating the sigmoid functional response feeds the system with significantly more fixed points than the hyperbolic response. (iii) Including carrying capacities, as in Eqns.(3.7), helps in feeding the system with more fixed points. Carrying capacities include an additional multiplicative term $1 - N_i/K_i$ that increases the order of the monomials in the isocline equations.

Thus, with so many fixed points fed into ecological models, what can functional responses tell us about how nature works? At this point, we can say that beyond two species (where the number of fixed points was in the range 1 to 3 in the studied models of Chapter 2), these models tell us little about how nature works if model parameters are not ecologically restricted. This is because these fixed points allow engineering any possible scenario. For instance, previous studies [21] have concluded that "combining two unstable two-dimensional systems (pest-predator and pest-pathogen) produces a stable three-dimensional system (pest-predator-pathogen)". Note that this model is a 3-species system that we have studied in this chapter, where the hyperbolic and sigmoid functional responses are used with a carrying capacity on the predator. In addition, specific model parameters are selected where the two dimensional models are unstable but with no ecological interpretation. However, knowing that the system is fed with so many fixed points, finding parameter models with no restriction to engineer a feasible and stable fixed point will not be difficult. In sum, the results that we have shown illustrate that is hard to get insights from multispecies models that incorporate functional responses as they allow to design any potential outcome.

Chapter 4

Conclusions and Future Work

4.1 Conclusions

Functional responses are considered a pillar in the field of ecology and they are mentioned in almost every major theoretical textbook in the field. The reason why functional responses have been incorporated in ecological models is to add realism or mechanistic understanding into ecological models. Previous studies have shown that models with functional responses can successfully mimic some of the dynamics of many 2-species systems. However, there has been little understanding about the effects of functional responses on these models. That is, it remains unclear whether the perceived benefits of adding functional responses are simply mathematical artefacts or not, especially in multispecies systems. Yet, it is necessary to fully understand the effect of functional responses on ecological models as it is directly linked to their explanatory power of ecological dynamics.

To address the problem above, in this thesis we have studied the number of fixed points, an important quantity of dynamical systems. We have introduced, for the first time, a methodology to count the number of interior fixed points present in a dynamical system with functional responses. We have shown that this number is linked to the capacity of a model to fit data and to the model's sensitivity to perturbation in its parameters. In particular, for 2-species models, we have uncoupled the 2-variable isocline equations (after some manipulations) into two separate single variable equations and examined them. We have shown that the order of these uncoupled polynomials is actually the number of interior fixed points of the original system. Furthermore, we have examined the effect of

functional responses in multispecies models. Due to the difficulty in uncoupling multivariate polynomial equations, we have computed the mixed volume (number of interior fixed points) of the system's isocline equations (after some manipulation) via the software package MixedVol-2.0. We have demonstrated that the number of interior fixed points increase in an multispecies model depending on: (i) how many nonlinear functional responses are present in the system, (ii) the type of the used functional responses (i.e., order of numerator and denominator of the functional responses), and (iii) whether carrying capacities are utilized in the model or not. Overall, these results have revealed that functional responses feed a dynamical multispecies model with many interior fixed points, which in turn can be engineered to reach any type of behavior. Hence, we conclude that the explanatory power of multispecies models with functional responses is drastically reduced if model parameters are not ecologically restricted.

The results above have also suggested that one should pay careful attention when selecting the number and type of functional responses for a model. This is due to the fact that the choice of the functional response can lead to models (such as the Logistic Predation model in 2-species communities) that violate basic ecological principles (e.g., predators and prey can coexist when the predators are starving and not attacking the prey). Also, our work has revealed that we should always consider parameter constraints on these models. This is because with so many fixed points in a system, the capacity of the model to fit any type of data increases. That is, beyond 2-species systems (where the number of fixed points was in the range 1 to 3 in the models studied in Chapter 2), multispecies models tell us little about how nature works if model parameters are not ecologically restricted. Note that these parameters can be obtained from field/lab experiments, or may rely on allometric and metabolic properties [31, 32]. Overall, we believe this work has shed new light onto the applicability of functional responses and opened a new dialogue of what constitutes a realistic model.

4.2 Future Work

In this work, we have discussed functional responses and show their potential link to LV models with higher-order interactions. For example, in a 3-species system, for which we know that the pair of species 1 and 2 and the pair 2 and 3 are interacting (the pair of

species 1 and 3 are not directly interacting), higher-order interaction models include the unseen effects of species 1 and 3 via the addition of higher-order polynomial terms into the model. Hence, it may be inferred that functional responses and higher-order interactions share common characteristics that can reveal more information about their effects and are worth investigating in future work.

While we have investigated in great deal the interior fixed points of models with functional responses, this work has not been an exhaustive exposition. There is still more room for rigour in the mathematical analysis of functional responses and their number and properties of interior fixed points. For example, we have used the MixedVol-2.0 package without a deep understanding of algebraic geometry. Yet, we believe that with a better understanding, it can be possible to derive exact mathematical expressions for the number of fixed points that exist in a system. Therefore, we foresee a promising avenue by bridging ecology with algebraic geometry in future work. Finally, there are several examples outside ecology, such as in fluid mechanics and structural mechanics, where by introducing randomness and stochasticity in a model it is possible to stabilize a system. In fact, it can be speculated that stochasticity feeds a dynamical model with many fixed points that are marginally stable. Hence, future work can also investigate the effect of stochasticity in ecological models following part of the methology proposed in this thesis. This future work can allow us to increase our understanding of the actual mechanisms operating in ecological systems.

Bibliography

[1] Peter Turchin. *Complex Population Dynamics: A Theoretical/Empirical Synthesis.* Princeton University Press, 2003.

[2] C Manuel Jr. *Ecology: concepts and applications.* 2008.

[3] Uwe C Täuber. Population oscillations in spatial stochastic lotka-volterra models: a field-theoretic perturbational analysis. *Journal of Physics A: Mathematical and Theoretical*, 45(40):405002, 2012.

[4] Alfred J. Lotka. Analytical note on certain rhythmic relations in organic systems. *Proceedings of the National Academy of Sciences*, 6:410–415, 1920.

[5] V. Volterra and M. Brelot. *Leçons sur la théorie mathématique de la lutte pour la vie.* Cahiers scientifiques. Gauthier-Villars, 1931.

[6] T. J. Case. *An Illustrated Guide to Theoretical Ecology.* Oxford Univ. Press, Oxford, 2000.

[7] Babak Momeni, Li Xie, and Wenying Shou. Lotka-volterra pairwise modeling fails to capture diverse pairwise microbial interactions. *eLife*, 6:e25051, 2017.

[8] C. S. Holling. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91(7):385–398, 1959.

[9] Yaghoub Fathipour and Bahador Maleknia. Mite predators. In *Ecofriendly pest management for food security*, pages 329–366. Elsevier, 2016.

[10] Rui Xu, Lansun Chen, and MAJ Chaplain. Persistence and global stability in a delayed predator-prey system with holling-type functional response. *The ANZIAM Journal*, 46(1):121–141, 2004.

[11] C. S. Holling. The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. *The Canadian Entomologist*, 91:293â320, 1959.

[12] Patrick H Leslie. Some further notes on the use of matrices in population mathematics. *Biometrika*, 35:213–245, 1948.

[13] Michael L Rosenzweig and Robert H MacArthur. Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist*, 97(895):209–223, 1963.

[14] AD Bazykin. Sistema volterra i uravnenie mihaelisa–menten. voprosy matematicheskoy genetiki, 1974.

[15] Robert McCredie May. *Stability and complexity in model ecosystems*, volume 6. Princeton university press, 2001.

[16] Donald Lee DeAngelis, RA Goldstein, and RV O'neill. A model for tropic interaction. *Ecology*, 56(4):881–892, 1975.

[17] Donald Ludwig, Dixon D Jones, and Crawford S Holling. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. *The Journal of Animal Ecology*, pages 315–332, 1978.

[18] Peter Yodzis. *Introduction to theoretical ecology.* Harpercollins College Div, 1989.

[19] LL Eberhardt. Is wolf predation ratio-dependent? *Canadian Journal of Zoology*, 75(11):1940–1944, 1997.

[20] Peter Turchin and George O Batzli. Availability of food and the population dynamics of arvicoline rodents. *Ecology*, 82(6):1521–1534, 2001.

[21] Theresa Wei Ying Ong and John H Vandermeer. Coupling unstable agents in biological control. *Nature communications*, 6:5991, 2015.

[22] Josef Hofbauer and Karl Sigmund. *Evolutionary games and population dynamics.* Cambridge university press, 1998.

[23] Peter F Stadler and Robert Happel. The probability of permanence. *Mathematical biosciences*, 113(1):25–50, 1993.

[24] Yasuhiro Takeuchi. *Global dynamical properties of Lotka-Volterra systems.* World Scientific, Danvers, 1996.

[25] Steven H. Strogatz. *Nonlinear dynamics and chaos : with applications to physics, biology, chemistry, and engineering.* Westview Press, Boulder, 2015.

[26] Lloyd N Trefethen and David Bau III. *Numerical linear algebra*, volume 50. Siam, 1997.

[27] R. Thom. *Stabilité structurelle et morphogenèse.* InterÉditions, Paris, 1972.

[28] Tomohiko Mizutani and Akiko Takeda. Demics: A software package for computing the mixed volume via dynamic enumeration of all mixed cells. pages 59–79. Springer, 2008.

[29] T. L. Lee and T. Y. Li. Mixed volume computation in solving polynomial systems. *Contemporary Mathematics*, 556:97–112, 2011.

[30] Tangan Gao, T. Y. Li, and Mengnien Wu. Algorithm 846: Mixedvol: A software package for mixed-volume computation. *ACM Trans. Math. Softw.*, 31:555–560, 2005.

[31] P. Yodzis and S. Innes. Body size and consumer-resource dynamics. *The American Naturalist*, pages 1151–1175, 1992.

[32] J. H. Brown, J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. Body size and consumer-resource dynamics. *Ecology*, pages 1771–1789, 2004.