

# On Equilibria and Feasibility of Ecological Polynomial Dynamical Systems

by

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## Abstract

Explaining and predicting the behavior of ecological systems has been one of the greatest challenges in ecology. One promising route to accomplish this challenge has been based on the mathematical modeling of species abundances over time. However, finding a compromise between tractability and realism has not been easy. Functional responses in 2-species models and higher-order interactions in 3-species systems have been proposed to reconcile part of this compromise. However, it remains unclear whether this compromise can be fulfilled and extended to multispecies models. Yet, answering this question is necessary in order to differentiate whether the explanatory power of a model comes from the general form of its polynomial or from a more realistic description of multispecies systems. Nevertheless, extracting the set of conditions compatible with feasibility (i.e, the necessary conditions for coexistence or of species, stability and permanence), even at the 2-species level, remains a big mathematical challenge. Currently, there is no methodology that can provide us with a full analytical understanding about feasibility for any given model.

Here, we develop a general method to quantify the mathematical consequences of adding higher-order terms in ecological models based on the number of *free-equilibrium* points that can emerge in a system (i.e., equilibria that can be feasible or unfeasible as a function of model parameters). We characterize complexity by the number of free-equilibrium points generated by a model, which is a function of the polynomial degree and system's dimension. We show that the probability of generating a feasible system in a model is an increasing function of its complexity, regardless of the specific mechanism invoked. Our results reveal that conclusions regarding the relevance of mechanisms embedded in complex models must be evaluated in relation to the expected explanatory power of their polynomial forms. Then, we propose a general formalism to analytically obtain feasibility conditions for any population dynamics model of any dimension. From our methodology, we establish mathematically how two or more model parameters are linked—a task that is impossible to perform with simulations. By showing how feasibility can be studied as a function of a given model, we establish the partial conditions for species coexistence, moving us a step closer to the goal of systematically understanding the behavior of ecological systems.

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# Chapter 1

## Introduction

### 1.1 Motivations and Overview

One of the long-standing questions in ecology is how can we know whether an observed set of species (e.g., bacteria, plant, insect, or mammal species) in a given place (e.g., human host, natural habitat) will coexist with one another across a period of time [1, 2]. The difficulty in answering this question resides in knowing the exact equations governing the dynamics of ecological systems, together with the high uncertainty regarding the initial conditions, parameter values, intrinsic randomness, and more importantly, how the changing external conditions (such as biotic and abiotic factors) will affect the dynamics [3–7]. This complexity of multidimensional and changing factors has typically taken both theoretical and empirical studies to choose between understanding and predicting species coexistence [8, 9].

Theoretical and empirical ecological studies are pushing community ecology into a more descriptive science. In doing so, modelling changes in species abundances over time has become common practice. With minimal assumptions (i.e., no spatial variety), these models yields a system of coupled ordinary differential or difference equations [10–12]. In essence, these equations connect the changes in a species abundance with its overall growth rate (i.e., difference between its growth and mortality rates). These rates, which are functions of the species intrinsic growth rate as well as its interaction with the other species in the community (i.e., its environment), are not uniquely defined. However, they are chosen to provide tractability (simplicity) and preserve realism (complexity) [11]. Indeed, finding a

compromise between tractability and realism has not been easy [13, 14].

It has been debated whether difference (i.e, discrete) or differential (i.e, continuous) models should be adapted in ecological studies [11, 15]. For instance, in the presence of a single species (or in the absence of species interactions), the simplest ordinary differential equation that has been used to model its abundance is the logistic model, whose solution (i.e., the sigmoid function) is available in closed form [16]. Note, however, that there is no general solution available for the logistic map, which is the discrete analogue of the logistic model [15]. Moreover, chaos is observed in the univariate discrete map, unlike its continuous analogue where chaos is observed in three dimensions and higher [17]. Due to the apparent high dynamical and mathematical complexity of ecological difference equations at the univariate level, continuous models have become more popular. As a result, extensive analytical work with continuous models has been done with two-species systems and numerical work has been primarily conducted study species coexistence, food-webs and species invasion with multispecies [18–29].

One of the simplest multispecies systems is the Lotka-Volterra (LV) model [18, 30]. In LV, the per-capita increase in species abundance is a linear function of all the species in the ecological system. The LV model has been known for its good predictive and forecasting capacities; however, it is an approximate model that cannot encapsulate all the complexities of an ecological system [12, 31–33]. Since the exact equations that govern the dynamics of ecological systems are unknown, researchers have been modifying the LV model to include higher-order terms in the hope of increasing realism (i.e., mimicking the observed data as close as possible). As a result, the linear functions in LV models are replaced by polynomial functions (i.e., higher-order terms) or polynomial fractions. Hence, polynomial systems appear almost everywhere in the theoretical ecology literature. They almost certainly take the form  $dN_i/dt = N_i f_i(\mathbf{N})/q_i(\mathbf{N})$ , where the  $f$ 's and the  $q$ 's are polynomials in species abundances  $\mathbf{N} = (N_1, N_2, \dots, N_n)^T$ . However, these models have been extensively utilized blindly and treated as black boxes without any deep understanding on their behavior. Recent studies have mistakenly perceived that mathematically there is nothing to prevent the inclusion of higher-order terms in ecological models [34].

Two of the simplest polynomial replacements or ecological concepts used to modify the LV model is the introduction of functional responses in 2-species models [11, 35] and higher-order interactions (HOIs) in 3-species systems [36]. Functional responses, which correspond



to the number of prey attacked, killed, and consumed per predator, enter the LV equations as polynomial fractions. These responses appear extensively in predator-prey models and food-webs, especially after Holling introduced three types of functional responses, which were successful in reproducing some of the dynamics of many 2-species systems [35]. On the other hand, HOIs correspond to the "unseen" effect of one species on the others. That is, the effect of species A on the per capita growth rate of species B might itself depend on the abundance of a third species C. These effects are typically translated as addition of higher-order terms in 3-species LV models [10, 37–40]. However, it remains unclear whether this compromise can be extended to multispecies models. Yet, answering this question is necessary in order to differentiate whether the explanatory power of a model comes from the general form of its polynomial or from a more realistic description of multispecies systems. In fact, even at the level of two-species systems, we do not have enough mathematical tools to fully analyze dynamical systems of the form mentioned earlier as closed form solutions. Therefore, research programs have been mainly focused on solving numerically dynamical systems. However, conclusions derived from this numerical work are typically specific of the input parameters (since it is generally impossible to simulate every possible scenario).

The main objective of this thesis is to build a general unifying framework to study analytically systems of the form  $dN_i/dt = N_i f_i(\mathbf{N})/q_i(\mathbf{N})$  for any dimension and level of complexity. In particular, this thesis will be focused on understanding the existence of feasible solutions, which we defined as the existence of steady state abundances whose components are all real and positive (ecologically, feasibility implies that all species abundances at equilibrium are positive). Importantly, feasibility is a necessary condition for species coexistence in equilibrium dynamics, persistence, and permanence in dynamical models of the form mentioned above. In fact, it has been proven that this type of models cannot even have bounded orbits in the feasibility domain without a feasible equilibrium point [41]. While analytic solutions for feasibility are known for simple 2-species systems, it has been unclear how to perform the same analysis for models with higher complexity. Thus, this thesis aims to contribute to the ecological literature by unlocking necessary mathematical tools to study natural ecological systems.

## 1.2 Thesis Outline

In this thesis, Chapter 2 examines the effects of adding higher-order terms in ecological models. In particular, it examines the effect of multiple-equilibrium points on a model's capacity to change its behaviour. We show that adding a single free-equilibrium point to a 2-species system, one can more easily move from feasible to unfeasible solutions, and vice versa, compared to the LV model. Then, we introduce a general method, based on Bernshtein's theorem, to count the number of free-equilibrium points of unrestricted polynomial dynamical systems. Then, we provide a formal mathematical proof based on Bernshtein's theorem to show that the number of free-equilibrium points in LV models with HOIs increases exponentially with the dimension of the system. Finally, we discuss how HOIs, not only increase the complexity of a model, but also its capacity to fit any empirical data, calling for a methodology to properly compare the explanatory capacity of an ecological model outside of its polynomial form. This will be answered in Chapter 3.

Chapter 3 examines and quantifies the effects of adding complexity into ecological models as a function of their polynomial form. The chapter expands on the models examined in Chapter 2, and characterizes the complexity of a model by the number of free-equilibrium points (equilibrium points whose feasibility depend on parameter values) generated by it, which is a function of the polynomial degree and system's dimension. First, using a 1-dimensional model, we show that its probability of feasibility increases as a function of its polynomial degree when parameter values are arbitrarily chosen from a given probability distribution. Next, we extend the univariate example into a multidimensional case to show that the probability of generating a feasible multispecies system is an increasing function of its complexity. Then, we study modifications to the linear LV model using HOIs and also functional responses where parameters are restricted. Finally, we discuss how the probability of feasibility can be used as a null model to assess the explanatory contribution to feasibility of complex ecological models. This probability analysis is numerical and in the next chapter we provide a general methodology to move to an analytic understanding.

In Chapter 4, we propose a general framework that can find the feasibility conditions of any model in any dimensions without the need to solve for the equilibrium locations. We start the chapter with a methodology that finds the feasibility conditions of a univariate system, 2-species systems, and multispecies systems. There are differences in such cases and we will

provide examples in each case to demonstrate the methodology and show that the obtained feasibility conditions are accurate. Also, the chapter includes application examples where we apply the methodology on the simplest ecological models that are impossible to solve for the location of equilibrium points analytically. The first example is a 2-species LV model with type II functional responses while the second example is a 3-species LV system with higher-order interactions. Specifically, we show how to find the range of parameters that are compatible with feasibility. Finally, we discuss advantages of our work and limitations of our formalism.

In Chapter 5, we summarize the thesis's findings in the conclusion section and discuss future avenues of research derived from our study. More specifically, we discuss how future work can focus on finding necessary and sufficient conditions for stability and permanence for LV models and to general polynomial ecological systems. This is important as these two conditions are not known, but represent the necessary and sufficient conditions for species coexistence. Lastly, we close the thesis by discussing the use of non-polynomial ecological systems, how to characterize their complexities, and how to compare fairly between two non-polynomial models. This last part has the aim of finding potential extensions of our work to any type of ecological model without restrictions.



# Chapter 2

## Adding Higher-Order Terms in Ecological Models

### 2.1 Introduction

Lotka-Volterra (LV) models [18, 30] have provided fundamental insights about ecological systems for almost a century [10]. Yet, it is known that LV models are parsimonious approximations [12, 31] and do not capture all the complexities arising from the dynamics of ecological systems under investigation [32, 33]. Many times, the prediction errors of LV models have been attributed to the existence of higher-order interactions (HOI) [42]. More broadly, HOIs can be seen as the “unseen” influences of one species on the others. That is, the effect of species A on the per capita growth rate of species B might itself depend on the abundance of a third species C due to either compensatory effects, supra-additivity, trait-mediated effects, functional effects, meta-community effects, or indirect effects [10, 37–40]. Therefore, HOIs have been typically translated as addition or modifications of higher-order terms in existing population dynamics models [36].

It has been shown that HOIs can stabilize dynamics in competition systems [43], promote diversity in ecological communities [44], capture unexplained complexity of LV models [45, 46], and dominate the functional landscape of microbial communities [47] (but it has been shown that HOIs play a non-significant role in predicting protozoan populations, [48]). While it is known that these perceived benefits come from an increasing number of alternative solutions given by the nature of multivariate polynomials [49], this math-

ematical “advantage” has not been formally quantified. In fact, it has been perceived that mathematically there is nothing to prevent the inclusion of higher-order terms in ecological models [34]. Yet, this formal quantification is important in order to increase our understanding about how to best investigate the role of higher-order interactions (and higher-order terms, in general) in shaping ecological dynamics.

In general, it is expected that adding HOIs into population dynamics models, the number of both solutions and parameters increases, introducing more complex dynamics and facilitating the capacity of the model to fit experimental data or empirical observations. While studies have been statistically penalizing for this increase [46, 50], it is still unclear whether the number of parameters is the main factor controlling the degrees of freedom of ecological models. For example, the existence of feasible equilibrium solutions is a crucial condition in the context of species coexistence in ecological dynamics of the form  $dN_i/dt = N_i f_i(\mathbf{N})/q_i(\mathbf{N})$  (i.e., a necessary condition for persistence, permanence, and the existence of bounded orbits in the feasibility domain, see [41, 51, 52]). Yet, two dynamical models with the same number of parameters can have different numbers of free-equilibrium points (i.e., solutions that can be either feasible or unfeasible as a function of model parameters). Note that it is possible to predict either species coexistence or non-coexistence by having free-equilibrium points that can turn into feasible or unfeasible solutions, respectively. In the classic LV model, there is only one free-equilibrium point regardless of the dimension of the system [53]. However, it is unclear exactly how much HOIs can increase the number of free-equilibrium points and multiply the ways of reaching any ecological dynamics, which standard statistical methods cannot penalize for [54, 55]. In other words, is the explanatory power of HOIs a mathematical construct that comes from feeding more free-equilibrium points into ecological models?

To answer the question above, first we investigate the effect of multiple free-equilibrium points on the capacity to alter the behavior of ecological systems. Specifically, we illustrate this effect through a simple example, which shows that by adding a single free-equilibrium point to a 2-species system, one can more easily move from feasible to unfeasible solutions compared to the LV model. Then, we introduce a general method, based on Bernshtein’s theorem [56], to formally count the number of free-equilibrium points of polynomial dynamical systems. Then, we apply this method to show that the number of free-equilibrium points in LV models with HOIs increases exponentially with the dimension of the system.

Finally, we discuss the implications of our findings in the context of fitting HOIs to empirical data, comparing the explanatory power of ecological models, and the use of higher-order terms in general.

## 2.2 Understanding the Effects of HOIs

To understand the effects of adding HOIs on the dynamics of ecological systems, we considered the simplest possible LV model with HOI terms. This model involves the classic 2-species LV system with an additional non-additive interaction term per capita  $N_1N_2$ :

$$\begin{cases} \frac{dN_1}{dt} = N_1(r_1 + a_{11}N_1 + a_{12}N_2 + b_1N_1N_2) \\ \frac{dN_2}{dt} = N_2(r_2 + a_{21}N_1 + a_{22}N_2 + b_2N_1N_2), \end{cases} \quad (2.1)$$

where  $N_i$  and  $r_i$  correspond to the abundance (biomass) and maximum per capita growth rate of species  $i$ , respectively. Additionally,  $a_{ii}$  corresponds to self-regulation terms,  $a_{ij}$  corresponds to interspecific terms, and  $b_i$  corresponds to HOI terms.

In general, it is known that the equilibrium points of a system like Eqn. (2.1) are given by the intersection points of the systems' isoclines, which are obtained by setting the time-derivatives to zero [12]. We can classify these equilibrium points into either *rigid* or *free*. We defined rigid-equilibrium points to be the ones restricted to particular subsurfaces of the space regardless of the values that the model parameters can take. Hence, there is less flexibility in terms of controlling their locations in space. For example, in the classic 2-species LV model (without HOI terms, i.e.,  $b_1 = b_2 = 0$  in Eqn. (2.1), no matter how we change the model parameters, one equilibrium point will be always at the origin, while two equilibrium points will lie always along each of the axes. Thus, in the LV model, rigid-equilibrium points can be defined as the ones which contain at least one zero coordinate (i.e., boundary-equilibrium points). On the other hand, we defined free-equilibrium points as the ones whose locations are not restricted in space and are completely dependent on model parameters. As mentioned before, it has already been proved that LV models without HOI terms have one single free-equilibrium point [53].

While previous studies [57–59] have focused on estimating numerically the total number of equilibrium points (i.e., without separating rigid- from free-equilibrium points), only free-

equilibrium points dictate the dynamics of a feasible system [60]. As we mentioned before, the existence of a feasible solution is a necessary condition for persistence and permanence in dynamical models of the form  $dN_i/dt = N_i f_i(\mathbf{N})/q_i(\mathbf{N})$  [41, 51]. Similarly, it has been proved that this type of models cannot have bounded orbits in the feasibility domain without a feasible free-equilibrium point [41]. In fact, due to the non-revival property of such models [53], the rigid-equilibrium points are the free-equilibrium points of the same model after substituting the corresponding zero abundances (of the species that die out) and deleting the equations which involve their time derivatives (as they will be zero as well). Therefore, for the purposes of this work, we will focus on the free-equilibrium points of LV models. Yet, for the interested reader, we have derived an analytic formula that depends solely on the number of free-equilibrium points to count the total number of equilibrium points in a LV model with or without HOI terms (see Chapter 2.6).

To obtain the free-equilibrium point(s) of a system and its (their) effect on the dynamics of a system, we need to obtain the *free*-isocline equations, which are the classic isocline equations but considering that no state variable can take a value of zero. For example, the free-isocline equations for System (2.1) read:

$$\begin{cases} r_1 + a_{11}N_1^* + a_{12}N_2^* + b_1N_1^*N_2^* = 0 \\ r_2 + a_{21}N_1^* + a_{22}N_2^* + b_2N_1^*N_2^* = 0, \end{cases} \quad (2.2)$$

where  $N_1^*$  and  $N_2^*$  are the steady-state abundances. Then, to provide the number of free-equilibrium points for this system, we can rewrite Eqns. (2.2) such that each equation is expressed in terms of a single state variable:

$$\begin{cases} (a_{11}b_2 - a_{21}b_1)N_1^{*2} + (r_1b_2 - r_2b_1 + a_{22}a_{11} - a_{21}a_{12})N_1^* + (r_1a_{22} - r_2a_{12}) = 0 \\ (a_{12}b_2 - a_{22}b_1)N_2^{*2} + (r_1b_2 - r_2b_1 - a_{22}a_{11} + a_{21}a_{12})N_2^* + (r_1a_{21} - r_2a_{11}) = 0. \end{cases} \quad (2.3)$$

The uncoupled Eqns. (2.3) can be solved independently via the quadratic formula. We denote the solutions of the first and second equations by  $N_1^{*\pm}$  and by  $N_2^{*\pm}$  respectively. Note that  $N_i^{*\pm}$  are the solutions to the quadratic equation where the sign of the square-root of the determinant is positive and negative, respectively. It is easy to check that  $(N_1^{*+}, N_2^{*-})$  and  $(N_1^{*-}, N_2^{*+})$  are the solutions to Eqns. (2.2). Therefore, necessary and sufficient



conditions for feasibility will be satisfied as long as either  $(N_1^{*+}, N_2^{*-})$  or  $(N_1^{*-}, N_2^{*+})$  is feasible. While closed form solutions of systems with more than two free-equilibrium points are not known, already the solutions expressed in Eqn. (2.3) reveal that System (2.1) has 2 free-equilibrium points.

Note that if  $b_1 = b_2 = 0$ , the two separate solutions  $(N_1^{*+}, N_2^{*-})$  and  $(N_1^{*-}, N_2^{*+})$  collapse into a single one (i.e.,  $N_1^*, N_2^*$ ). Under this condition (i.e., the classic 2-species LV model without HOI terms), species will coexist when the only free-equilibrium point is both feasible (i.e., positive) and stable [61]. However, if  $b_1$  and  $b_2$  are not zeros, species coexistence will be attained when at least one free-equilibrium point (out of the 2) is feasible and keeps the trajectory of the initial condition close to it at all times. Note that the characteristic equation of Eqns. (2.2) can be written as  $\lambda^2 - \text{tr}(\mathbf{J})\lambda + \det(\mathbf{J}) = 0$ , where  $\mathbf{J} = [\frac{\partial^2 N_i}{\partial t \partial N_j}]$ . Thus, for any 2-dimensional system, the necessary and sufficient conditions for an equilibrium point to be asymptotically stable are  $\text{tr}(\mathbf{J}) < 0$  and  $\det(\mathbf{J}) > 0$  [12]. These conditions are, in fact, incorporated into the feasibility conditions, resulting in two sets of conditions that at least one needs to be fulfilled. That is, the existence of the second free-equilibrium point gives an additional opportunity to have a feasible system, and potentially stable if no parameter restrictions are imposed a priori. Of course, the answer to the question of which of the two free-equilibrium points will be stable completely depends on the choice of model parameters.

Because of the additional conditions that are introduced via extra free-equilibrium points, one may be tempted to conclude that HOI terms do promote species coexistence (feasible and stable solutions). However, it is easy to show that the conditions to achieve non-coexistence (unfeasible or unstable solutions) also increase by adding HOIs. For instance, apart from changing the species abundances in the real domain, we can impose that any one of the following quantities  $N_1^{*+}, N_1^{*-}, N_2^{*+}$ , or  $N_2^{*-}$  has an imaginary component, making both solutions  $(N_1^{*+}, N_2^{*-})$  and  $(N_1^{*-}, N_2^{*+})$  to be outside of the feasibility domain (due to the quadratic formulation of the uncoupled Eqns. (2.3)—imposing  $N_1^{*+}$  to have an imaginary component implies that its complex conjugate in the other solution tuple  $N_1^{*-}$  has an imaginary component as well. Note that reaching imaginary steady-state abundances from real model parameters is impossible to attain in the classic LV model without HOIs [53]. Therefore, HOIs increase the capacity of the system to reach either coexistence or non-coexistence (given that the imaginary domain for abundances has become accessible).

However, the exact number and identity of the potential locally stable points fully depend on the model selected: order of the HOI terms, number of species, and the parameter space under consideration. Note that this choice is typically associated with the specific research question. For example, if parameters are restricted in a region that yields no feasible free-equilibrium points, coexistence is impossible. If one restricts model parameters in a LV model with HOIs to have exactly one feasible free-equilibrium point, the model will be topologically equivalent to a classic LV model [62]. Similarly, by considering other sets of model parameters, competitive exclusion or coexistence can be made more or less likely. Therefore, whether the addition of HOIs makes competitive exclusion or co-existence more likely is all dependent on the choice of model parameters.

Finally, it is important to notice that the overall flexibility gained by adding extra HOI terms can further increase depending on the model. For example, by adding quadratic terms per capita (i.e.,  $N_1^2$  and  $N_2^2$ ) to Eqn. (2.1), it can be shown that the system will have 4 free-equilibrium points and 4 sets of separate solution tuples, from which at least one of them has to change to reach coexistence (or non-coexistence). That is, HOIs can increase the number of free-equilibrium points, and in turn, increase the flexibility of the system to reach any possible dynamics. In the context of fitting data into models [46], while the free-equilibrium points can be feasible or unfeasible, without parameter constraints the equilibrium points can always yield feasible solutions. For example, in the analysis of time-dependent quantities (such as species abundances), the most typical approach is to use the initial time points as the initial conditions to fit the dynamics of a system. Unfortunately, this initialization already biases the solution [63], which is relatively easier to achieve with higher-order terms. Therefore, the number of free-equilibrium points is a measure of how easy it is to fit data to a dynamical model (which is not necessarily linked to the number of parameters or species), but not necessarily about the ecological mechanisms of a system. This is a key problem we turn our attention in the next section.

## 2.3 Quantifying the Effects of HOIs

To introduce a general methodology to quantify the number of free-equilibrium points in ecological models, we used a generic system of polynomial dynamical equations for  $n$  species of the form:

$$\left\{ \begin{array}{l} \frac{dN_1}{dt} = \frac{N_1 f_1(N_1, \dots, N_n)}{q_1(N_1, \dots, N_n)} \\ \vdots \\ \frac{dN_n}{dt} = \frac{N_n f_n(N_1, \dots, N_n)}{q_n(N_1, \dots, N_n)}, \end{array} \right. \quad (2.4)$$

where  $f_1, f_2, \dots, f_n$  and  $q_1, q_2, \dots, q_n$  are multivariate polynomials in species abundances. As mentioned in the previous section, to find the free-equilibrium points of System (2.4), we can set all time-derivatives to zero in order to obtain a system of multivariate polynomials in steady-state abundances  $N_1^*, \dots, N_n^*$  as follows

$$\left\{ \begin{array}{l} f_1(N_1^*, \dots, N_n^*) = 0 \\ \vdots \\ f_n(N_1^*, \dots, N_n^*) = 0. \end{array} \right. \quad (2.5)$$

The number of free-equilibrium points of System (2.4) is given by the number of non-zero roots of System (2.5). While it is not a trivial problem, the number of non-zero roots can be calculated based on Bernshtein's theorem [56]: Let us assume that the polynomial System (2.5) has finitely many roots in  $(C^*)^n$ . Then the number of these roots is bounded from above by the mixed volume of its Newton polytopes  $P_k$ ,  $1 \leq k \leq n$ . The upper bound of the number of non-zero roots is tight and achieved (exactly) for any generic choice of coefficients inside the polynomials  $f_1, f_2, \dots, f_n$  (note that in the LV model, when the vector of growth rates is not in the column space of the interaction matrix, there will be no solution and we can neglect such special cases). Therefore, Bernshtein's theorem is the multivariate extension to the fact that a single variable polynomial of degree  $n$  will have  $n$ -complex roots for any generic coefficients.

To illustrate the quantification of non-zero roots of a polynomial system based on Bernshtein's theorem, we show the details of how to compute Newton's polytopes, the mixed volumes, and the evaluation of the number of complex roots using the following hypothetical system of equations (free-isoclines):

$$\left\{ \begin{array}{l} f_1(N_1^*, N_2^*) = 9N_1^* - 3N_1^*N_2^* + 9N_1^{*2} + 2N_2^{*2} \\ f_2(N_1^*, N_2^*) = 8 + 2N_1^* - 9N_1^*N_2^*. \end{array} \right. \quad (2.6)$$

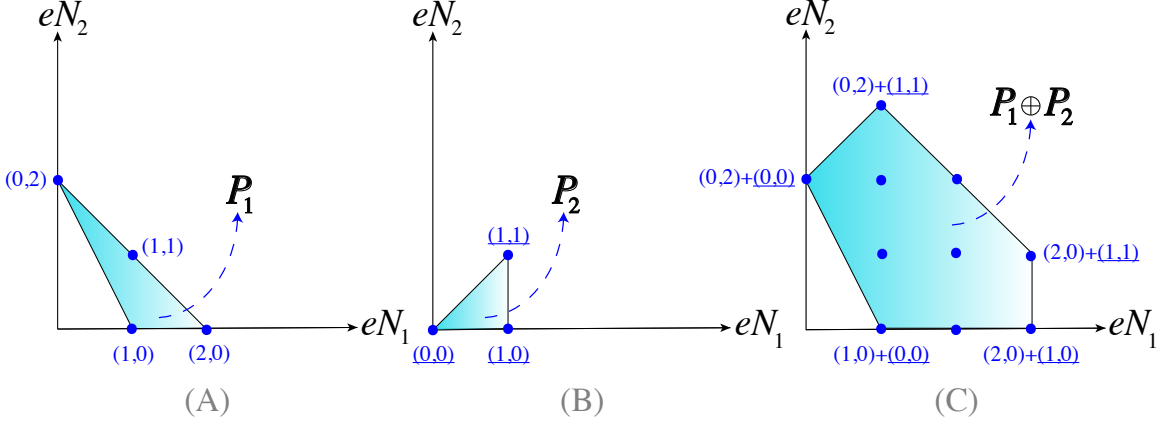


Figure 2-1: Illustration of the quantification of the number of complex roots of a polynomial system. For the hypothetical 2-species system defined by the set of Eqns. (2.6), the figure illustrates the construction of the mixed volume of Newton polytopes  $P_i$  of  $f_i$  for  $i = 1, 2$ . Panels (A) and (B) represent the Newton polytopes  $P_1$  and  $P_2$ , respectively. Note that the coordinates (blue symbols) correspond to the different supports. Panel (C) represents the Minkowski sum of the first and second polytopes  $P_1 \oplus P_2$ . Note that the mixed volume (number of complex roots) of this system is defined by  $M(P_1, P_2) = \text{vol}_2(P_1 \oplus P_2) - \text{vol}_2(P_1) - \text{vol}_2(P_2)$ . The axes are the exponents of the supports' monomials.

To compute the number of complex roots from Eqns. (2.6), we need to follow four basic concepts in algebraic geometry [64]. For  $i = 1, 2$ :

1. We need to obtain the support  $S_i$  of  $f_i$ , which is defined as the set of exponents of its monomials  $eN_i$ 's. In System (2.6), the support  $S_1$  of  $f_1$  contains the points  $(eN_1, eN_2)$  in the set  $\{(1,0), (1,1), (2,0), (0,2)\}$ ; while the support  $S_2$  of  $f_2$  contains the points  $(eN_1, eN_2)$  in the set  $\{(0,0), (1,0), (1,1)\}$ .
2. We need to obtain the Newton polytope  $P_i$  of  $f_i$ , which is defined as the convex hull of the support  $S_i$ . Fig. 1 (Panels A and B, respectively) shows the Newton polytopes  $P_1$  and  $P_2$  of System (2.6).
3. We need to perform the Minkowski sum  $P_i \oplus P_j = \{p_i + p_j | p_i \in P_i \text{ and } p_j \in P_j\}$  for  $j > i$ , which is defined as the convex hull of all possible summations of the supports  $S_i$  and  $S_j$ . Fig. 1 (Panel C) shows  $P_1 \oplus P_2$  of System (2.6).
4. We need to obtain the mixed volume of the Newton polytopes  $M(P_1, P_2)$ , which is defined as the difference in area between  $P_1 \oplus P_2$  and the sum of the areas of  $P_1$  and  $P_2$ . The mixed volume corresponds to the exact number of roots that a multivariate polynomial system has. In System (2.6), the number of roots  $M(P_1, P_2)$  is given by

$$M(P_1, P_2) = \text{vol}_2(P_1 \oplus P_2) - \text{vol}_2(P_1) - \text{vol}_2(P_2) = \frac{11}{2} - 1 - \frac{1}{2} = 4.$$

The calculation of the non-zero roots in the example above can be generalized to System (2.5) using the earlier steps and the formula of the mixed volume of  $P_1, \dots, P_n$  [64] shown in Eqn. (2.7) below, which only requires computing the volumes of the Minkowski sums of all possible subsets of  $P_1, \dots, P_n$  (see [65, 66] for methods and software packages to compute Eqn. (2.7) efficiently).

$$\begin{cases} M(P_1, P_2, \dots, P_n) = \sum_{k=1}^n (-1)^{n-k} \sum_{1 \leq j_1 < j_2 < \dots < j_k \leq n} \text{vol}_k(P_{j_1} \oplus \dots \oplus P_{j_k}), \\ \text{where } P_{j_1} \oplus \dots \oplus P_{j_k} = \{p_{j_1} + \dots + p_{j_k} \mid p_{j_1} \in P_{j_1}, \dots, p_{j_k} \in P_{j_k}\}. \end{cases} \quad (2.7)$$

Note that if we remove the term  $-3N_1^*N_2^*$  from  $f_1(N_1^*, N_2^*)$  in Eqn. (2.6), then the number of non-zero roots of the system will not change. This is because the point  $(1, 1)$  in the support set  $S_1$  of  $f_1$  is not a corner point of the Newton polytope  $P_1$  (as it can be seen from Fig. 2-1A). Thus, removing that term (and parameter) will not affect the shape of  $P_1$ . Importantly, this simple example illustrates that having more parameters in a multivariate polynomial system does not imply having more non-zero roots (i.e., more free-equilibrium points). Generally, all terms whose support coordinates are not corner points of the corresponding Newton polytope do not influence the number of non-zero roots in the multivariate polynomial system. This makes necessary to separate the problem of adding parameters to the problem of adding free-equilibrium points.

## 2.4 Effects of HOIs on LV Models

To investigate the difference in the number of free-equilibrium points between LV models with and without HOI terms, we followed our general methodology to calculate the number of non-zero roots in polynomial systems. In particular, we analytically computed the number of free-equilibrium points from the following 3 commonly used systems:

$$\begin{aligned}
\text{System 1:} \quad & \frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^n a_{ij}N_j), \\
\text{System 2:} \quad & \frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^n a_{ij}N_j + \sum_{1 \leq j < k \leq n} b_{ijk}N_jN_k), \\
\text{System 3:} \quad & \frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^n a_{ij}N_j + \sum_{1 \leq j < k \leq n} b_{ijk}N_jN_k + \sum_{j=1}^n c_{ij}N_j^2),
\end{aligned} \tag{2.8}$$

System 1 corresponds to the classic LV model without HOIs. While it is known that this system has only one free-equilibrium point [53], using Bernshtein's theorem [56] we confirmed the existence of one single non-zero root. In turn, Systems 2 and 3 correspond to the simplest extensions of LV models with HOI terms. Note that System 3 has an additional higher-order self-regulation term. We found that Systems 2 and 3 have exactly  $2^n - n$  and  $2^n$  free-equilibrium points, respectively. Importantly, the increase in the number of parameters in a polynomial dynamical system does not imply an equal increase in the number of free-equilibrium points. For example, while System 3 has  $n^2$  terms more than System 2, it only has  $n$  free-equilibrium points more. Recall that only the corner terms to the corresponding Newton polytope determine the number of free-equilibrium points. In Systems 1 and 2, all the terms inside the brackets are corner terms. Similarly, in System 3, the  $r$ 's and the terms associated with the coefficients  $c$ 's are corner terms. However, the terms associated with the coefficients  $a$ 's and  $b$ 's are non-corner terms (see next section for the mathematical derivations). This confirms that parameters and free-equilibrium points are two different descriptors of a dynamical model. More generally, for the system

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{l=1}^{m'-1} \sum_{1 \leq j_1 \leq j_2 \leq \dots \leq j_l \leq n} a_{ij_1 j_2 \dots j_l} N_{j_1} N_{j_2} \dots N_{j_l}), \quad i = 1, \dots, n, \tag{2.9}$$

which represents  $m'$ -order interactions in a LV model with HOI terms and  $n$  species, we found that the number of free-equilibrium points is given by  $(m' - 1)^n$  (see next section for the mathematical derivation). This result reveals that adding HOI terms to the LV model increases the number of free-equilibrium points exponentially with the dimension  $n$  of the system.

## 2.5 Counting the Number of Equilibrium Points

In the previous section, we presented the findings of the number of free-equilibrium points in three different LV models (one with and two without HOI terms). Here, we present the formal proof of their derivation. Free-equilibrium points are considered first while the total number of points are considered after that (free + rigid) for the following studied systems

$$\begin{aligned}
 \text{System 1:} \quad & \frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^n a_{ij}N_j), & i = 1, \dots, n \\
 \text{System 2:} \quad & \frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^n a_{ij}N_j + \sum_{1 \leq j < k \leq n} b_{ijk}N_jN_k), & i = 1, \dots, n \\
 \text{System 3:} \quad & \frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^n a_{ij}N_j + \sum_{1 \leq j < k \leq n} b_{ijk}N_jN_k + \sum_{j=1}^n c_{ij}N_j^2), & i = 1, \dots, n.
 \end{aligned}$$

To find the free-equilibrium points, we set all time-derivatives to zero in the systems above. We ignore the  $N_i$  terms outside the brackets because they produce solutions which have at least one zero component (rigid-equilibrium points) which will be considered in Part 2 of this section. Therefore, the equations we need to study are

$$\begin{aligned}
 \text{System 1:} \quad & r_i + \sum_{j=1}^n a_{ij}N_j^* = 0, & i = 1, \dots, n \\
 \text{System 2:} \quad & r_i + \sum_{j=1}^n a_{ij}N_j^* + \sum_{1 \leq j < k \leq n} b_{ijk}N_j^*N_k^* = 0, & i = 1, \dots, n \\
 \text{System 3:} \quad & r_i + \sum_{j=1}^n a_{ij}N_j^* + \sum_{1 \leq j < k \leq n} b_{ijk}N_j^*N_k^* + \sum_{j=1}^n c_{ij}N_j^{*2} = 0, & i = 1, \dots, n.
 \end{aligned}$$

Note that all the equations for each of the 3 systems are functions of the species abundances and contain the exact same terms. Hence, the support of each equation, and thus the Newton polytopes, are identical and we will denote them by  $S_{(1)}$  and  $P(S_{(1)})$ , respectively. Let  $S_{(k)}$  be defined as  $\underbrace{S_{(1)} \oplus \dots \oplus S_{(1)}}_{k \text{ times}}$ . Furthermore, let us define  $e_i$  to be the point in space with its  $i^{\text{th}}$  component to be 1 and the rest are all zeros. It is also important to note that the operations of the Minkowski summation and those of forming convex hulls

are commuting [67], that is

$$P(S_{(k)}) = \underbrace{P(S_{(1)}) \oplus \dots \oplus P(S_{(1)})}_{k \text{ times}}.$$

Focusing on System 1, it is easy to see that the vertices of  $P(S_{(1)})$  are the origin and  $e_i$  for  $i = 1, \dots, n$ . Note that all the terms in System 1 are corner points. To perform the induction step, let us assume that the vertices of  $P(S_{(k)})$  are the origin and  $ke_i$  for  $i = 1, \dots, n$ .  $P(S_{(k+1)}) = P(S_{(k)}) \oplus P(S_{(1)})$  imply that the vertices of  $P(S_{(k+1)})$  are contained in the Minkowski sum of the vertices of  $P(S_{(k)})$  and  $P(S_{(1)})$ , which are the origin,  $e_i$ ,  $ke_i$  and  $ke_i + e_j$  for  $i, j = 1, \dots, n$ . It is useful to isolate the case  $i = j$  from the term  $ke_i + e_j$  to the standalone term  $(k+1)e_i$ . Hence, the Minkowski sum of the vertices of  $P(S_{(k)})$  and  $P(S_{(1)})$  are the origin,  $e_i$ ,  $ke_i$ ,  $ke_i + e_j$  and  $(k+1)e_i$  for  $i, j = 1, \dots, n$  and  $i \neq j$ . Note that both  $e_i$  and  $ke_i$  lie in the line connecting the origin and  $(k+1)e_i$  for  $i = 1, \dots, n$ , hence, they cannot be vertices of  $P(S_{(k+1)})$ . Moreover,  $ke_i + e_j$  lie in the line connecting  $(k+1)e_i$  and  $(k+1)e_j$  for  $i, j = 1, \dots, n$  and  $i \neq j$ . Hence, the vertices of  $P(S_{(k+1)})$  are the origin and  $(k+1)e_i$  for  $i = 1, \dots, n$ . Thus, induction is complete. Therefore for all, positive integers  $k$ , the vertices of  $P(S_{(k)})$  are the origin and  $ke_i$  for  $i = 1, \dots, n$ .

The computation of the volume of  $P(S_{(k)})$  is simply equivalent to finding the volume of the generalized-tetrahedron that is bounded by the coordinate hyperplanes and the hyperplane  $eN_1 + \dots + eN_n = k$ , which is

$$\begin{aligned} \text{vol}_n(P(S_{(k)})) &= \int_0^k \int_0^{k-N_1} \dots \int_0^{k-N_1-N_2-\dots-N_{n-1}} dN_n \dots dN_2 dN_1 \\ &= \int_0^k \int_0^{N_1} \dots \int_0^{N_{n-1}} dN_n \dots dN_2 dN_1 = \frac{k^n}{n!} \end{aligned}$$

under a change of variables to the upper limits of the integrands. To find the number of non-zero roots, we just need to compute the mixed volume, which is

$$M(\underbrace{P, \dots, P}_{k \text{ times}}) = \sum_{k=1}^n (-1)^{n-k} \binom{n}{k} \text{vol}_n(P(S_{(k)})) = \sum_{k=1}^n (-1)^{n-k} \binom{n}{k} \frac{k^n}{n!} = 1.$$

Thus, we have provided an alternative proof to confirm that the classic LV model has only 1 free-equilibrium point.



Coordinates	Starting points	Ending points
[0]	-	-
$[e_i]$	0	$(k+1)e_i$
$[e_i + e_j]$	0	$(k+1)e_i + (k+1)e_j$
$[ke_i]$	0	$(k+1)e_i$
$[ke_i] + [e_j]$	$(k+1)e_i$	$(k+1)e_j$
$(k+1)e_i$	-	-
$[e_i + e_j] + [ke_l]$	$(k+1)e_i + (k+1)e_j$	$(k+1)e_l$
$(k+1)e_i + e_j$	$(k+1)e_i$	$(k+1)e_i + (k+1)e_j$
$[ke_i + ke_j]$	0	$(k+1)e_i + (k+1)e_j$
$[ke_i + ke_j] + [e_l]$	$(k+1)e_i + (k+1)e_j$	$(k+1)e_l$
$(k+1)e_i + ke_j$	$(k+1)e_i$	$(k+1)e_i + (k+1)e_j$
$[ke_i + ke_j] + [e_l + e_m]$	$(k+1)e_i + (k+1)e_j$	$(k+1)e_l + (k+1)e_m$
$(k+1)e_i + ke_j + e_l$	$(k+1)e_i + (k+1)e_j$	$(k+1)e_i + (k+1)e_l$
$(k+1)e_i + (k+1)e_j$	-	-

Table 2.1: The table shows the Minkowski sum between the vertices of  $P(S_{(k)})$  (which are the origin,  $ke_i$ , and  $ke_i + ke_j$ ) and the vertices of  $P(S_{(1)})$  (which are the origin,  $e_i$ , and  $e_i + e_j$  for  $i, j, l, m = 1, \dots, n$  where  $i \neq j \neq l \neq m$ ). All single bracketed terms are the result of the Minkowski sum of these terms with the origin. Double bracketed terms are the Minkowski sum of the expression in the first bracket with that in the second one. All coordinates which contain  $(k+1)$  are special cases of the latter double bracketed expression in the table when a term in the second bracket combines with one in the first bracket. Note that in the 8<sup>th</sup> line  $(k+1)e_i + e_j$  is mentioned without any mentioning to  $e_i + (k+1)e_j$  as the entire set of coordinates generated by both expressions are identical for  $i, j = 1, \dots, n$  and  $i \neq j$ .

,

Focusing on System 2, the vertices of  $P(S_{(1)})$  are the origin,  $e_i$ , and  $e_i + e_j$  for  $i, j = 1, \dots, n$  and  $i < j$ . Note that all the terms in System 2 are corner points. To perform an induction step, let us assume that the vertices of  $P(S_{(k)})$  are the origin,  $ke_i$ , and  $ke_i + ke_j$  for  $i, j = 1, \dots, n$  and  $i < j$ . Again, since  $P(S_{(k+1)}) = P(S_{(k)}) \oplus P(S_{(1)})$ , then the vertices of  $P(S_{(k+1)})$  are contained in the Minkowski sum of the vertices of  $P(S_{(k)})$  and  $P(S_{(1)})$ , which are shown in Table 2.1. Note that for the points that are not corner points, their starting and ending points are also included in the table. From Table 2.1, it is easy to see that the vertices of  $P(S_{(k+1)})$  are the origin,  $(k+1)e_i$  and  $(k+1)e_i + (k+1)e_j$  for  $i, j = 1, \dots, n$  and  $i < j$ . Thus, induction is complete. Therefore, for all positive integers  $k$ , the vertices of  $P(S_{(k)})$  are the origin,  $ke_i$ , and  $ke_i + ke_j$  for  $i, j = 1, \dots, n$  and  $i < j$ .

To compute the mixed volume (hence the number of non-zero roots), let us define  $S'_{(2k)}$  as the union of the vertices of  $P(S_{(k)})$  as well as  $2ke_i$  for  $i = 1, \dots, n$ . Note that the vertices of  $P(S'_{(2k)})$  are simply the origin and  $2ke_i$  for  $i = 1, \dots, n$ . This is true given that  $ke_i$  lies

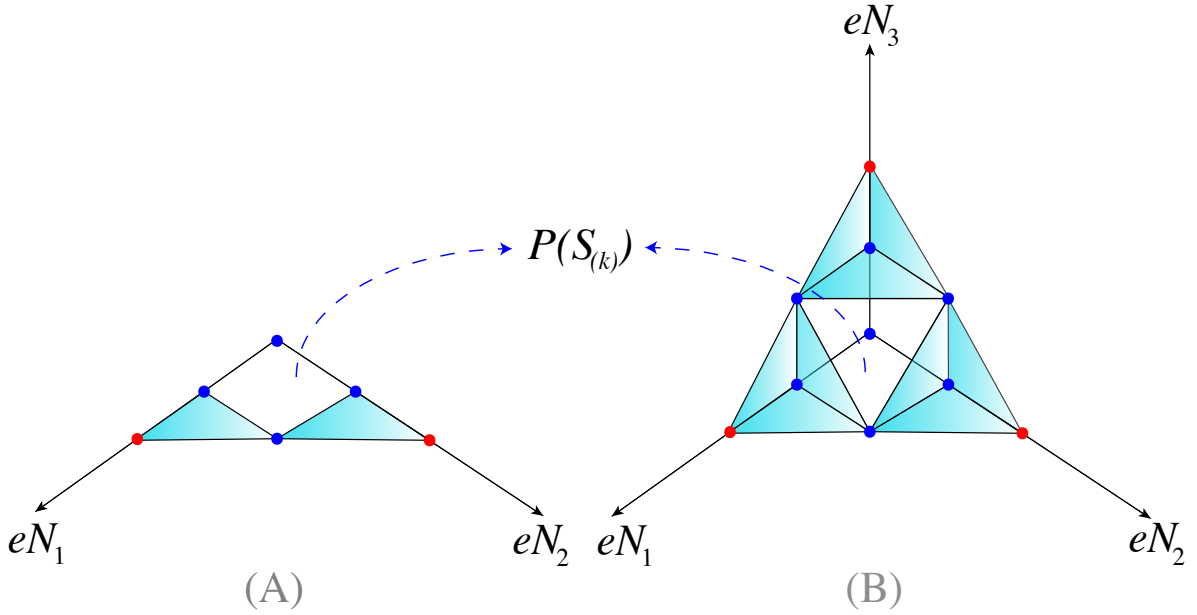


Figure 2-2: Illustration of the difference in volumes between  $P(S'_{(2k)})$  (which are the cyan plus white regions) and  $P(S_{(k)})$  (which are the white regions) for two and three species equations is shown in panels (A) and (B) respectively. The blue dots are vertices of  $P(S_{(k)})$ , which are spaced uniformly by  $k$  units along the axes, while the red and the origin are vertices of  $P(S'_{(2k)})$ . The axes are the exponents of the supports' monomials.

in the interior of the line connecting the origin and  $2ke_i$ , whereas  $ke_i + ke_j$  lies in the line connecting  $2ke_i$  and  $2ke_j$  for  $i, j = 1, \dots, n$  and  $i < j$ . Also note that  $P(S_{(k)})$  is contained in  $P(S'_{(2k)})$  and the difference in their volumes is the sum of the individual volumes of the generalized-tetrahedron $_i$  for  $i = 1, \dots, n$ —whose vertices are  $ke_i$ ,  $ke_i + ke_j$ , and  $2ke_i$  (we just exclude the origin) for  $j = 1, \dots, n$  and  $j \neq i$  (see Figure 2-2). These volumes are all identical and there are  $n$  of them. To help to visualize this, we can shift each of these coordinates of the generalized-tetrahedron $_i$  by  $ke_i$  to get the shifted structure, whose vertices are the origin and  $ke_i$  for  $i = 1, \dots, n$ —which is exactly  $P(S'_{(k)})$ . Thus, the volume of  $P(S_{(k)})$  is

$$\text{vol}_n(P(S_{(k)})) = \text{vol}_n(P(S'_{(2k)})) - n \text{vol}_n(P(S'_{(k)})) = \frac{(2k)^n}{n!} - \frac{nk^n}{n!} = \frac{(2^n - n)k^n}{n!}.$$

To find the number of non-zero roots, we just need to compute the mixed volume which is

$$M(\underbrace{P, \dots, P}_{k \text{ times}}) = \sum_{k=1}^n (-1)^{n-k} \binom{n}{k} \text{vol}_n(P(S_{(k)})) = (2^n - n) \underbrace{\sum_{k=1}^n (-1)^{n-k} \binom{n}{k} \frac{k^n}{n!}}_{=1} = 2^n - n.$$

Focusing on System 3, the support  $S_{(1)}$  contains the origin,  $e_i$ ,  $e_i + e_j$ , and  $2e_i$  for  $i, j = 1, \dots, n$  and  $i < j$ . Therefore, the vertices of  $P(S_{(1)})$  are the origin and  $2e_i$  for  $i = 1, \dots, n$ . This is true given that  $e_i$  and  $e_i + e_j$  are not corner points of  $P(S_{(1)})$  for  $i, j = 1, \dots, n$  and  $i < j$ . That is in System 3, the  $r$ 's and the terms associated with the coefficients  $c$ 's are corner terms. However, the terms associated with the coefficients  $a$ 's and  $b$ 's are non-corner terms. To perform an induction step, let us assume that the vertices of  $P(S_{(k)})$  are the origin and  $2ke_i$  for  $i = 1, \dots, n$ .  $P(S_{(k+1)}) = P(S_{(k)}) \oplus P(S_{(1)})$  imply that the vertices of  $P(S_{(k+1)})$  are contained in the Minkowski sum of the vertices of  $P(S_{(k)})$  and  $P(S_{(1)})$ —which are the origin,  $2e_i$ ,  $2ke_i$  and  $2ke_i + 2e_j$  for  $i, j = 1, \dots, n$ . It is useful to isolate the case  $i = j$  from the term  $2ke_i + 2e_j$  to the standalone term  $2(k+1)e_i$ . Hence, the Minkowski sum of the vertices of  $P(S_{(k)})$  and  $P(S_{(1)})$  are the origin,  $2e_i$ ,  $2ke_i$ ,  $2ke_i + 2e_j$ , and  $2(k+1)e_i$  for  $i, j = 1, \dots, n$  and  $i \neq j$ . Note that both  $2e_i$  and  $2ke_i$  lie in the line connecting the origin and  $2(k+1)e_i$  for  $i = 1, \dots, n$ , hence, they cannot be vertices of  $P(S_{(k+1)})$ . Moreover,  $2ke_i + 2e_j$  lies in the line connecting  $2(k+1)e_i$  and  $2(k+1)e_j$  for  $i, j = 1, \dots, n$  and  $i \neq j$ . Hence, the vertices of  $P(S_{(k+1)})$  are the origin and  $2(k+1)e_i$  for  $i = 1, \dots, n$ . Thus, induction is complete. Therefore, for all positive integers  $k$ , the vertices of  $P(S_{(k)})$  are the origin and  $2ke_i$  for  $i = 1, \dots, n$ . From the derivation in System 1, we already know that the volume of  $P(S_{(k)})$  is  $(2k)^n/n!$  (it is the volume of the generalized-tetrahedron that is bounded by the coordinate hyperplanes and the hyperplane  $eN_1 + \dots + eN_n = 2k$ ). Then, to find the number of non-zero roots, we just need to compute the mixed volume which is

$$M(\underbrace{P, \dots, P}_{k \text{ times}}) = \sum_{k=1}^n (-1)^{n-k} \binom{n}{k} \text{vol}_n(P(S_{(k)})) = 2^n \underbrace{\sum_{k=1}^n (-1)^{n-k} \binom{n}{k} \frac{k^n}{n!}}_{=1} = 2^n.$$

Here, we calculate  $M_T$ —the total number of equilibrium-points for any of the 3 systems under investigation, including their rigid-equilibrium points (the ones which have one or more zero-components). Note that rigid-equilibrium points of LV model with or with-

out HOI terms are the free-equilibrium points of the same model after substituting the corresponding zero abundances in them and deleting the lines which involve their time derivative as they will be zero as well. To see this, we can always start with an LV model with or without higher-order interaction terms and focus on the rigid-equilibrium point  $O_m$  in which species  $m$  dies out. That is,  $N_m = 0$  in  $O_m$ . Note that these models do not allow revival of species. Therefore, when a species dies out, the value  $N_m = 0$  will stay the same forever (i.e.,  $dN_m/dt = 0$ ). Upon substituting  $N_m = 0$  into the original dynamical system and deleting the line  $dN_m/dt = 0$  from it, we get a model which is one species less for which  $O_m$  but with the point/coordinate  $N_m = 0$  is deleted from it to be its free-equilibrium point. The remaining  $n - 1$  equations will have identical polytopes but with all the terms involving  $N_m$  being removed. Therefore, the new systems will have exactly  $M_{n-1}$  free-equilibrium points, providing  $n$  ways to eliminate a single species. Under the same logic, by letting  $k$  species go extinct, the new systems will have  $M_{n-k}$  free-equilibrium points with  $nC_k$  ways to do it. Hence,

$$M_T = \sum_{k=0}^n \binom{n}{k} M_{n-k},$$

Recall that from Part 1 we already know that for  $k$  species, the number of free-equilibrium points for systems 1, 2, and 3 are  $1$ ,  $2^k - k$ , and  $2^k$ , respectively. Therefore,

$$\begin{aligned} \text{System 1:} \quad M_T &= \sum_{k=0}^n \binom{n}{k} (1) = 2^n, \\ \text{System 2:} \quad M_T &= \sum_{k=0}^n \binom{n}{k} (2^{n-k} - (n - k)) = 3^n - n2^{n-1}, \\ \text{System 3:} \quad M_T &= \sum_{k=0}^n \binom{n}{k} (2^{n-k}) = 3^n. \end{aligned}$$

The results above confirm that the LV model has a total of  $2^n$  equilibrium points (i.e., free-equilibrium points + rigid-equilibrium points) [53]. Importantly, we can also clearly see that adding higher-order terms makes the total number of equilibrium points jump from  $2^n$  to  $3^n - n2^{n-1}$  when we add non-additive pairwise interactions terms per capita (System 2), furthermore, these number jumps to  $3^n$  when we include the non-additive quadratic terms per capita (System 3). Next, for the general system shown below:

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{l=1}^{m'-1} \sum_{1 \leq j_1 \leq j_2 \leq \dots \leq j_l \leq n} a_{ij_1 j_2 \dots j_l} N_{j_1} N_{j_2} \dots N_{j_l}), \quad i = 1, \dots, n,$$

The support  $S_{(1)}$  contains the origin,  $e_{i_1}$ ,  $e_{i_1} + e_{i_2}$ ,  $\dots$  and  $e_{i_1} + e_{i_2} + \dots + e_{i_{m'-1}}$  for  $i_1, i_2, \dots, i_{m'-1} = 1, 2, \dots, n$ . All these coordinates are bounded by the coordinate hyperplanes and the hyperplane  $eN_1 + \dots + eN_n = (m' - 1)$ . Hence, the origin and  $(m' - 1)e_i$  for  $i = 1, \dots, n$  are the vertices of  $P(S_{(1)})$  where the term  $(m' - 1)e_i$  is obtained by setting  $i_1 = i_2 = \dots = i_{m'-1} \equiv i$  in  $e_{i_1} + e_{i_2} + \dots + e_{i_{m'-1}}$ . To perform an induction step, let us assume that the vertices of  $P(S_{(k)})$  are the origin and  $(m' - 1)ke_i$  for  $i = 1, \dots, n$ . Since  $P(S_{(k+1)}) = P(S_{(k)}) \oplus P(S_{(1)})$ , then the vertices of  $P(S_{(k+1)})$  are contained in the Minkowski sum of the vertices of  $P(S_{(k)})$  and  $P(S_{(1)})$ —which are the origin,  $(m' - 1)e_i$ ,  $(m' - 1)ke_i$  and  $(m' - 1)ke_i + (m' - 1)e_j$  for  $i, j = 1, \dots, n$ . It is useful to isolate the case  $i = j$  from the term  $(m' - 1)ke_i + (m' - 1)e_j$  to the standalone term  $(m' - 1)(k + 1)e_i$ . Therefore, the vertices of  $P(S_{(k+1)})$  are the origin,  $(m' - 1)e_i$ ,  $(m' - 1)ke_i$ ,  $(m' - 1)ke_i + (m' - 1)e_j$ , and  $(m' - 1)(k + 1)e_i$  for  $i, j = 1, \dots, n$  and  $i \neq j$ . Note that both  $(m' - 1)e_i$  and  $(m' - 1)ke_i$  lie in the line connecting the origin and  $(m' - 1)(k + 1)e_i$  for  $i = 1, \dots, n$ , hence, they cannot be vertices of  $P(S_{(k+1)})$ . Moreover,  $(m' - 1)ke_i + (m' - 1)e_j$  lies in the line connecting  $(m' - 1)(k + 1)e_i$  and  $(m' - 1)(k + 1)e_j$  for  $i, j = 1, \dots, n$  and  $i \neq j$ . Hence, the vertices of  $P(S_{(k+1)})$  are the origin and  $(m' - 1)(k + 1)e_i$  for  $i = 1, \dots, n$ . Thus, induction is complete. Therefore, for all positive integers  $k$ , the vertices of  $P(S_{(k)})$  are the origin and  $(m' - 1)ke_i$  for  $i = 1, \dots, n$ . From the derivation in System 1, we already know that the volume of  $P(S_{(k)})$  is  $((m' - 1)k)^n / n!$  (it is the volume of the generalized-tetrahedron that is bounded by the coordinate hyperplanes and the hyperplane  $eN_1 + \dots + eN_n = (m' - 1)k$ ). Then, to find the number of non-zero roots, we just need to compute the mixed volume which is

$$M(\underbrace{P, \dots, P}_{k \text{ times}}) = \sum_{k=1}^n (-1)^{n-k} \binom{n}{k} \text{vol}_n(P(S_{(k)})) = (m' - 1)^n \underbrace{\sum_{k=1}^n (-1)^{n-k} \binom{n}{k} \frac{k^n}{n!}}_{=1} = (m' - 1)^n.$$

It is worth noting that this result matches the upper bound of Bezout's inequality which states that the number of common zeros is less than or equals to the product of the degree of each polynomial [68]. Also, unlike corner terms, if non-corner terms are removed from

the generalized model (non-corner points of the generalized-tetrahedron that is bounded by the coordinate hyperplanes and the hyperplane  $eN_1 + \dots + eN_n = m' - 1$ ), the number of free-equilibrium points will not be affected. However, removing corner points will reduce that number as we have seen in System 2 which is essentially System 3 but with some of its corner points being removed. Regards to the number of total (rigid+free) equilibrium points for this general system, it is given by

$$M_T = \sum_{k=0}^n \binom{n}{k} M_{n-k} = \sum_{k=0}^n \binom{n}{k} (m' - 1)^{n-k} = (m')^n,$$

## 2.6 Is the Addition of HOIs Increasing the Understanding of Ecological Dynamics?

Recent work has shown that higher-order interactions can increase the stability [43], promote the diversity [44], and better explain the dynamics of ecological communities [45, 46]. While it is known that these perceived benefits come from an increasing number of alternative solutions given by the nature of multivariate polynomials, this mathematical advantage has not been formally quantified. In fact, it has been perceived that mathematically there is nothing to prevent the inclusion of higher-order terms in ecological models [34].

Here, we have shown analytically that by adding HOI terms to ecological models, the number of free-equilibrium points increases exponentially with the dimension of the system. Recall that the classic LV model without HOI terms has a single free-equilibrium point, regardless of the number of parameters [53]. Importantly, we have shown that the more free-equilibrium points present in an ecological dynamical system, the more flexibility the system has to reach any type of dynamics. This reveals that HOI terms cannot provide additional explanatory power of ecological dynamics if model parameters are not ecologically restricted.

The mathematical advantages coming from adding HOI terms into LV models can be easily seen in the mapping from the free-equilibrium point space of these systems (i.e., the steady-state species abundances). This mapping is one-to-one for the classic LV model, i.e., from  $\mathbb{R}^{\theta(n)}$  (where  $\theta(n)$  is the number of parameters in the model with  $n$  species) to  $\mathbb{R}^n$ . However, when HOI terms are added to LV models, the mapping becomes from  $\mathbb{R}^{\theta'(n)}$

to  $\mathbb{C}^n$ , where  $\theta'(n) \geq \theta(n)$ . Thus, the mapping becomes one to exponentially many when HOI terms are included. Also, the co-domains for both mappings are different, it is  $\mathbb{R}^n$  for the classic LV model and  $\mathbb{C}^n$  for LV model with HOI terms. These explain why the number of both feasible and unfeasible solutions of a system increases when HOI terms are added. Note that even if studies penalize for the increase in the number of parameters  $\theta'(n) - \theta(n)$  between these models (e.g., using AIC, [54]), the mappings for HOI terms will continue to be from one to exponentially many, and the mathematical advantages will continue to be present. This reveals that models with and without HOI terms are fundamentally different and direct comparisons between them (e.g., dynamical properties or explanatory power) cannot be made without parameter restrictions.

It is also expected that adding HOIs into ecological models can lead to an enrichment of dynamics. To see this, we can consider the following 1-dimensional system with  $m$ -order HOIs terms:  $dN_1/dt = N_1 f(N_1)$ , where  $f(N_1)$  is a univariate polynomial of degree  $m - 1$ . Importantly, this 1-dimensional system is a special case of the general System (2.9), which has  $(m' - 1)^n$  free-equilibrium points and whose parameters (coefficients of the  $N$ 's) are all zero except for some of the terms in the first line (involving  $dN_1/dt$ ). The univariate system has one rigid-equilibrium point (the origin) and  $m - 1$  free-equilibrium points. If  $f$  is quadratic, the system is known to have a pitchfork bifurcation diagram with a single feasible branch. Instead, if  $f$  is cubic, the system is known to have a hysteresis loop with multiple locally stable free-equilibrium points in the feasibility domain [12]. In fact, more dynamical phenomena are observed for higher degrees of  $f$ . For instance, in the presence of  $k$  feasible free-equilibrium points, without multiple or complex roots, a stable feasible free-equilibrium point is followed by an unstable one, making the number of feasible and stable free-equilibrium points in this case to be either floor or ceil  $k/2$  for  $k = 0, 1, \dots, m - 1$ . This suggests that for higher dimensions, when parameters are restricted in regions with more feasible free-equilibrium points, this will imply an inherited increase in the likelihood of stability. These phenomena, which are associated with systems having multiple free-equilibrium points, cannot occur in classical LV models (without HOIs) regardless of the number of species [12]. In fact, any LV model with HOI terms is a special case of another LV model with HOI (with more species and/or higher order). Hence, the dynamics observed in a model with HOIs can also be observed in a more complex version of the model. This reveals that the explanatory power of models should only be compared when their number

of free-equilibrium points have been made comparable through parameter restrictions.

To illustrate the point above on a practical setting, one can focus on the problem of fitting data to ecological models [34, 46]. In this process, both parameters and initial conditions need to be tuned, introducing a bias. If a model has exponentially many free-equilibrium points, it is easier to reach a feasible solution, especially without parameter restrictions. Thus fitting will be facilitated in models with higher-order terms (mainly due to the number of free-equilibrium points and not necessarily due to the number of parameters) and one may be tempted to conclude that feasibility is an ecological mechanism derived from higher-order interactions (while this is just a mathematical construct).

In general, one should address the problems above and reach explanatory power by exploring parameter values restricted within key ecological quantities. Yet, this is often an overlooked or difficult task within ecological research. For example, parameters are often changed randomly [69], are not changed so that certain ecological quantities that are fully descriptive of a certain dynamics of interest are greater than unity [70, 71], are freely changed in order to fit data [46], or are chosen such that ecological quantities derived from a simpler model are used as the descriptive quantities of a more complicated model [72]. Moreover, the parameter space should be restricted to physical or ecological cases only (recall that by adding HOI terms it is possible to have imaginary equilibrium points but this is not possible in the classic LV model). In fact, although there are many ecological quantities that exist in the literature and they are typically associated with different research questions [60, 73], those ecological quantities generally increase in number and change along with the dimension of the system. Indeed, for systems with more than two free-equilibrium points, given that closed form solutions of steady state abundances for this type of systems are not known yet, it is unclear which specific quantities are ecologically the most important to deduce feasibility. Hence, if the aim is to add more complexity in ecological models, we hope this study can serve as a call for more work on parameter restrictions.



# Chapter 3

## Adding Mechanisms and Complexity into Ecological Models

### 3.1 Introduction

Understanding and predicting the behavior of ecological systems has been one of the greatest challenges in ecological research [3, 4, 74, 75]. One promising route to accomplish this challenge has been based on the mathematical modeling of species abundances over time by assuming different functions of species interactions, growth and decline rates [10]. However, these terms are not uniquely represented, they are either arbitrarily or specifically chosen to provide tractability (such as the ability to analytically understand the effect of a change in a parameter) and preserve realism (such as mimicking as much as possible ecological mechanisms) [11]. Indeed, in principle, a tractable, realistic, mathematical model of a system can allow us to apply conventional methods to deduce and have a mechanistic knowledge about the behavior of real-world systems [12, 76]. Yet, finding a compromise between tractability and realism has not been easy [77–79].

Importantly, it has already been shown that in order to explain complex dynamics, it is not always necessary to have complex models [14]. For example, complex behavior, such as transitions from point attractors to chaotic behavior can already emerge from population dynamics models with low-order polynomials (e.g., the 1-dimensional deterministic logistic model) [13]. In fact, one of the best examples of simple tractable models in ecology is the well known linear Lotka-Volterra (LV) model [18, 30]. Yet, this model must be understood

just as a first-order approximation to how complex ecological systems behave [12]. As a consequence, many modifications have been done to the linear LV model in the hope of adding realism and increasing their explanatory power [10]. In general, these modifications yield models of the form  $dN_i/dt = N_i f_i(\mathbf{N})/q_i(\mathbf{N})$  for  $i = 1, 2, \dots, n$ , where the  $f$ 's and  $q$ 's are multivariate polynomials (in general with higher-order terms) in species abundances  $\mathbf{N} = (N_1, N_2, \dots, N_n)^T$  [14].

A clear example of complexity added to the linear LV model, as discussed in the previous chapter, is the incorporation of higher-order interactions (HOIs) that involve more than two variables [49]. The introduction of these higher-order terms has been justified in order to account for the possibility that the effect of a species  $i$  on the per capita growth rate of a species  $j$  might itself depend on the abundance of a third species  $k$  due to either compensatory effects or supra-additivity [10, 80]. The addition of HOIs has been shown to stabilize dynamics in competition systems [43], promote diversity in ecological communities [44], and capture unexplained dynamics of linear LV models [46]. However, it has been debatable whether these terms are derived from fundamental principles [42], whether mathematically there is anything to prevent their inclusion into ecological models [81], or whether they are indeed useful to explain observed ecological dynamics [48].

Another example of complexity is the addition of functional responses, which have been one of the most studied and ecologically motivated polynomial fraction forms added to linear LV models [10, 11, 35, 48]. Typically, functional responses correspond to the mechanistic (or phenomenological) description of how predators (consumers) search, attack, and handle their prey (resources). Although the name of functional response was first introduced by Solomon [82], functional responses were broadly adopted after Holling [35] identified three types of responses: linear (Type I - linear LV model), hyperbolic (Type II), and sigmoid (Type III). For instance, the Beddington-DeAngelis functional response [83, 84], which is a variation of Type II, has been one of the most widely used responses for modeling food webs [85]. Importantly, the introduction of functional responses has appeared to reconcile part of the compromise between tractability and realism across a variety of ecological models [10]. Yet, most of the analytical (tractable) work incorporating nonlinear functional responses (Types II and III) has been limited to 2-species systems [10, 11, 35], remaining unclear whether this compromise can be extended to larger multispecies cases [72, 81].

In general, one of the big questions derived from the addition of complexity (e.g., either

HOIs or functional responses) is whether the explanatory power of a modified model comes from the general form of its polynomial or from a more realistic description of multispecies systems. To answer this question, we study the probability of feasibility in complex models (i.e., modifications to the linear LV model using multivariate polynomials) under an arbitrary choice of parameter values. Note that the observability or adaptability of an ecological system is associated with how much its structure can change while retaining its feasibility [86, 87]. Thus, it is important to distinguish the minimum amount of information necessary in a model to explain such observability. Specifically, we study the probability of feasibility as a function of three key properties of these complex models: their polynomial degree (interaction order), dimension (number of species), and parameter restrictions (sign restrictions). We define the probability of feasibility as the frequency of finding in a model at least one feasible solution (i.e., a feasible free-equilibrium point where all its coordinates are real and positive) by randomly choosing parameter values under a given distribution [88]. Note that the existence of feasible equilibrium solutions is a crucial condition in the context of species coexistence in equilibrium dynamics, i.e., a necessary condition for persistence, permanence, and the existence of bounded orbits in the feasibility domain [41].

We start illustrating our study using a 1-dimensional toy model and demonstrating that its probability of feasibility increases as a function of its polynomial degree (and consequently its number of parameters) when parameter values are arbitrarily chosen from a given probability distribution. Next, we extend the toy example into a multidimensional case to show that the probability of generating a feasible multispecies system is an increasing function of its complexity. Specifically, we characterize complexity by the number of free-equilibrium points generated by a model, which is a function of the polynomial degree and system's dimension. Then, to illustrate the expected behavior of complex models across different dimensions and parameter restrictions, we study modifications to the linear LV model using HOIs and functional responses. Finally, we discuss the implications of our results for the explanatory contribution to feasibility of complex ecological models.

## 3.2 Univariate Complex Models

To investigate the probability of feasibility of ecological systems using complex models, we start illustrating our methodology in 1-dimensional (univariate) systems. For this purpose,

let us consider the following 1-dimensional dynamical system characterized by the state variable  $N$  as shown below

$$\frac{dN}{dt} = \frac{Nf(N)}{q(N)}, \quad (3.1)$$

where  $f(N) = a_m N^m + a_{m-1} N^{m-1} + \dots + a_1 N + a_0$  is a polynomial of degree  $m$  and  $q(N)$  can be any other polynomial that shares no common factor with  $Nf(N)$ . Note that in the case when  $f(N)$  is linear and  $q(N) = 1$ , we recover the 1-dimensional version of the linear LV model (i.e., logistic growth model when  $a_1 < 0$ , [10]).

As mentioned before, we study the feasibility of a system as defined by its capacity to have at least one feasible equilibrium point (the equilibrium point is both real and positive) under an arbitrary choice of parameter values. This implies that the feasibility problem of Model (3.1) is identical to the feasibility problem of the system defined by the model  $dN/dt = Nf(N)$ , as they both involve analyzing the real and positive roots of the polynomial  $f(N)$ . Therefore, we can think of the feasibility problem in Model (3.1) as the same as the feasibility problem of the modified 1-dimensional linear LV model with higher-order terms. Note that the dynamical stability criteria can be relaxed in this case, as it is linked to the feasibility problem [89]. That is, when Model (3.1) has  $k$  positive equilibrium points (without multiple or complex roots), a stable feasible free-equilibrium point is followed by an unstable one, making the number of positive stable equilibrium points to be either floor or ceil  $k/2$  for  $k = 0, 1, \dots, m$  [81]. This implies that one can derive the stability problem from the feasibility one.

It is well known that the feasibility of any system depends on the specifics given by the model parameterization and constraints [90]. However, in the absence of information about the exact parameter values, as in most of the ecological research, these values are randomly chosen from a probability distribution [79, 91]. This parameter uncertainty transfers the feasibility problem to the probability of having at least one feasible equilibrium point by randomly choosing parameter values under given conditions [61, 88]. For illustration purposes, let us consider the case when the  $a$ 's are all Gaussians i.i.d. centered on zero (mean zero), and let us denote  $p_G(m)$  the probability that at least one root of  $f(N)$  is positive (i.e., feasible). Note that  $p_G(m)$  is independent of the distribution's variance simply because  $f(N)$  and  $cf(N)$  have identical roots for any constant  $c \neq 0$ . Under this

Gaussian case, it has been demonstrated [92] that the expected number of positive real roots  $E(m)$  as  $m \rightarrow \infty$  is given by

$$E(m) = \frac{R(m)}{2}, \text{ where} \quad (3.2)$$

$$R(m) = \frac{2}{\pi} \log(m) + 0.6257358072 \dots + O(1/m). \quad (3.3)$$

Note that  $R(m)$  corresponds to the expected number of real roots, while  $E(m)$  assumes no a priori tendency for positive or negative roots in  $R(m)$ . That is, the density of real zeros is an even function [92].

Next, let us try to find how Eqn. (3.2) can be inserted into the expression of the probability of feasibility  $p_G(m)$ . To provide a numerical approximation, let us assume that the location of the  $m$  roots of  $f(N)$  are independent of each other and positive with probability  $p_i$  for  $i = 1, 2, \dots, m$ . Therefore, the probability of feasibility (to have at least one positive and real root) becomes  $p_G(m) = 1 - (1 - p_1)(1 - p_2) \dots (1 - p_m)$ . By applying Jensen's inequality (i.e.,  $f(p_1) + f(p_2) + \dots + f(p_m) \geq mf((p_1 + p_2 + \dots + p_m)/m)$ ) to the convex function  $f(x) = -\log(1 - x)$ , we obtain  $p_G(m) \geq 1 - (1 - E(m)/m)^m$ , where the expected number of positive roots  $E(m) = p_1 + p_2 + \dots + p_m$ . From the formula of  $p_G(m)$ , one can derive the upper bound  $p_G(m) \leq 1 - (1 - \max(p_1, p_2, \dots, p_m))^m$ . Assuming that  $p_G(m)$  is continuous for any  $m \geq 1$  implies the existence of  $\hat{E}(m)$  such that the probability of feasibility can be written as

$$p_G(m) = 1 - (1 - \hat{E}(m)/m)^m, \quad (3.4)$$

where  $\hat{E}(m)$  is an overestimate of the expected number of positive roots (that is,  $E(m) \leq \hat{E}(m) \leq m \max(p_1, p_2, \dots, p_m)$ ). This allows us to infer the mathematical form of  $E(m)$  by finding  $\hat{E}(m)$  such that  $p_G(m)$  is the best fit of  $1 - (1 - \hat{E}(m)/m)^m$ .

Figure 3-1 provides a numerical confirmation of the positive relationship between the probability of feasibility  $p_G(m)$  and the degree  $m$  of the polynomial  $f(N)$  under an arbitrary choice of parameter values (no parameter restrictions). The probability is calculated numerically over  $10^4$  simulations using i.i.d. parameters from a Gaussian distribution with mean zero and standard deviation one. The figure shows the best fit to the data using Eqn. (3.4), where  $\hat{E}(m) = a \log(m) + b + c/m$ ,  $a = 0.391$ ,  $b = 0.356$  and  $c = 0.141$ . Note that these values are close (still an overestimate) to  $1/\pi$  and to the constant term in Eqn

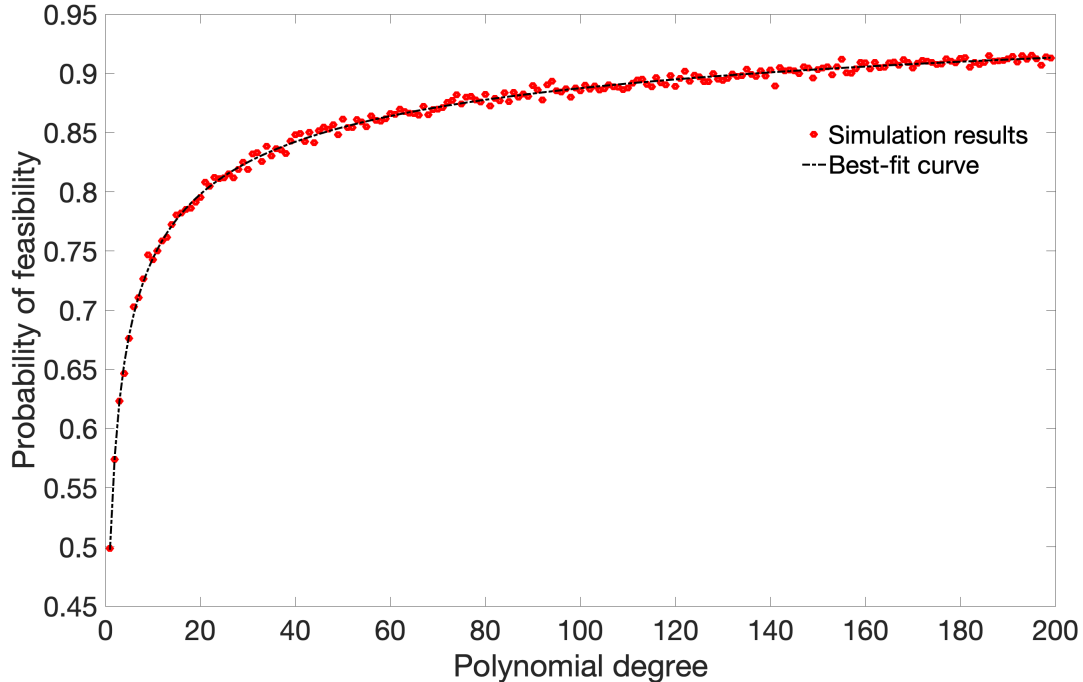


Figure 3-1: Probability of feasibility increases as a function of the polynomial degree in 1-dimensional systems. The figure shows the probability that at least one root is feasible  $p_G(m)$  in Model (3.1) as a function of the degree  $m \geq 1$  of the polynomial  $f(N)$  (using  $10^4$  trial points for each polynomial degree  $m$ ). Note that parameters are all i.i.d. Gaussian with mean zero and standard deviation one. The probability  $p_G(n)$  is independent of the distribution's variance. By plotting (solid line)  $p_G(m)$  and fitting it with  $1 - (1 - \hat{E}(m)/m)^m$  (where  $\hat{E}(m) = a \log(m) + b + c/m$ ), we find that the best-fit parameters ( $R^2 = 0.9966$ ) are  $a = 0.391 \pm 0.004$  (an overestimate value that is close to  $1/\pi$  in the expression of  $E(m)$  in Eqns. (2-3)),  $b = 0.356 \pm 0.013$  (an overestimate value that is close to the constant term in the expression of  $E(m)$  in Eqns. (2-3)) and  $c = 0.141 \pm 0.016$ . The term  $c/m$ , which is present in both  $E(m)$  (as an order quantity  $O(1/m)$ ) and  $\hat{E}(m)$ , is not significant for large polynomial degrees  $m$  (as it is small compared to either the log or the constant term in both  $\hat{E}(m)$  and  $E(m)$ ). However, the best fit of  $c$  takes care of fitting the probability of feasibility with low polynomial degrees without altering the fact that the values of  $a$  and  $b$  in  $\hat{E}(m)$  are overestimate values and are close to the ones in the expression of  $E(m)$ .

(3.2). Also, notice the sharp increase in the probability of feasibility for small  $m$ 's. That is, when the polynomial degree  $m$  is relatively small, only a few extra terms are needed to add a noticeable increase in the probability of feasibility. Once  $m$  is large enough, the rate of increase in the probability of feasibility diminishes sharply even if considerably more extra terms are added.

Importantly, the example above illustrating a monotonic and saturating behavior of the probability of feasibility as a function of the polynomial degree is robust to the choice of the probability distribution (see next section). This is true as long as the addition of

parameters does not decrease the probability of obtaining an odd sign sequence in the coefficients of  $f(N)$  (i.e., the number of consecutive sign changes in  $a_m, a_{m-1}, \dots, a_1, a_0$  is an odd integer—see next section).

### 3.3 Robustness Properties of the Probability of Feasibility

In the previous section, we found that there is an increasing relationship between the probability of feasibility  $p_G(m)$  and the polynomial degree  $m$  in 1-dimensional systems by using i.i.d. parameters drawn from a Gaussian distribution with mean zero. Here, we show that this result is robust to the choice of the probability distribution of parameter values.

To support our statement above, we start by repeating the same analysis with a uniform distribution with mean zero and computing the probability of feasibility  $p_U(m)$  (note that we use  $p_G(m)$  and  $p_U(m)$  for Gaussian and uniform, respectively). Figure 3-2 shows that the monotonicity pattern remains as shown in Figure 3-1. Furthermore, let us suppose that  $a_0, a_1, \dots, a_m$  are independent normally distributed, and the distribution has a mean that is uniformly distributed between  $-c$  and  $c$  (i.e., centered on zero) with a standard deviation that is uniform between 0 and  $d$ . Figure 3-3 confirms numerically that the expected number of positive roots still has the form  $a \log(m) + b + O(1/m)$ , and the probability of feasibility behaves similarly to Figures 3-1 and 3-2 for any value of  $c$  and  $d$  (as  $c$  decreases or  $d$  increases, the coefficient of the log increases implying that the expected number of positive roots increases).

In the previous examples, we have illustrated probability distributions with some underlying centrality around zero. Next, let us discuss distributions that center somewhere else. It has been demonstrated [92] that when all parameters have an i.i.d. Gaussian distribution with non-zero mean and variance, the expected number of positive roots is asymptotic to a constant which depends on a single quantity  $\lambda$ . This quantity  $\lambda$  is the mean divided by the standard deviation, yielding

$$E(m) = \frac{1}{2} - \frac{1}{2} \operatorname{erf}^2\left(\frac{|\lambda|}{\sqrt{2}}\right) + \frac{1}{\pi} \Gamma[0, \lambda^2] + O(1/m). \quad (3.5)$$

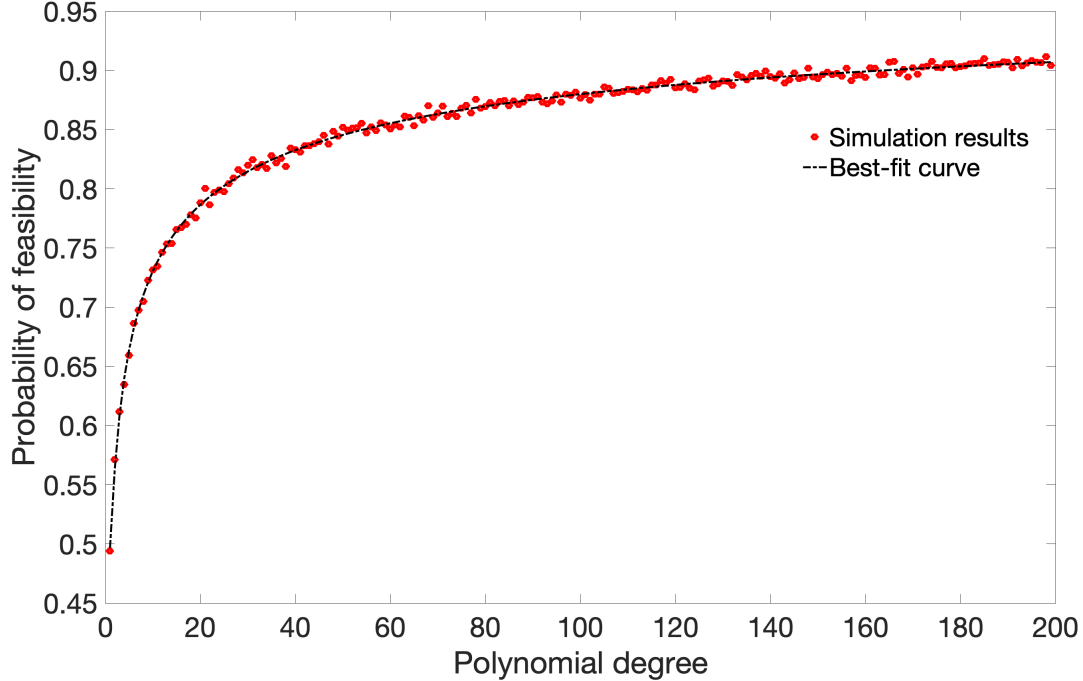


Figure 3-2: Same as in Figure 3-1 but using a uniform distribution with mean zero. Specifically, we plot  $p_U(m)$  and fit it with  $1 - (1 - \hat{E}(m)/m)^m$ , where  $\hat{E}(m) = a \log(m) + b + c/m$ . We find that the best-fit parameters ( $R^2 = 0.9968$ ) are  $a = 0.384 \pm 0.003$  (close to  $1/\pi$ ),  $b = 0.326 \pm 0.012$  (close to the constant term in the expression of  $E(m)$  in Eqns. (3.2-3.3)) and  $c = 0.170 \pm 0.015$ .

This implies that the new probability of feasibility  $p_{G_s}$  of this 1-dimensional system will asymptote to a constant smaller than 1. Figure 3-4 shows the probability of feasibility  $p_{G_s}$  and its fit using the function  $1 - (1 - \hat{E}(m)/m)^m$ , where  $\hat{E}(m) = a + b/m$  and  $b < 0$  to ensure that  $\hat{E}(m)$  is increasing with  $m$ . The best-fit parameter is  $a = 0.585$ , which is an overestimate yet close to the theoretical value of 0.536515 that is obtained by plugging  $\lambda = 5/7$  in the expression of  $E(m)$ . Also, Eqn. (3.5) demonstrates that the probability of feasibility is maximized when parameters are randomized around a mean zero (i.e.,  $\lambda = 0$ ) in the case of parameters that are i.i.d. That is, the probability of feasibility can be increased by reducing the absolute value of the mean and/or increasing the standard deviation given that  $E(m)$  is a decreasing function of  $|\lambda|$ . Additionally, let us suppose that  $a_m, a_{m-1}, \dots, a_1, a_0$  are independent and each parameter is normally distributed with a mean that is uniformly distributed between  $c_1$  and  $c_2$  and standard deviation that is uniform between 0 and  $d$ . Figure 3-5 shows numerical simulations confirming that the probability of feasibility behaves similarly to the previous cases and also asymptotes to a value less than 1. This result is robust even if each of  $a_m, a_{m-1}, \dots, a_1, a_0$  is not normal and



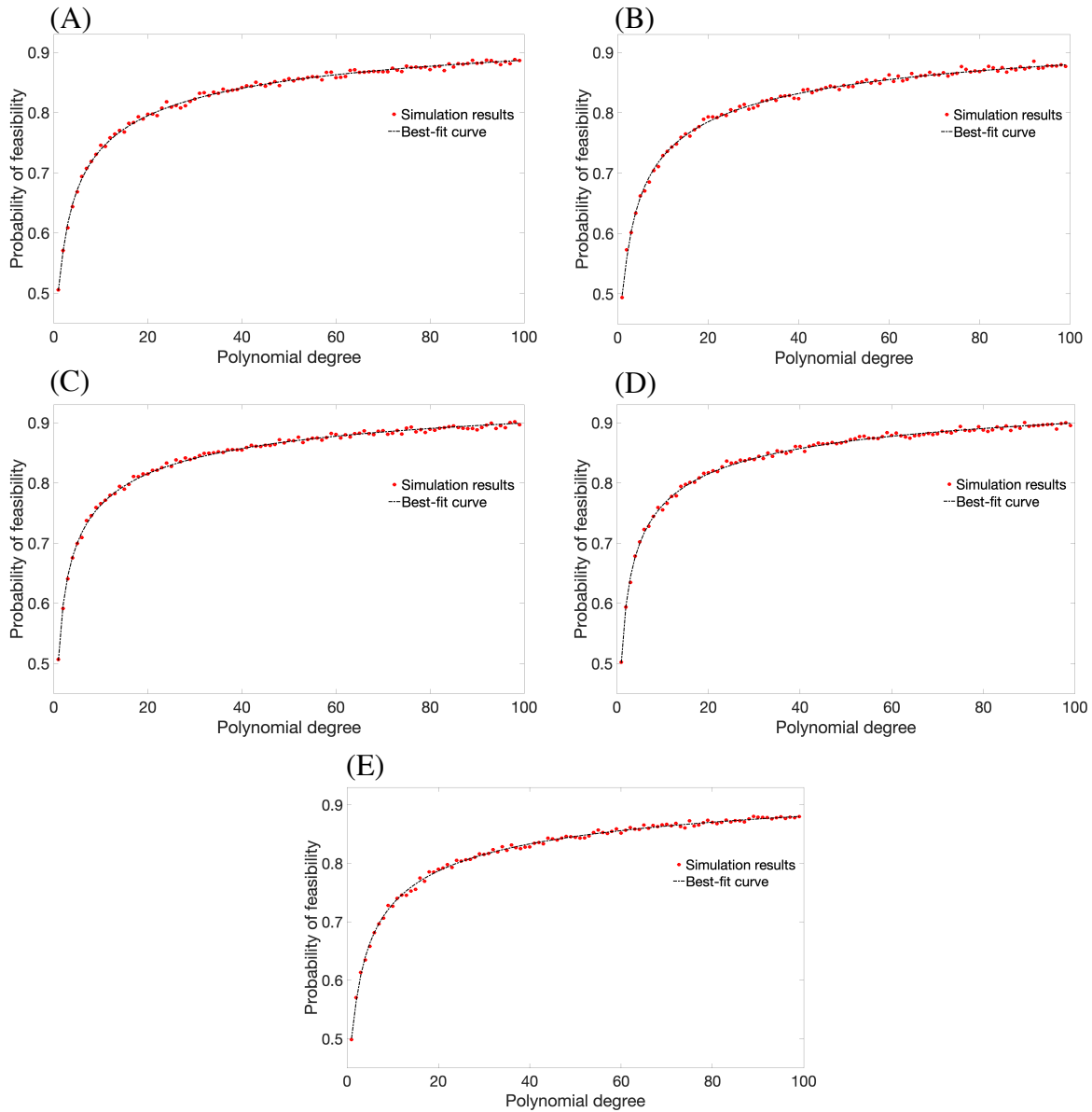


Figure 3-3: Similar to Figure 3-1 but parameters are normally distributed with a mean that is uniformly distributed between  $-c$  and  $c$  (i.e., centered on 0) with a standard deviation that is uniform between 0 and  $d$ : Panel A ( $c = 1, d = 1$ ), Panel B ( $c = 1, d = 0.01$ ), Panel C ( $c = 1, d = 100$ ), Panel D ( $c = 0.01, d = 1$ ), and Panel E ( $c = 100, d = 1$ ). All probabilities were fit with  $1 - (1 - \hat{E}(m)/m)^m$ , where  $\hat{E}(m) = a \log(m) + b + c/m$ . We find that the best-fit parameters are  $a = 0.398 \pm 0.004$ ,  $b = 0.320 \pm 0.016$  and  $c = 0.184 \pm 0.019$  for Panel A,  $a = 0.389 \pm 0.005$ ,  $b = 0.304 \pm 0.017$  and  $c = 0.193 \pm 0.021$  for Panel B,  $a = 0.408 \pm 0.004$ ,  $b = 0.388 \pm 0.015$  and  $c = 0.115 \pm 0.018$  for Panel C,  $a = 0.409 \pm 0.005$ ,  $b = 0.386 \pm 0.016$  and  $c = 0.114 \pm 0.019$  for Panel D,  $a = 0.387 \pm 0.004$ ,  $b = 0.318 \pm 0.014$  and  $c = 0.181 \pm 0.018$  for Panel E. The fit in all panels has  $R^2 > 0.996$ . As  $c$  decreases or  $d$  increases, the coefficient of the log increases (i.e  $a$ ) implying that the expected number of positive roots increases.

each have a specific PDF. In addition, fixing a few  $a$ 's to fixed values (including zero) will not change the monotonicity (simulations not shown).

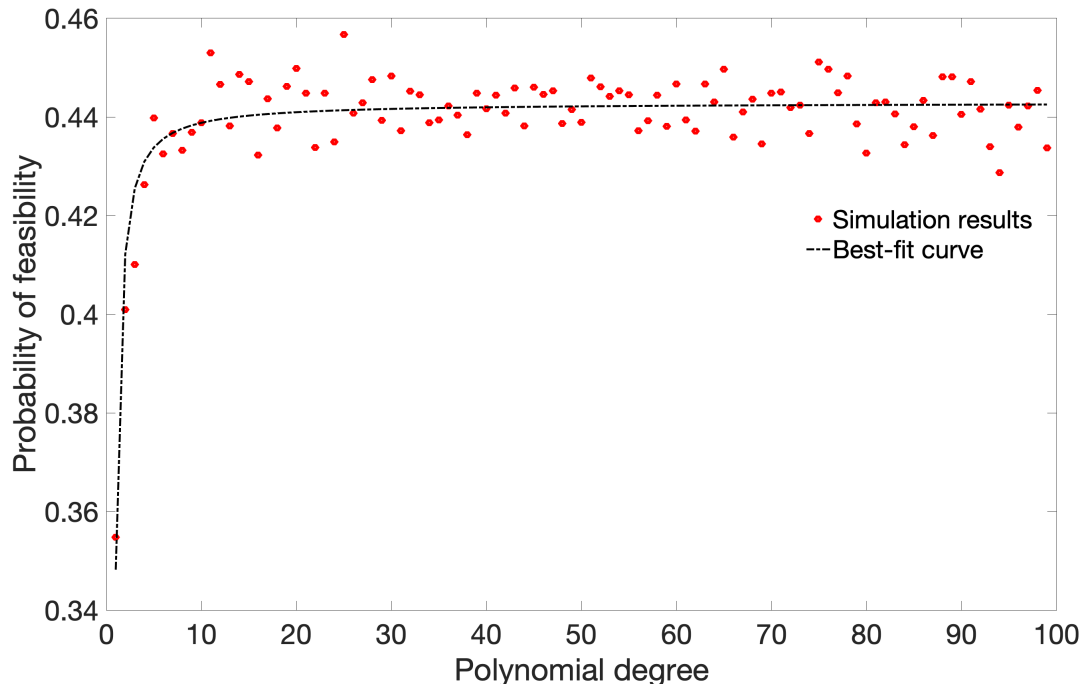


Figure 3-4: Similar to Figure 3-1 but parameters are all i.i.d. uniformly distributed with mean 5 and standard deviation 7. The probability of feasibility increases as  $m$  increases, and asymptotes to a constant smaller than 0.5. The probability of feasibility was fit with  $1 - (1 - \hat{E}(m)/m)^m$ , where  $\hat{E}(m) = a + b/m$ . We find that the best-fit parameters are  $a = 0.585 \pm 0.002$  and  $b = -0.237 \pm 0.010$ . Notice that  $\hat{E}(m)$  is an increasing function of  $m$  which is evident from the negative  $b$ . If we include the term  $\log(m)$  in the expression of  $\hat{E}(m)$ , we find that the best-fit parameter for the coefficient of  $\log(m)$  to be of order  $10^{-4}$ , which is close to zero. This rules out the dependence of  $\hat{E}(m)$  on  $\log(m)$ .

Finally, we can see that the probability of feasibility is not sensitive to the formula of the parameter distribution and is dependent on their centrality. Indeed, according to Descartes's rule of sign, the number of positive roots of the polynomial  $f(N)$  equals to or is less than (by an even number) the number of consecutive sign changes of the coefficients of  $f(N)$ . That is, if for example  $f(N) = 3N^2 + 5N - 4$ , then there is only one consecutive sign change from 5 to  $-4$  and this polynomial has exactly one positive root. Alternatively, if for example  $f(N) = -3N^2 + 5N - 4$ , then there are two consecutive sign changes and the polynomial has either two or zero positive roots (in this case, it has zero roots). Hence, from Descartes's rule of signs, we can conclude that if the number of consecutive sign changes is an odd integer, then it must have a positive root irrelevant of the distribution formula. This illustrates that if a distribution increases the likelihood of odd numbers of consecutive sign changes, the probability of feasibility increases as well.

For instance, if a distribution only allows for odd sign sequences, the probability of feasibil-

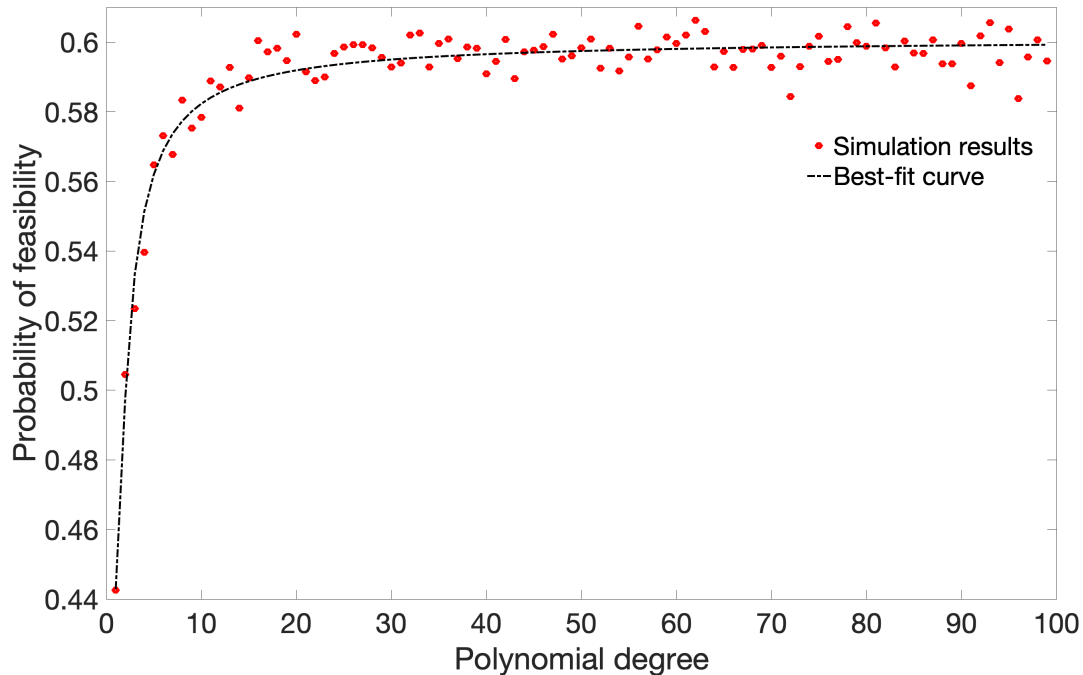


Figure 3-5: Similar to Figure 3-1 but parameters are normally distributed with a mean that is uniformly distributed between  $c_1 = -7.5$  and  $c_2 = 17.5$  and standard deviation that is uniform between 0 and  $d = 14$  (as an illustrative example). The probability of feasibility  $p_{Gs}(m)$  increases as  $m$  increases, and asymptotes to a constant smaller than 0.6. The probability of feasibility was fit with  $1 - (1 - \hat{E}(m)/m)^m$ , where  $\hat{E}(m) = a + b/m + c/m^2$ . The  $1/m^2$  term is the next leading term after  $1/m$  in the expression of  $\hat{E}(m)$  which does not influence the value of  $\hat{E}(m)$  for higher polynomial degrees. We added it to fit the lower data points better. We find that the best-fit parameters are  $a = 0.9189 \pm 0.003$ ,  $b = -0.868 \pm 0.042$  and  $c = 0.392 \pm 0.043$ . Notice that  $\hat{E}(m)$  is an increasing function of  $m$  for all  $m \geq 1$ . Also, if we include the term  $\log(m)$  in the expression of  $\hat{E}(m)$ , the best fit parameter for its coefficient is of order  $10^{-3}$  which is close to zero. This rules out the dependence of  $\hat{E}(m)$  on  $\log(m)$ .

ity is guaranteed to be 1. Therefore, in order to explain the reduction in the probability of feasibility in the previous examples (centered vs non-centered distributions around zero), we need to remember that in the case of symmetric distributions, the probability of an odd number of consecutive sign sequence is 0.5 for all polynomial degrees given that there are an equal number of sign sequences with even or odd numbers of consecutive sign changes. However, in the example where all parameters are i.i.d. with non-zero mean, that probability becomes  $2p(1-p)$  for all polynomial degrees where  $p$  is the fraction of the PDF of that distribution that is positive (i.e.,  $p = P(X > 0)$  where  $X$  is the parameters' distribution)—see the proof at the end of this section. This quantity is maximized at  $p = 0.5$  (distributions centered on zero) and decreases as we move farther away from it. The probability of an odd number of consecutive sign changes behaves similarly with the behaviour of  $\lambda$  in  $E(m)$

that is displayed in Eqn. (3.5) (i.e.,  $E(m)$  decreases as  $|\lambda|$  increases).

This simple example above explains the reduction in the probability of feasibility when we deviate from centered distributions without the need to know the formula nor the shape of the distribution. Thus, we can see that if we fix a polynomial degree in a model, the more a parameter distribution injects odd sign sequences, the higher the increase in the probability of feasibility. Similarly, as the polynomial degree increases in a model, if the new parameters do not decrease the process of injecting odd sign sequences to  $f(N)$ , then the probability of feasibility increases. As an example, let us focus on  $a_m, a_{m-1}, \dots, a_1, a_0$ , if the parameters with even and odd indices are i.i.d. normal with standard deviation of 1 and mean of  $-100$  and  $100$ , respectively, then the probability of feasibility will be 1 if the polynomial degree is odd and zero if the polynomial degree is even. This oscillatory behavior is due to the same oscillation in the probability of odd sign sequences which is 1 for an odd polynomial degree and zero for an even.

### 3.3.1 Effect of Consecutive Sign Changes on The Probability of Feasibility

Theorem: Let  $f(N) = a_m N^m + a_{m-1} N^{m-1} + \dots + a_1 N + a_0$ , whose parameters are independent and identically distributed. Let  $X$  be the parameters' distribution and  $p = P(X > 0)$ . The probability that the number of consecutive sign changes in the sequence  $a_m, a_{m-1}, \dots, a_1, a_0$  is an odd integer is  $2p(1 - p)$ .

Proof: Let us consider a linear polynomial  $f(N) = a_1 N + a_0$ . We have consecutive sign changes when  $(a_1, a_0) = (-, +)$  or  $(+, -)$ . With  $p = P(X > 0)$ , the probability of obtaining those two sign sequences is  $(1 - p)p + p(1 - p) = 2p(1 - p)$ . In the general case, consider a polynomial of degree  $k - 1$  whose coefficients are represented by the sequence  $\mathbf{a}_k = (a_{k-1}, a_{k-2}, \dots, a_1, a_0)$ . Let  $s(\mathbf{a}_k) = (\text{sign}(a_{k-1}), \text{sign}(a_{k-2}), \dots, \text{sign}(a_1), \text{sign}(a_0))$  be the 'symbolic' sign sequence of  $\mathbf{a}_k$  and let  $c(\mathbf{a}_k)$  be the number of consecutive sign changes in  $\mathbf{a}_k$ . Assign binary numbers 0 and 1 if  $\text{sign}(a_k)$  is negative or positive, respectively, in  $s(\mathbf{a}_k)$  and let  $b(\mathbf{a}_k)$  be the resulting binary number. Finally, let  $d(\mathbf{a}_k)$  be the decimal representation of  $b(\mathbf{a}_k)$ . For example, the coefficients of the quadratic polynomial  $f(N) = N^2 - 2N + 3$  is represented by the sequence  $\mathbf{a}_3 = (1, -2, 3)$  whose related quantities are given by  $s(\mathbf{a}_3) = (+, -, +)$ ,  $c(\mathbf{a}_3) = 2$ ,  $b(\mathbf{a}_3) = 101$  and  $d(\mathbf{a}_3) = 5$ .

Lemma 1:  $c(\mathbf{a}_k)$  is odd if and only if  $d(\mathbf{a}_k)$  is odd when it is less than or equals to  $2^{k-1} - 1$  and even when it is greater than or equals to  $2^{k-1}$ .

Proof of Lemma 1: With a linear function  $f(N)$ , we only have the four sign sequences  $(-, -), (-, +), (+, -), (+, +)$  whose decimal representation are the numbers 0,1,2,3 respectively. Only sequences with decimal numbers 1 (odd number  $\leq 2^1 - 1 = 1$ ) and 2 (even number  $\geq 2^1 = 2$ ) have odd number of consecutive sign changes. Before carrying out with induction, let  $\mathbf{A}_k^{O\downarrow}$  be all sequences  $\mathbf{a}_k$  with an odd  $c(\mathbf{a}_k)$  and with a  $d(\mathbf{a}_k)$  that is less than or equals to  $2^{k-1} - 1$ . When  $E$  instead of  $O$  is used, it indicates an even  $c$  instead of an odd one. Also, when the up arrow is used instead of the lower one it indicates that  $d$  is greater than or equals to  $2^{k-1}$ . Hence, for a fixed  $k$ , any sequence  $\mathbf{a}_k$  must belong to either  $\mathbf{A}_k^{O\downarrow}$ ,  $\mathbf{A}_k^{E\downarrow}$ ,  $\mathbf{A}_k^{O\uparrow}$  or  $\mathbf{A}_k^{E\uparrow}$ . Note that for  $k+1$ , any sequence  $\mathbf{a}_{k+1}$  will have  $a_k$  leading the sequence followed by a sequence that belongs to either  $\mathbf{A}_k^{O\downarrow}$ ,  $\mathbf{A}_k^{E\downarrow}$ ,  $\mathbf{A}_k^{O\uparrow}$  or  $\mathbf{A}_k^{E\uparrow}$ . Also, note that the leading sign of any sequence that belongs to either  $\mathbf{A}_k^{O\downarrow}$  or  $\mathbf{A}_k^{E\downarrow}$  is negative (i.e.,  $a_{k-1}$  has negative sign or binary digit 0) as  $d$  is less than or equals to  $2^{k-1} - 1$ . The opposite is true (i.e.,  $a_{k-1}$  has positive sign or binary digit 1) when the up arrow is used. For example, when  $a_k < 0$  then the sequences  $a_k^-; \mathbf{A}_k^{O\downarrow}$ , which stacks the negative  $a_k$  in front of all sequences  $\mathbf{A}_k^{O\downarrow}$ , will start with two consecutive minus signs implying  $c(a_k^-; \mathbf{A}_k^{O\downarrow}) = c(\mathbf{A}_k^{O\downarrow})$  which is odd. Also since the leading sign is negative, then  $d(a_k^-; \mathbf{A}_k^{O\downarrow}) \leq 2^k - 1$  which both imply that the sequences  $a_k^-; \mathbf{A}_k^{O\downarrow} \subseteq \mathbf{A}_{k+1}^{O\downarrow}$ . Another example, when  $a_k > 0$  then the sequences  $a_k^+; \mathbf{A}_k^{O\downarrow}$  will start with a consecutive sign change (i.e., a  $+$  followed by a  $-$ ) followed by an odd number of consecutive sign changes which results in  $c(a_k^+; \mathbf{A}_k^{O\downarrow})$  being even. Also since the leading sign is positive, then  $d(a_k^+; \mathbf{A}_k^{O\downarrow}) \geq 2^k$  and the sequences  $a_k^+; \mathbf{A}_k^{O\downarrow} \subseteq \mathbf{A}_{k+1}^{E\uparrow}$ . With the same procedure,

1.  $\mathbf{A}_{k+1}^{O\downarrow}$  is the union of both  $a_k^-; \mathbf{A}_k^{O\downarrow}$  and  $a_k^-; \mathbf{A}_k^{E\uparrow}$ .
2.  $\mathbf{A}_{k+1}^{O\uparrow}$  is the union of both  $a_k^+; \mathbf{A}_k^{O\uparrow}$  and  $a_k^+; \mathbf{A}_k^{E\downarrow}$ .
3.  $\mathbf{A}_{k+1}^{E\downarrow}$  is the union of both  $a_k^-; \mathbf{A}_k^{O\uparrow}$  and  $a_k^-; \mathbf{A}_k^{E\downarrow}$ .
4.  $\mathbf{A}_{k+1}^{E\uparrow}$  is the union of both  $a_k^+; \mathbf{A}_k^{O\downarrow}$  and  $a_k^+; \mathbf{A}_k^{E\uparrow}$ .

For induction, let us assume that  $d(\mathbf{A}_k^{O\downarrow})$  is odd,  $d(\mathbf{A}_k^{O\uparrow})$  is even,  $d(\mathbf{A}_k^{E\downarrow})$  is even and  $d(\mathbf{A}_k^{E\uparrow})$  is odd. Looking at (1) since  $d(a_k^-; \mathbf{A}_k^{O\downarrow}) = d(\mathbf{A}_k^{O\downarrow})$  is odd and  $d(a_k^-; \mathbf{A}_k^{E\uparrow}) = d(\mathbf{A}_k^{E\uparrow})$  is odd, then  $d(\mathbf{A}_{k+1}^{O\downarrow})$  is odd. Similarly looking at (2), since  $d(a_k^+; \mathbf{A}_k^{O\uparrow}) = 2^k + d(\mathbf{A}_k^{O\uparrow})$  is even and

$d(a_k^+; \mathbf{A}_k^{E\downarrow}) = 2^k + d(\mathbf{A}_k^{E\downarrow})$  is even, then  $d(\mathbf{A}_{k+1}^{O\uparrow})$  is even. With the same procedure, then for (3) and (4)  $d(\mathbf{A}_{k+1}^{E\downarrow})$  is even while  $d(\mathbf{A}_{k+1}^{E\uparrow})$  is odd. This completes the inductive step and the proof is complete.

Lemma 2: The probability that  $d(\mathbf{a}_k)$  is odd when  $d(\mathbf{a}_k) \leq 2^{k-1} - 1$  is  $(1-p)p$ . Also, the probability that  $d(\mathbf{a}_k)$  is even when  $d(\mathbf{a}_k) \geq 2^{k-1}$  is  $(1-p)p$ .

Proof of Lemma 2: For the first part, since  $d(\mathbf{a}_k)$  is odd, then the sign of the trailing term (i.e.,  $a_0$ ) is positive which has a binary representation of 1. Also, since  $d(\mathbf{a}_k) \leq 2^{k-1} - 1$  then the sign of the leading term (i.e.,  $a_{k-1}$ ) is negative which has a binary representation of 0. All intermediate terms can be either positive or negative. The probability of obtaining a sequence that leads with a minus sign and ends up with a plus sign is precisely  $(1-p)p$ . For the second part, since  $d(\mathbf{a}_k)$  is even, then the sign of the trailing term (i.e.,  $a_0$ ) is negative which has a binary representation of 0. Also, since  $d(\mathbf{a}_k) \geq 2^{k-1}$  then the sign of the leading term (i.e.,  $a_{k-1}$ ) is positive which has a binary representation of 1. All intermediate terms can be either positive or negative. The probability of obtaining a sequence that leads with a plus sign and ends up with a minus sign is precisely  $(1-p)p$ . This completes the proof.

From Lemma 1 and 2, the probability that  $c(\mathbf{a}_k)$  is odd is precisely the sum of the probability that  $d(\mathbf{a}_k)$  is odd when  $d(\mathbf{a}_k) \leq 2^{k-1} - 1$  and the the probability that  $d(\mathbf{a}_k)$  is even when  $d(\mathbf{a}_k) \geq 2^{k-1}$ , which is  $2p(1-p)$  and the proof is complete.

### 3.4 Complex Multispecies Models

To investigate whether the probability of feasibility in complex multispecies models has similar patterns to those shown in 1-dimensional models, we focus on the multivariate generalization of Model (3.1):

$$\frac{dN_i}{dt} = \frac{N_i f_i(\mathbf{N})}{q_i(\mathbf{N})}, \quad i = 1, \dots, n, \quad (3.6)$$

where  $\mathbf{N}$  is a vector of species abundances. Model (3.6) can be characterized by two quantities: its number of free-equilibrium points and the joint distribution of its parameters.

Equilibrium points (known as  $N_i^*$ ) are the solutions to all  $N_i$  in Eqn. (3.6) when the left-hand side (LHS) of the equation is equal to zero. These equilibrium points, as mentioned

in the previous chapter, can be classified as free or rigid [81]. Free-equilibrium points have non-zero components (can be complex) and can move freely within the state space as a function of parameter values, while rigid-equilibrium points are restricted in space such that they contain at least one zero (i.e.,  $N_i^* = 0$ ). That is, rigid-equilibrium points are restricted to particular regions of the state space regardless of the values that model parameters can take and contain at least one zero coordinate (i.e., boundary-equilibrium points). Instead, the location of free-equilibrium points are not restricted in space and are completely dependent on model parameters. This implies that only free-equilibrium points can lead to feasible systems (i.e.,  $N_i^* > 0$  for  $i = 1, \dots, n$ ). These definitions further reveal that the number of free-equilibrium points ( $\Theta$ ) is, in fact, the multivariate generalization of the polynomial degree  $m$  seen in the 1-dimensional case.

Following the definitions above, we use  $\Theta$  as the measure of complexity of a model. When parameters of  $f_i(\mathbf{N})$  are independent and unrestricted for all  $i$ ,  $\Theta$  can be analytically obtained by computing the number of complex roots of Eqn. (3.6) [64, 81]. However, when parameters are not independent or restricted, that  $\Theta$  becomes an upper bound and the exact value can be computed using the software PHClab package [93]. Note that other measures of complexity have been used in the literature [11, 94]. However, these other measures are either at the level of system complexity (such as dimensionality or connectivity) or at the level of assumed mechanisms in a model (e.g., Type I vs Type II functional responses). Instead our measure of complexity makes no prior assumption about the complexity of a model, but integrates all this information to provide a measure of the enrichment in dynamics that can be derived from a model [81].

Assuming Eqn. (3.4) as the expression for the probability of feasibility in multidimensional systems where  $m$  is replaced by  $\Theta$ ,  $p(\Theta)$  can be further simplified under two key observations: (i) The number of free-equilibrium points  $\Theta$  is expected to be large in multidimensional systems. This observation has been shown for LV models with HOIs under an arbitrary choice of parameter values, where  $\Theta$  increases exponentially with the dimension of the system [81]. (ii) The overestimate  $\hat{E}(\Theta)$  is very small compared to  $\Theta$  (i.e.,  $\hat{E}(\Theta)/\Theta \ll 1$ ). This second observation has been shown for 1-dimensional systems with standard Gaussian distributions (see Chapter 3.2). Specifically,  $E(m) \approx \log(m)/\pi$ , which is much smaller than  $m$  for large  $m$ . Building on these two observations, we can rewrite

the expected probability of feasibility in multidimensional systems as

$$p(\Theta) \approx 1 - \exp(-\hat{E}(\Theta)). \quad (3.7)$$

The goodness in the approximation of Eqn. (3.7) to Eqn. (3.4) can be shown by sampling over the  $\Theta$ - $\hat{E}$  space. For example, setting  $\Theta = 1000$  and  $\hat{E} = 1$ , the evaluated expression  $1 - (1 - \hat{E}(\Theta)/\Theta)^\Theta = 0.632305$  is close to the evaluated expression  $1 - \exp(-\hat{E}(\Theta)) = 0.63212$ . Importantly, the joint distribution of parameters in Model (3.6) affects how  $\hat{E}$  is related to  $\Theta$ . As we have shown, in 1-dimensional systems with i.i.d. probability distributions,  $\hat{E}$  increases with the polynomial degree  $m$ . Thus, following Eqn.(3.7), the assumption  $\hat{E}(\Theta_1) > \hat{E}(\Theta_2)$  when  $\Theta_1 > \Theta_2$  implies that  $p(\Theta_1) > p(\Theta_2)$ . That is, we expect that  $p(\Theta)$  increases with  $\Theta$  in multidimensional systems as well. However, as in the univariate case, there are also exceptions to this pattern. Specifically, when  $\Theta > 1$  is small, the relationship  $\hat{E}(\Theta) > \hat{E}(1)$  can be violated. This is because models with  $\Theta = 1$  and  $\Theta > 1$  are fundamentally different. Using arbitrary model parameters with the LV model (i.e.,  $\Theta = 1$ ), the solo free-equilibrium point must have real coordinates. Instead, for complex models (i.e.,  $\Theta > 1$ ) free-equilibrium points are generally complex [81]. Thus, when  $\Theta$  is small but  $\Theta > 1$ , the comparison between  $\hat{E}(\Theta)$  and  $\hat{E}(1)$  is unclear and becomes dependent on the distribution. However,  $\hat{E}(\Theta) > \hat{E}(1)$  is expected to hold with the increase of free-equilibrium points. These results show that the complexity of a model can be characterized by its number of free-equilibrium points ( $\Theta$ ), which are a function of the polynomial degree and system's dimension.

As in the univariate case, stability in the multivariate case is related to the feasibility problem [89]. In multidimensional systems, we do not necessarily need an asymptotically stable free equilibrium point for the existence of species coexistence [41, 95]. For example, species coexistence can be possible when there exists both a trajectory from the initial condition towards any of the feasible free-equilibria and if after some sufficiently large time, the maximum distance between the feasible equilibrium and the trajectory is bounded [96]. That is, in the presence of an attracting direction in any of the feasible free-equilibrium points, species coexistence is possible given an appropriate initial condition [81]. Thus, as we have discussed for the 1-dimensional case (where a stable equilibrium is typically followed by an unstable one), increasing the number of feasible free-equilibrium points alone



increases on average the probability of the existence of at least one trajectory compatible with such points. For example, let us assume a scenario where we have all repelling feasible free-equilibrium points (i.e., given an unstable system), then adding an extra feasible free-equilibrium point increases the probability of the existence of a non-repelling direction and consequently attaining coexistence. In the next sections, we test our hypotheses above by illustrating the expected behavior of specific multidimensional models using modifications to the linear LV model with HOIs and nonlinear functional responses.

### 3.4.1 Revisiting Higher-Order Interactions

The multidimensional model with HOIs can be generally written as [48]:

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{l=1}^{m'-1} \sum_{1 \leq j_1 \leq j_2 \leq \dots \leq j_l \leq n} a_{ij_1 j_2, \dots, j_l} N_{j_1} N_{j_2} \dots N_{j_l}), \quad i = 1, \dots, n, \quad (3.8)$$

where the  $r$ 's represent species growth rates,  $m'$  is the interaction order (with  $m' = 2$  we recover the linear LV model), double indexed  $a$ 's represent pairwise species interaction coefficients, and the remaining  $a$ 's correspond to HOIs. Note that the feasibility problem in Model (3.8) is identical to the feasibility problem of  $dN_i/dt = N_i f_i(\mathbf{N})$ —which is the same as the feasibility problem studied in Model (3.6). That is, in both cases, the feasibility problem involves solving the multivariate polynomial system  $f_i(\mathbf{N}^*) = 0$  for  $i = 1, 2, \dots, n$ . Hence, without loss of generalization, we can think of the feasibility problem of a general fractional polynomial system as that of an LV model with HOIs.

Following our analysis of 1-dimensional systems, let us assume that in Model (3.8), the  $r$ 's and the  $a$ 's are all Gaussians i.i.d. with mean zero (the variance does not affect the probability of feasibility or the location of free-equilibrium points since for any constants  $c \neq 0$ , the roots of the multivariate polynomial system  $cf_i(\mathbf{N}^*) = 0$  for  $i = 1, 2, \dots, n$  do not change). For illustration purposes, let us consider multispecies systems of dimension two, three, and four (i.e.,  $n = 2, 3, 4$ ) with interaction order given by  $m' = 2, 3, 4, 5, 6$ . Then, we define  $p_G(n, m')$  as the probability of feasibility with  $n$  species and interaction order  $m'$ . The probability of feasibility is calculated using the PHClab package [93], which numerically solves the polynomial system defined by Eqns. (3.8) after setting  $dN_i/dt = 0$  and deleting  $N_i$  from the right-hand side (RHS). Under a generic choice of parameter values,

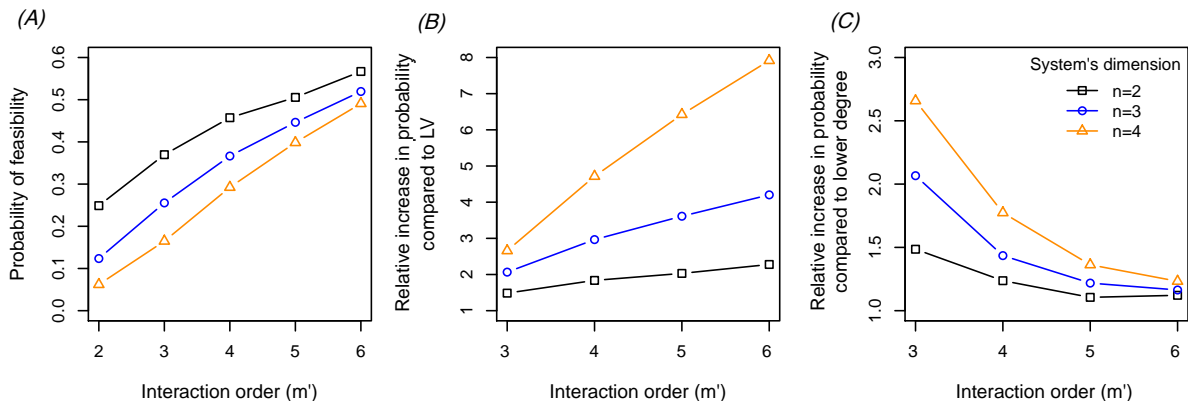


Figure 3-6: Probability of feasibility increases as a function of systems' dimension and polynomial degree. Panel (A) shows the probability of feasibility (i.e.,  $p(n, m')$ ) as a function of system size  $n$  and interaction order  $m'$  in the linear Lotka-Volterra (LV) model (i.e.,  $p(n, m' = 2)$ ) and modifications with higher-order interactions (i.e.,  $p(n, m' > 2)$ ). In general, probabilities decrease with system size, but increase as a function of interaction order. Panel (B) shows the relative increase in the probability of feasibility of modified models compared to the linear LV model (i.e.,  $p(n, m')/p(n, 2)$ ). The higher the system size and interaction order, the higher the relative increase. Panel (C) shows the relative increase in the probability of feasibility of modified models compared to lower degree models (i.e.,  $p(n, m')/p(n, m' - 1)$ ) for  $n = 2, 3, 4$  species communities. The higher the interaction order, the higher the saturation and, in turn, the lower the relative increase. Note that parameters ( $r$ 's and the  $a$ 's) in Eqn. (3.8) are all assumed to be standard Gaussians i.i.d. with zero mean and unit variance.

we showed [81] that the number of free-equilibrium points is given by  $\Theta = (m' - 1)^n$ . It is also well known that in the case of the linear LV model (i.e.,  $m' = 2, \Theta = 1$ ) under an arbitrary choice of parameter values (distribution centered on zero), the probability of feasibility is given by  $p_G(n, 2) = 1/2^n$  for all  $n$  [97, 98]. However, as in the 1-dimensional case, Figure 3-6A shows that when HOIs are added, the probability of feasibility increases as a function of the polynomial degree  $m'$ . The figure also shows that if two multispecies models have the same polynomial degree  $m'$ , the one with the lower dimension  $n$  exhibits a higher probability of feasibility (i.e.,  $p_G(n_1, m') > p_G(n_2, m')$  for all  $m'$  if and only if  $n_1 < n_2$ ). This result can be expected from the fact that the probability of feasibility in a system decreases on average as the number of species increases [98, 99]. Note that if two multispecies models have the same interaction order  $m'$ , but different dimension  $n$ , they also differ in the number of model parameters and free-equilibrium points  $\Theta$ .

Next, we use the results above to study how the explanatory power of feasibility with complex models change relative to the linear LV model. Figure 3-6B shows that multispecies

models with the same interaction order  $m' > 2$  exhibit a relative increase in the probability of feasibility compared to the linear LV model (i.e.,  $p_G(n, m')/p_G(n, 2)$ ) as a function of their dimension  $n$ . For example, adding up to quadratic terms (i.e.,  $m' = 3$ ), the relative probability of feasibility increases by a factor of 1.5, 2, and 2.6 for 2, 3, and 4 species, respectively. Note that increasing the interaction order substantially increases the number of model parameters in a high dimensional system, which turns into high amplifications in probability. Nevertheless, Figure 3-6C shows that this relative increase in the probability of feasibility reduces as more parameters are added (i.e.,  $p_G(n, m')/p_G(n, m' - 1)$ ). That is, adding extra parameters to a multispecies model, that is already defined by a large number of parameters, increases the relative probability of feasibility less than in a multispecies model with fewer number of parameters. This implies that the largest relative increase in the probability of feasibility will happen when adding HOIs to the linear LV model with a large number of species.

### 3.4.2 Functional Responses and Parameter Restrictions

The cases above did not consider any sort of parameter restrictions, hence we now shift our focus to study how the probability of feasibility with complex multispecies models changes as a function of sign restrictions. Typically, these restrictions are imposed into models to specify particular structures and dynamics, such as antagonistic, competitive, and mutualistic [10]. In particular, these dynamics are expressed and modified through a variety of nonlinear functional responses [11, 35]. Hence, to explicitly incorporate functional responses into our general multidimensional model (Eqn. 3.6), we use the form:

$$\frac{dN_i}{dt} = N_i(r_i + a_{ii}N_i - \sum_{\substack{1 \leq j \leq n \\ j \neq i}} a_{ij}N_j\phi_{ij}), \quad i = 1, \dots, n, \text{ where} \quad (3.9)$$

$$\phi_{ij} = \frac{N_i^{m''-2}}{1 + \sum_{k \in I'_{q(i,j)}} h_{k,q(i,j)} N_k^{m''-1}}, \quad m'' = 2, 3, \dots \quad (3.10)$$

Define  $\phi_{ij} = 1$  when  $m' = 1$ . Functional responses (i.e.,  $\phi$ 's), which are quotients of two polynomials determined by the abundances of the prey, are dependent on the parameters:  $m''$ ,  $p$ 's,  $q$ 's,  $I$ 's, and  $h$ 's. The parameter  $m''$  in Eqn. (3.10) indicates the type of the functional response (i.e., Type I, Type II, and Type III functional responses are represented

by  $m'' = 1$ ,  $m'' = 2$ , and  $m'' = 3$ , respectively). For any pair of species  $(i, j)$ , the functions  $p(i, j)$  and  $q(i, j)$  represent the indices of the prey (or resource) and predator (or consumer), respectively (i.e., if  $i$  is the prey of  $j$  then  $p(i, j) = i$  and  $q(i, j) = j$ ). For each species  $k$ , we define  $I_k$  to be the set of indices that represent all their prey. By defining  $I_k$  for each species, all connections between species are known. To allow for different responses within the same species, for every predator  $q(i, j)$ , we define  $I'_{q(i, j)}$  to be a subset of  $I_{q(i, j)}$  which contains the index of the prey  $p(i, j)$  (i.e., that is  $p(i, j) \in I'_{q(i, j)} \subseteq I_{q(i, j)}$ ). The  $h$ 's in Eqn. (3.10) are constants and represent prey handling time in Type II functional responses. Note that the  $r$ 's and the  $a$ 's continue to represent species' growth rates and interaction coefficients, respectively.

It has been common to use forms of functional responses where the  $\phi$ 's are functions of the abundance of a single prey for which  $p(i, j)$  is the only element in  $I'_{q(i, j)}$  [11]. Nevertheless, the  $\phi$ 's can also be functions of the abundances of all prey, making  $I'_{q(i, j)} = I_{q(i, j)}$ . Here, we consider four commonly used cases: Type I, Type II with  $I'_{q(i, j)} = I_{q(i, j)}$  (i.e., Beddington-DeAngelis functional response), Type II with  $I'_{q(i, j)} = \{p(i, j)\}$ , and Type III with  $I'_{q(i, j)} = \{p(i, j)\}$ . We denote these responses by  $T_1$ ,  $T_{2m}$ ,  $T_{2s}$ , and  $T_{3s}$ , respectively. Note that in Eqn. (3.10)  $\phi_{ij} = \phi_{ji}$ , however, this symmetry can be broken to allow for more generalized types of functional responses by replacing the double subscript constant  $h_{k, q(i, j)}$  with a triple subscript constant  $h_{k, i, j}$  in Eqn. (3.10).

In Model (3.9) the  $a$ 's are not necessarily restricted to any particular value or sign. However, in predator-prey models,  $a_{ij}$  and  $a_{ji}$  have opposite signs for every  $i \neq j$ . Moreover, the ratio  $|a_{q(i, j), p(i, j)}|/|a_{p(i, j), q(i, j)}|$ , which is denoted by  $\epsilon_{ij}$ , is usually a constant between 0 and 1, and reflects the fraction of prey that is converted into a predator's abundance. This implies that the probability of feasibility with functional responses (or higher-order terms in general) can be different when adding or not parameter restrictions (e.g., sign restrictions defining who eats whom). Thus, to study the effect of sign restrictions in the coefficients of  $a$ 's, we rewrite Model (3.9) as

$$\frac{dN_i}{dt} = N_i(r_i + a_{ii}N_i - \sum_{j \in S_i \setminus I_i} a_{ij}N_j\phi_{ij} + \sum_{j \in I_i} \epsilon_{ji}a_{ji}N_j\phi_{ij}), \quad i = 1, \dots, n, \quad (3.11)$$

where  $S_i = \{1, 2, \dots, n\} \setminus \{i\}$  (backslash symbol means set difference) and all  $a_{ij}$ 's are non-negative except when  $i = j$  (unrestricted in sign).

Additionally, it is worth noticing that the feasibility in Model (3.9) is dependent on the common numerator of its RHS, and the solution becomes similar to the previous case of an LV model with HOIs, where parameters are linked. That is, the higher the diversity and order of functional responses added into a model, the higher the order of terms added to the numerator of the RHS of Eqn. (3.9). To show this, let us write all  $\phi_{ij}$ 's as quotients of two polynomials  $\phi_{ij} = \phi_{ij}^U / \phi_{ij}^D$ . Thus, Eqn. (3.9) has a common denominator given by  $\Phi_i = \prod_{k \in S_i} \phi_{ik}^D$ , whose number of terms and leading order depend on the specified functional responses. Then, let us define  $\bar{\Phi}_{ij} = \Phi_i \phi_{ij}^U / \phi_{ij}^D$ , where  $\bar{\Phi}_{ij}$  is the same as  $\Phi_i$  but with the term  $\phi_{ij}^D$  replaced by  $\phi_{ij}^U$ —which also depends on the specified functional responses. This process implies that the common numerator of the RHS of Eqn. (3.9) (after deleting  $N_i$  outside the bracket) is a multivariate polynomial expressed in terms of species abundances given by the following expression:

$$r_i \bar{\Phi}_i + a_{ii} N_i \bar{\Phi}_i - \sum_{\substack{1 \leq j \leq n \\ j \neq i}} a_{ij} N_j \bar{\Phi}_{ij}, \quad i = 1, 2, \dots, n. \quad (3.12)$$

Therefore, the roots of Eqns. (3.12) determine the free-equilibrium points of Eqns. (3.9), allowing the common numerator of the RHS of Eqn. (3.11) to be written in a form similar to Eqn. (3.12). Note that when moving from Type  $T_1$  to  $T_{2s}$  and then to  $T_{3s}$ , the order of added terms increases. Moreover, when  $T_{2m}$  functional responses are used, which are functions of all prey abundances of a specific predator, there will be less distinct denominators in each line of Eqn. (3.9). This is because all prey of a specific predator will have the identical denominator of Eqn. (3.10), and, in return, it will have fewer higher-order terms added to the numerator in Eqn. (3.12) than what would be added by  $T_{2s}$ .

To numerically compute the probability of feasibility for different types of functional responses (i.e.,  $T_1$ ,  $T_{2m}$ ,  $T_{2s}$  and  $T_{3s}$ ), we consider the following models and parameter distributions. Unrestricted Model ( $M_U$ ): Model (3.9) is used to represent species dynamics (the parameters are  $a$ 's,  $h$ 's and  $r$ 's) and the distribution of parameters is given by (i) all  $a$ 's are uniform in  $[-\sqrt{3}, \sqrt{3}]$ , (ii) all  $r$ 's are uniform in  $[-\sqrt{3}, \sqrt{3}]$  except for  $r_1$  (uniform in  $[0, 2\sqrt{3}]$ ) and  $r_n$  (uniform in  $[-2\sqrt{3}, 0]$ ), and (iii) all  $h$ 's are uniform in  $[0, 2\sqrt{3}]$  (notice that all these parameters have a unit variance). Restricted Model ( $M_R$ ): Model (3.11) is used to represent species dynamics (the parameters are  $a$ 's,  $h$ 's,  $r$ 's and the  $\epsilon$ 's) and the distribution of parameters is given by (i) all  $a_{ij}$ 's are uniform in  $[0, 2\sqrt{3}]$  except when  $i = j$

2*Type / Size	<b>n=2</b>			<b>n=3</b>			<b>n=4</b>		
	$\Theta$	$p_U$	$p_R$	$\Theta$	$p_U$	$p_R$	$\Theta$	$p_U$	$p_R$
$T_1$	1	0.2543	0.5378	1	0.1256	0.2299	1	0.0662	0.0923
$T_{2m}$	3	0.2661	0.3248	10	0.1391	0.1817	23	0.0760	0.0957
$T_{2s}$	Same as $T_{2m}$			12	0.1457	0.2031	62	0.0920	0.1226
$T_{3s}$	5	0.2842	0.3486	33	0.1807	0.2802	289	0.1347	0.2422

Table 3.1: Probability of feasibility and number of free-equilibrium points as a function of system's size and polynomial degree (functional response). For  $n = 2, 3, 4$  species systems (columns) and four different types of functional responses  $T_1, T_{2m}, T_{2s}, T_{3s}$  (rows), the table shows the probability of feasibility for sign-unrestricted models ( $p_U \equiv p(n, \text{type}, M_U)$ ) and sign-restricted models ( $p_R \equiv p(n, \text{type}, M_R)$ ). For each of these combinations, the table also shows the average number of free-equilibrium points ( $\Theta$ ) computed using the solver PHCLab. Note that  $\Theta$  can numerically fluctuate due to either parameters yield less roots or because the solver eliminates leading terms with small coefficients (which do not affect the existence of a feasible root). Probabilities decrease with systems size. Both probabilities and free-equilibrium points tend to increase with polynomial degree. For each system size,  $p_U$  increases with the value of  $\Theta$ . Similarly, for  $\Theta > 1$ ,  $p_R$  increases with the value of  $\Theta$ .

( $a_{ii}$ 's are uniform between  $[-\sqrt{3}, \sqrt{3}]$ ), (ii) all  $r$ 's are uniform in  $[-\sqrt{3}, \sqrt{3}]$  except for  $r_1$  (uniform in  $[0, 2\sqrt{3}]$ ) and  $r_n$  (uniform in  $[-2\sqrt{3}, 0]$ ), (iii) all  $h$ 's are uniform in  $[0, 2\sqrt{3}]$ , and (iv) all  $\epsilon$ 's are uniform in  $[0, 1]$ . In addition, we assume an interaction network defined by  $p(i, j) = \min(i, j)$  for every  $1 \leq i, j \leq n$ , where  $i \neq j$  (i.e., all species are connected to each other). This assumption requires that  $I_k = \{1, 2, \dots, k-1\}$  for all  $k$  where  $I_1$  is an empty set (i.e., every species is a predator of all lower indexed species and is a prey to all higher indexed species). Next, we compute the probability of feasibility  $p(n, \text{type}, \text{model})$  for  $n$ -species systems ( $n = 2, 3, 4$ ). Note that  $p(2, T_{2m}, M_i) = p(2, T_{2s}, M_i)$  for  $i = \{M, U\}$  as the solo predator in the network has a single prey. These parameter values are chosen to simply illustrate the effect of sign restrictions and are not intended to reflect any specific ecological process.

In general, as the complexity of a model increases (either with dimension or with adding extra processes), its number of roots (free-equilibrium points) also increases, which leads to an increase in the computational time needed to solve multivariate polynomials for a single trial. Thus, any exponential increase in the number of free-equilibrium points makes computing the probability of feasibility a hard task. Thus, to reasonably compute these probabilities, we use 25,000 trials for each combination  $p(n, \text{type}, M_i)$ . The results are presented in Table 3.1. Note that the probability of feasibility agrees with the theoretical value  $p(n, T_1, M_U) = 1/2^n$  up to 2 digits, which is a good indicator for comparison purposes.

Table 3.1 shows that the number of free-equilibrium points ( $\Theta$ ) of both models ( $M_U$  and  $M_R$ ) increases as a function of the polynomial degree, i.e., functional responses  $T_1$ ,  $T_{2m}$ ,  $T_{2s}$  and  $T_{3s}$  in that order. Focusing on the unrestricted model ( $M_U$ ) and controlling for the number of species  $n$  (for any  $n$ , columns in table), Table 3.1 shows that the increase in the probability of feasibility is consistent with the increase in  $\Theta$  (i.e., complexity). That is,  $p(n, T_1, M_U) < p(n, T_{2m}, M_U) < p(n, T_{2s}, M_U) < p(n, T_{3s}, M_U)$ . These inequalities are also present in the restricted model ( $M_R$ ), except for  $n = 2$  and  $n = 3$ , where  $p(n, T_1, M_R) > p(n, T_{2m}, M_R)$ . However, at  $n = 4$  (under a higher  $\Theta$  when  $T_{2m}$  is used) the inequality is recovered again. It is worth mentioning that unlike the case of the LV model with HOIs, where both the number of free-equilibrium points and the number of parameters increase as a function of the polynomial degree, in the case of functional responses  $T_{2m}$ ,  $T_{2s}$  and  $T_{3s}$ , the number of parameters is constant. Nevertheless, the increase in the probability of feasibility, while not as high as in the LV model with HOIs, is still observed despite fixing the number of parameters and whether the  $a$ 's are restricted in sign or not.

The analysis above allows us to make a distinction between complex models and the linear LV model. Table 3.1 reveals that the probability of feasibility is a monotonic and saturating function of complexity when  $\Theta > 1$  (e.g., moving from type  $T_{2m}$  to  $T_{2s}$  to  $T_{3s}$ ). However, when we compare cases with  $\Theta = 1$  against cases with  $\Theta > 1$ , the probability of feasibility of a linear LV model (i.e.,  $\Theta = 1$ ) will be exceeded only as soon as a minimum level of complexity ( $\Theta^*$ ) is reached. For example, under the restricted model  $M_R$ , the probability of feasibility will exceed that of the linear LV model when  $\Theta \geq 23$  for  $n = 2, 3, 4$ . This level of complexity ( $\Theta$ ) differs for each distribution. By contrast, under the unrestricted model  $M_U$ , this level decreases to  $\Theta \geq 3$  for all  $n$ 's regardless of functional response.

The previous results can be explained by noticing the fundamental difference between complex models and the linear LV model. Under arbitrary model parameters, the solo free-equilibrium point in LV model must be real (i.e., all its coordinates are real). Instead, in complex models free-equilibrium points are generally complex [81]. Thus, the initial entrance to the complex domain represents a handicap for complex models, yet this is quickly recovered by the increase of free-equilibrium points. These concepts can be verified analytically: defining the probability of feasibility  $p(\Theta)$  by the form  $1 - (1 - \hat{E}(\Theta)/\Theta)^\Theta$ , let us assume that  $p(\Theta) < p(1)$ , leading to  $\hat{E}(\Theta) \leq \Theta(1 - (1 - \hat{E}(1))^{1/\Theta})$ . If  $\Theta$  increases, the RHS of the inequality will approach  $-\ln(1 - \hat{E}(1))$  independently of  $\Theta$ . However, we

know already that  $\hat{E}(\Theta)$  increases with  $\Theta$ . This implies the existence of a minimum  $\Theta^*$  for which  $\hat{E}(\Theta^*) > -\ln(1 - \hat{E}(1))$  and subsequently  $p(\Theta^*) > p(1)$ . Because of the expected drastic increase in  $\Theta$  as a function of the dimension of the system [81], it can be proved that no matter the parameter restrictions imposed in a model,  $\Theta^*$  can always be exceeded by increasing either dimensionality or polynomial degree. This increase will yield a higher probability of feasibility than in the linear LV model regardless of the specific mechanisms invoked.

Indeed, Table 3.1 shows that the relative increase in the probability of feasibility compared to the linear LV model (i.e.,  $p(n, \text{type}, M_i)/p(n, T_1, M_i)$ , for  $i = \{U, R\}$ ) is a function of  $n$  for any given functional response. For instance, when  $T_{3s}$  is used as functional response, the probability for models  $M_U$  and  $M_R$  increases by a factor of 1.1, 1.4, 2 and 0.6, 1.2, 2.6 for  $n = 2, 3, 4$  species, respectively. This increasing pattern is also consistent using  $T_{2m}$  and  $T_{2s}$ . Therefore, adding nonlinear processes to a linear LV model ( $T_1$ ) increases the number of free-equilibrium points; which, in turn, contributes to the increase in the probability of feasibility—this is further magnified as the number of species increases. Additionally, note that the number of parameters is fixed for the functional responses  $T_{2m}$ ,  $T_{2s}$  and  $T_{3s}$ , which differ only by a few terms (the  $h$ 's) compared to  $T_1$ . Therefore, unlike the case of HOIs, the relative increase in the probability of feasibility is not necessarily larger when moving from Type I to Type II (either  $T_{2m}$  or  $T_{2s}$ ) than the increase observed when moving from Type II to Type III. For example, focusing on the model  $M_R$  with  $n = 4$  species and moving from  $T_1$  to  $T_{2s}$  and then from  $T_{2s}$  to  $T_{3s}$ , the relative increase is 1.3 and 2, respectively.

It is also worth noticing that while functional responses  $T_{2m}$ ,  $T_{2s}$  and  $T_{3s}$  are widely used in the literature, the functional response  $T_{2m}$  can be considered a more realistic type [11]. Interestingly, Table 3.1 shows that models with  $T_{2m}$  have less free-equilibrium points (less complexity) than the other types, and their probability of feasibility is the closest to the linear LV model. This can suggest that realistic models should deviate the least from the probability of feasibility of the linear LV model. Nevertheless, the difference in its probability of feasibility compared to the linear LV model will increase with dimensionality. This is evident by the number of free-equilibrium points, which exceeds that obtained from the LV model with HOIs at interaction order  $m' = 3$  (i.e., adding up to quadratic terms to the linear LV model results in  $2^n$  free equilibrium points) at  $n \geq 3$ —implying at least an exponential increase in  $\Theta$  with dimensionality. Focusing on  $T_{2m}$ , if the symmetry is broken



in Eqn. (3.10) by replacing a few  $h_{k,q(i,j)}$  with  $h_{k,i,j}$  (which can differ only slightly from  $h_{k,q(i,j)}$ ), the number of free-equilibrium points can go beyond that of  $T_{3s}$ , increasing the probability of feasibility significantly. Furthermore, the probability of feasibility with functional responses (under parameter restrictions) is smaller than in the linear LV model for  $n = 2, 3$  species except when  $n = 3$  and the functional response  $T_{3s}$  is used. However, this pattern already disappears with 4 species, confirming that one cannot directly extrapolate our understanding of ecological dynamics from low to high dimensions [61, 100, 101].

### 3.5 Ecological models: Higher Complexity In, Higher Feasibility Out

One of the main goals in ecological research is to understand the main factors that contribute to the persistence of multispecies systems [2, 10]. While simple ecological models (such as the linear LV model) are typically modified for the purpose of adding realism and dynamical richness, tractability is usually compromised [11, 14]. For example, it is well known that in the linear LV model (Type I), the number of feasible equilibrium solutions (a crucial condition for the persistence of ecological systems) is always one regardless of the dimension of the system, making this a limited but tractable model [41, 53]. By contrast, the addition of higher-order terms (specifically, polynomial fractions such as non-linear functional responses and higher-order interactions) invariantly increases the number of free-equilibrium solutions, making these rich but untractable models [81]. This reveals that without knowing the exact parameter values in a model, it is necessary to study from a probabilistic point of view the contribution of ecological processes (both mechanistic and phenomenological) to explaining the dynamics of multispecies systems.

Focusing on the feasibility of ecological systems (defined here as the probability of exhibiting at least one positive real root under an arbitrary choice of parameter values) in complex models (defined here as modifications to the LV model using multivariate polynomial fractions and with  $\Theta > 1$ ), we have shown that the probability of feasibility is a monotonic and saturating function of its complexity, regardless of the specific mechanism invoked. We have characterized this complexity by the number of free-equilibrium points ( $\Theta$ ) generated by a model, which is a function of the model's polynomial degree and dimension. We have

found that the probability of feasibility in a complex model ( $\Theta > 1$ ) will exceed the one in a linear LV model ( $\Theta = 1$ ) as soon as a minimum level of complexity ( $\Theta^*$ ) is reached. Importantly, this minimum level is modulated by parameter restrictions, but can always be exceeded via increasing the polynomial degree or system's dimension.

It is worth recalling that the number of free-equilibrium points in a model and its number of parameters are two different descriptors [81]. For example, the LV model with Type II functional responses has the same number of parameters as that of Type III, yet the number of free-equilibrium points is different in both models. This difference is important as we have shown that it is expected that the model with more free-equilibrium points will have a higher probability of feasibility. These findings could be perceived as a desirable advantage for complex models, as they can provide a higher probability of generating a feasible multispecies system (and richer dynamics). Unfortunately, this increase in probability happens no matter what type of specific mechanism is added, it all depends on its polynomial form—limiting the capacity to distinguish the actual contribution of a specific ecological process to the feasibility of a multispecies system.

For example, studies have investigated population dynamics resulting from mutualism by employing functional responses based on density-dependent benefits and costs [102–104], i.e., the  $\phi$ 's in Eqn. (3.9) are replaced with  $\phi - \phi^{\text{cost}}$  where functional responses are modified to add a cost term. However, as we have shown, adding cost terms to penalize for some benefits will not decrease the probability of feasibility, actually they will increase it. Similarly, in the study of food-web models [85], it is common practice to use multispecies functional responses (i.e., polynomial fractions of more than a single species) in order to include the effect of other predators or prey [105]. Note that the Types I, II, III functional responses are functions of the prey density only—a single species. But, as we have shown, any of these modifications can only increase the probability of feasibility. As a third example, the simple and ecologically-motivated idea of introducing carrying capacities to limit the growth of species (i.e., the total growth rate  $G_i$  of species  $i$  is replaced by  $G_i(1 - N_i/K_i)$ , where  $K_i$  is its carrying capacity) [72] also increases the probability of feasibility. Thus, regardless of whether a higher-order term (nonlinear mechanism) is well-ecologically motivated, expected to limit or enrich dynamics, or has absolutely no meaning, it is expected to increase the probability of feasibility in a multispecies model. This suggests that the explanatory contribution to feasibility of a proposed ecological mechanism must

be evaluated by its deviation from the expected behavior of its polynomial form.

The contribution of different ecological processes has been studied by showing how additional terms can help us to fit observed data [103]. Yet, fitting data has the same effect as introducing parameter restrictions [81]. Hence, under this fitting process, it is only expected that any additional process will increase on average the probability of explaining the dynamics of the feasible system. Furthermore, under certain cases, adding more process into a model can leave the probability the same as in the original restricted case (e.g., a linear LV mutualistic model with no self-regulation: adding negative-density dependence will increase the probability, while adding positive density-dependence will leave the probability invariant. Yet, this involves modifying an already restricted model rather than restricting a modified model). Thus, studies using fitting methodologies should contrast their results by using out-of-sample validations [106].

Our results motivate us to reconsider what constitutes a realistic model, or how much complexity can be appropriate to add into a model to mimic realistic ecological mechanisms. Do we need models to fit perfectly data? Or do we need models to explain and predict dynamics with minimal available information? Because it is virtually impossible to know the exact form of the equations governing the dynamics of multispecies systems, as well as the exact value of initial conditions, we believe that a first step towards answering these questions implies understanding the extent to which the complexity of a model provides an advantage over other models by virtue of their specific mechanisms invoked and not simply by their polynomial form. Otherwise, any mechanism can explain equally well any ecological dynamics, introducing the problem of model or structural unidentifiability [107]. Thus, in order to advance our causative knowledge of ecological dynamics, we need to understand the expected outcomes of our proposed models and their alternative hypotheses.



# Chapter 4

## Closed-Form Feasibility Conditions of Ecological Models

### 4.1 Introduction

Over more than 100 years, ecological research has been striving to derive the biotic and abiotic conditions compatible with the coexistence of a given group of interacting species (also known as an ecological system or community) [3–7]. These conditions can provide the keys to understand the mechanisms responsible for the maintenance of biodiversity and the tolerance of ecological systems to external perturbations [108, 109]. Because of the nature of this question, many efforts have been centered on developing phenomenological and mechanistic models to represent the dynamics of ecological systems and predict their behavior [10]. However, even if we had knowledge about the exact equations governing the dynamics of interacting species, extracting and solving the set of conditions compatible with the coexistence of such species remains a big mathematical challenge [11, 110]. Indeed, due to mathematical limitations, most of the analytical work looking at these coexistence conditions has focused on relatively simple 2-species systems or strictly particular cases of higher-dimensional systems [10, 12, 111]. In fact, even at the 2-species level, currently there is no general methodology that can provide us with a full analytical understanding about coexistence conditions for any given model. Therefore, the majority of work has relied on numerical simulations, which only provide a partial view of the dynamics conditioned by the choice of parameter values. Thus, because of the varying complexity of ecological

models and the arbitrary choice of model parameters, it has been difficult to derive general knowledge about coexistence conditions [11, 36].

Recent work has started to address the challenge above by focusing on the necessary conditions for species coexistence in equilibrium dynamics: feasibility [61]. Mathematically, the feasibility of a generic  $n$ -species dynamical system  $dN_i/dt = N_i f_i(\mathbf{N})/q_i(\mathbf{N})$ , where the  $f$ 's and  $q$ 's are multivariate polynomials in species abundances  $\mathbf{N} = (N_1, N_2, \dots, N_n)^T$ , corresponds to the existence of at least one equilibrium point  $\mathbf{N}^* = (N_1^*, N_2^*, \dots, N_n^*)^T > \mathbf{0}$  that satisfies  $dN_i/dt = 0 \forall i$ . Feasibility conditions are typically represented by inequalities as a function of model parameters. Traditionally, feasibility conditions have been attained by finding the isocline equations  $f_i(\mathbf{N}^*) = 0 \forall i$  and then solving for  $\mathbf{N}^*$  before finding the conditions that satisfy  $\mathbf{N}^* > \mathbf{0}$  [12, 61]. For example, let us focus on the Lotka-Volterra (LV) model of the form  $dN_i/dt = N_i(r_i + \sum_{j=1}^n a_{ij}N_j)$ , where  $a$ 's and  $r$ 's represent the interaction coefficients and the intrinsic growth rates, respectively. In the LV model, the isocline equations (for any dimension) can be written as  $\mathbf{r} + \mathbf{A}\mathbf{N}^* = \mathbf{0}$ , whose unique root is given by  $\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{r}$ . Therefore, feasibility conditions in this case are simply given by the inequality  $-\mathbf{A}^{-1}\mathbf{r} > \mathbf{0}$ . However, adding nonlinear functional responses or higher-order terms can increase exponentially the number of roots of the system [81]. Importantly, it is known from elimination theory (via Grobner basis) and Abel's impossibility theorem that it is impossible to solve analytically for  $\mathbf{N}^*$  when the number of roots of the system is five or more [112–114]. Similarly, using numerical approaches, it has been demonstrated that the probability of feasibility (the probability of finding at least one equilibrium point whose components are all positive by randomly choosing parameter values) is an increasing function of the model's complexity regardless of the invoked mechanism, whether they are ecologically motivated or have no meaning whatsoever [115]. This implies that traditional approaches are also unsuitable for finding the necessary conditions for coexistence in generic systems.

Here, we propose a general formalism to obtain for any population dynamics model the set of necessary conditions leading to the coexistence of a given ecological system. In this work, we propose a general framework that can find the feasibility conditions of any model in any dimensions without the need to solve for the equilibrium locations. In fact, we can separate those feasibility conditions to find conditions that guarantee exactly  $k$  feasible equilibrium points for any value  $k$ . In addition, we propose a methodology to compact these

conditions into smaller mathematical expressions that allow us analyze complex systems analytically where it was previously impossible to attain. With these tools in hand, we can find the range of parameters in any ecological model that are compatible with feasibility. With these in hand, we start with a methodology that finds the feasibility conditions of a univariate system, 2-species systems and multispecies systems. In each case, we will provide examples in each case to demonstrate the methodology and show that the obtained feasibility conditions are accurate. Also, for two and multispecies systems, we included application sections where we apply the methodology on the simplest ecological models, that are impossible to solve for the location of equilibrium points analytically, to find the range of parameters that are compatible with feasibility. The first example is a 2-species LV model with type III functional responses while the second example is a 3-species LV system with higher-order interactions. Finally, we discuss potential applications of our work, advantages and limitations of our formalism, and future avenues of research derived from our study.

## 4.2 One-Dimensional Systems (1 species)

In this section, we focus on univariate polynomial systems. The aim here is to find a closed form expression for the number of feasible roots in the system  $F(\Psi)$ , which is a function of model parameters  $\Psi$ . From the expression of  $F$  and exploiting its property, we can deduce feasibility conditions which are sets of polynomial inequalities. For this section, let us consider the following polynomial dynamical system of a single variable  $N$  as shown below

$$\frac{dN}{dt} = \frac{Nf(N)}{q(N)} \quad (4.1)$$

where  $f(N)$  is a polynomial of degree  $n$  whose coefficients are in  $\Psi$ . We already know that the number of roots of  $f(N)$  is  $n$ , a consequence of the Fundamental Theorem of Algebra. In this section, we derive the formula of  $F(\Psi)$  and derive feasibility conditions from it. The procedure involves the following steps:

1. Consider the monomial map  $m(N) = [1, N, N^2, \dots, N^{n-1}]^T$  which is of length  $n$  and let  $Q(N) = N$ . Next, denote the roots of  $f(N)$  by  $\eta_1, \eta_2, \dots, \eta_n$  then denote the

symmetric sums of the roots  $\eta_1^k + \eta_2^k + \dots + \eta_n^k$  by  $\Sigma_k$  for  $k = 0, 1, 2, \dots$

2. Construct the symmetric matrix  $S(s_1) = W\Delta W^t$  where  $W_{ij} = m_i(\eta_j)$  and  $\Delta_{ii} = Q(\eta_i - s_1)$  is a diagonal matrix. Note that all entries of  $S(s_1)$  contains only symmetric sums of the  $\eta$ 's (i.e,  $S(s_1)$  only contains  $s_1$ 's and  $\Sigma$ 's).
3. Construct the generating function  $G(N) = f'(N)/f(N)$  and evaluate the Laurent series of  $G(N)$  at  $N = \infty$ . The purpose of the series is to evaluate the  $\Sigma$ 's from looking at the coefficients of the Laurent series of  $G(N)$ , which are functions of model parameters  $\Psi$  (or coefficients of  $f(N)$ ). Assuming that  $\Sigma_k^*$  is the highest symmetric sum that is needed to be evaluated, the following identity is valid:

$$G(N) = \frac{\Sigma_0}{N} + \frac{\Sigma_1}{N^2} + \frac{\Sigma_2}{N^3} + \dots + \frac{\Sigma_{k^*}}{N^{k^*+1}} + O(N^{-k^*-2})$$

4. After evaluating the Laurent series up to order  $O(N^{-k^*+2})$ ,  $S(s_1)$  is a function of  $s_1$  and model parameters only, evaluate the characteristic polynomial of  $S(s_1)$  and write it in the form  $\det(S(s_1) - \lambda I) = (-1)^n \lambda^n + v_{n-1}(s_1) \lambda^{n-1} + \dots + v_0(s_1)$ . After that consider the sequence  $\mathbf{v} = [v_n(s_1) = (-1)^n, v_{n-1}(s_1), \dots, v_0(s_1)]$  and let  $V(s_1)$  be the number of consecutive sign changes in  $\mathbf{v}$ .
5. Define the function  $\text{sign}(x)$  to be 1 when  $x > 0$ , 0 when  $x = 0$  and  $-1$  when  $x < 0$ . Before writing down the expression of  $V(s_1)$ , note that in order to determine whether there is a sign change between two real numbers  $x$  and  $y$ , we simply evaluate  $[1 - \text{sign}(xy)]/2$ , which is 0 when  $x$  and  $y$  have the same sign and 1 otherwise. With this expression, the formula of  $V(s_1)$  is

$$V(s_1) = \sum_{i=0}^{n-1} \frac{1 - \text{sign}(v_i(s_1)v_{i+1}(s_1))}{2}.$$

6. For any interval  $(a, b]$ , the number of real roots of  $f(N)$  in  $(a, b]$  is exactly  $V(a) - V(b)$ . Hence, to obtain the analytical expression for  $F(\Psi)$ , we consider the interval  $(0, \infty)$  to obtain  $F(\Psi) = V(0) - V(\infty)$  or simply

$$F(\Psi) = \sum_{i=0}^{n-1} \frac{\text{sign}(v_i(\infty)v_{i+1}(\infty)) - \text{sign}(v_i(0)v_{i+1}(0))}{2}$$



7. Call  $v_0(0), \dots, v_{n-1}(0), v_0(\infty), \dots, v_{n-1}(\infty)$  the feasibility basis. Since each of the  $v_i$ 's can take a positive or a negative sign, then there are  $2^{2n}$  sign combinations the feasibility basis can take. Many of those combinations are impossible to occur (empty) for any choice of real  $\Psi$ . To detect the non-empty sign combinations, we compute the signs of all  $v_i$ 's as well as  $F(\Psi)$  for a range of parameters  $\Psi$ , where each component of  $\Psi$  varies independently in a large domain (say uniformly between  $-100$  and  $100$ ). This operation is cheaply computed as it is evaluation a few functions and not solving systems of equations. After that, we extract unique sign combinations of the  $v_i$ 's which yield  $F(\Psi) \geq 1$  and put them in a feasibility table whose rows are the signs of the  $v_i$ 's and columns are the individual feasibility conditions. For a cleaner representation of feasibility conditions, we can investigate all sign combinations of all the factors of each of the  $v_i$ 's (feasibility basis) and deleting all perfect square factors from them (if possible).
8. After we obtain the table, we perform minimization to it by combining the feasibility conditions (the columns). If two columns with the same value of  $F(\Psi)$  differ by a single sign (in one row), combine the two columns into one and place X in the row where there is a single sign difference to indicate that that no condition is needed to be imposed for the quantity associated with that row. We can combine columns with different values of  $F(\Psi)$  if the user does not care about separating the conditions based on the value of  $F$ . Then we iterate through the process until it terminates (no two columns differ by a single sign). For further minimization, we eliminate redundant signs where the sign of one or more quantities that constitute the basis implies the sign of another quantity in the same basis. For example, if the quantities  $ac$  and  $a^2 + b^2 - 3ac$  are in the basis, then  $ac < 0$  implies  $a^2 + b^2 - 3ac > 0$  making the later inequality redundant. Sometimes, the quantity in the basis is always positive or negative regardless of the sign of the others (e.g  $a^2 + b^2 > 0$  is always true). To find these cases, we go through a single column at a time and iterate through each quantity in the basis then compute the conditional probability that the quantity in the basis takes its correspondent sign given that all other remaining quantities in the same basis have their correspondent signs. If one or more conditional probabilities are 1, any of those quantities may be replaced by **X** in the table. We then repeat computing the same conditional probabilities which were 1 but without the **X**'ed quantity being

part of the calculation. Then, we check whether the conditional probabilities are still 1 or not. If any is 1, we delete a redundant sign and keep repeating the process until no conditional probability is 1. We then go through all columns and repeat the same process until it terminates

### 4.2.1 Illustrative example

Consider the following dynamical system

$$\frac{dN}{dt} = N(aN^2 + bN + c)$$

Consider the quadratic polynomial  $f(N) = aN^2 + bN + c$  in Eqn. (4.1) with  $\Psi = (a, b, c)$ . This example has the same mathematical form of a population model with an Allee effect [116]. Denote the roots of  $f(N)$  by  $\eta_1$  and  $\eta_2$ . Let  $m(N) = [1, N]$  be a monomial map of length  $n = 2$  and  $Q(N) = N$ . Now, compute the matrix  $S(s_1) = W\Delta W^t$  where  $W_{ij} = m_i(\eta_j)$  and  $\Delta_{ii} = Q(\eta_i - s_1)$  is a diagonal matrix as follows:

$$S(s_1) = \begin{bmatrix} 1 & 1 \\ \eta_1 & \eta_2 \end{bmatrix} \begin{bmatrix} \eta_1 - s_1 & 0 \\ 0 & \eta_2 - s_1 \end{bmatrix} \begin{bmatrix} 1 & \eta_1 \\ 1 & \eta_2 \end{bmatrix} = \begin{bmatrix} \eta_1 + \eta_2 - 2s_1 & \eta_1^2 + \eta_2^2 - s_1(\eta_1 + \eta_2) \\ \eta_1^2 + \eta_2^2 - s_1(\eta_1 + \eta_2) & \eta_1^3 + \eta_2^3 - s_1(\eta_1^2 + \eta_2^2) \end{bmatrix}$$

Note that we only have symmetric sums of  $\eta$ 's up to power of  $2n - 1 = 3$  (i.e,  $\eta_1^k + \eta_2^k$  where  $k = 1, 2, 3$ ). To evaluate these symmetric sums, we need to evaluate the Laurent series of the generating function  $G(N) = f'(N)/f(N)$  at  $N = \infty$  up to order  $O(N^{-5})$  as shown below

$$G(N) = \frac{2aN + b}{aN^2 + bN + c} = \frac{2}{N} + \frac{-b}{aN^2} + \frac{b^2 - 2ac}{a^2N^3} + \frac{-b^3 + 3abc}{a^3N^4} + O(N^{-5})$$

Hence,  $\eta_1 + \eta_2 = -b/a$ ,  $\eta_1^2 + \eta_2^2 = (b^2 - 2ac)/a^2$  and  $\eta_1^3 + \eta_2^3 = (-b^3 + 3abc)/a^3$ . Denote to these sums by  $\Sigma_1, \Sigma_2$  and  $\Sigma_3$  respectively. Now, the characteristic equation of  $S(s_1)$  is

$$\det(S(s_1) - \lambda I) = \lambda^2 + \lambda[-\Sigma_1 - \Sigma_3 + s_1(2 + \Sigma_2)] + [\Sigma_1\Sigma_3 - \Sigma_2^2 + s_1(\Sigma_1\Sigma_2 - 2\Sigma_3) + s_1^2(2\Sigma_2 - \Sigma_1^2)]$$

After constructing the characteristic equation whose coefficients are  $[v_2(s_1) = 1, v_1(s_1), v_0(s_1)]$ , we evaluate the signs of  $v$ 's at both  $s_1 = 0$  and  $s_1 = \infty$  as follows

$$\begin{cases} \text{sign}(v_2(0)) = 1, & \text{sign}(v_1(0)) = \text{sign}(-\Sigma_1 - \Sigma_3), & \text{sign}(v_0(0)) = \text{sign}(\Sigma_1\Sigma_3 - \Sigma_2^2) \\ \text{sign}(v_2(\infty)) = 1, & \text{sign}(v_1(\infty)) = \text{sign}(2 + \Sigma_2), & \text{sign}(v_0(\infty)) = \text{sign}(2\Sigma_2 - \Sigma_1^2). \end{cases}$$

where  $v_i(0)$  and  $v_i(\infty)$  are the coefficient of the trailing (constant) and leading term of  $v_i(s_1)$  respectively. Now, we compute  $V(0)$  and  $V(\infty)$  to have

$$V(0) = \frac{1 - \text{sign}(-\Sigma_1 - \Sigma_3)}{2} + \frac{1 - \text{sign}(-\Sigma_1 - \Sigma_3)\text{sign}(\Sigma_1\Sigma_3 - \Sigma_2^2)}{2}$$

$$V(\infty) = \frac{1 - \text{sign}(2 + \Sigma_2)}{2} + \frac{1 - \text{sign}(2 + \Sigma_2)\text{sign}(2\Sigma_2 - \Sigma_1^2)}{2}$$

Next, using the formula  $F(a, b, c) = V(0) - V(\infty)$  together with two basic properties of sign functions, namely  $\text{sign}(xy) = \text{sign}(x)\text{sign}(y)$  and  $\text{sign}(y) = 1/\text{sign}(y)$  for any non-zero real numbers  $x$  and  $y$ , we obtain the expression of  $F(a, b, c)$ , which is

$$F(a, b, c) = - \frac{\text{sign}(ab(a^2 + b^2 - 3ac))[1 + \text{sign}(ac(b^2 - 4ac))]}{2} + \frac{\text{sign}(2a^2 + b^2 - 2ac)[1 + \text{sign}(b^2 - 4ac)]}{2}$$

The feasibility basis in this case is given by  $v_0(0), v_1(0), v_0(\infty), v_1(\infty)$  and we can use it as our basis in the table. Instead, we use the factors shown in the expression of  $F(a, b, c)$  as our basis in the feasibility table. The five quantities which constitute the basis are  $Q_1 = ab, Q_2 = a^2 + b^2 - 3ac, Q_3 = ac, Q_4 = b^2 - 4ac, Q_5 = 2a^2 + b^2 - 2ac$ . Next, randomize  $a, b$  and  $c$  uniformly between  $-100$  to  $100$  and evaluate the signs of the  $Q_i$ 's as well as  $F(a, b, c)$ . We find that there are only 3 sign combinations that yield to  $F(a, b, c) \geq 1$  are given by the feasibility conditions  $C_1, C_2$  and  $C_3$  that are shown below

	$C_1$	$C_2$	$C_3$
$ab$	+	-	-
$a^2 + b^2 - 3ac$	+	+	+
$ac$	-	-	+
$b^2 - 4ac$	+	+	+
$2a^2 + b^2 - 2ac$	+	+	+
$F(a, b, c)$	1	1	2

Once the table is obtained, we start the minimization process. It is clear that from columns 1 and 2 that the sign of  $Q_1$  does not matter and thus can be replaced by an X symbol and that concludes the first minimization step as no two columns differ by a single sign and we end up with the feasibility conditions  $C_{1+2} = \{Q_2 > 0, Q_3 < 0, Q_4 > 0, Q_5 > 0\}$  and  $C_3 = \{Q_1 < 0, Q_2 > 0, Q_3 > 0, Q_4 > 0, Q_5 > 0\}$ . For the second minimization step, we follow the procedure outlined in item 8. For example, for column  $C_{1+2}$ , we find that the conditional probabilities  $P(Q_2 > 0|Q_3 < 0, Q_4 > 0, Q_5 > 0) = 1$ ,  $P(Q_3 < 0|Q_2 > 0, Q_4 > 0, Q_5 > 0) \neq 1$ ,  $P(Q_4 > 0|Q_2 > 0, Q_3 < 0, Q_5 > 0) = 1$  and  $P(Q_5 > 0|Q_2 > 0, Q_3 < 0, Q_4 > 0) = 1$  concluding that the sign of  $Q_2$ ,  $Q_4$  or  $Q_5$  can be replaced by **X** in that column. Let's replace the sign of  $Q_2$  by **X**. Then, we repeat computing the conditional properties that were 1 but without the condition  $Q_2 > 0$ . We find that  $P(Q_4 > 0|Q_3 < 0, Q_5 > 0) = 1$  and  $P(Q_5 > 0|Q_3 < 0, Q_4 > 0) = 1$  concluding that we can replace the sign of  $Q_4$  or  $Q_5$  by **X**. Let's replace the sign of  $Q_4$  by **X** and eliminate it from the latter conditional probability to find that  $P(Q_5 > 0|Q_3 < 0) = 1$ . Hence, the sign of  $Q_4$  can be replaced by **X** in column  $C_{1+2}$ . We repeat the same process with the column  $C_3$  and obtain the feasibility table including the 2-step minimization that is shown below

	$C_1$	$C_2$	$C_3$		$C_{1+2}$	$C_3$		$C_{1+2}$	$C_3$
$ab$	+	-	-		X	-		X	-
$a^2 + b^2 - 3ac$	+	+	+		+	+		X	X
$ac$	-	-	+	→	-	+	→	-	+
$b^2 - 4ac$	+	+	+		+	+		X	+
$2a^2 + b^2 - 2ac$	+	+	+		+	+		X	X
$F(a, b, c)$	1	1	2		1	2		1	2

From the table, we conclude that the condition  $ac < 0$  guarantees exactly 1 feasible equilibrium point (i.e,  $F(a, b, c) = 1$ ) while the condition  $ab < 0, ac > 0, b^2 - 4ac > 0$  guarantees exactly 2 feasible equilibrium points (i.e,  $F(a, b, c) = 2$ ). A special case of the discussed illustrative example is the Allee effect model that has the following form [116]:

$$\frac{dN}{dt} = N \left( \frac{N}{A} - 1 \right) \left( 1 - \frac{N}{K} \right) = N \left( \left( \frac{-1}{AK} \right) N^2 + \left( \frac{1}{K} + \frac{1}{A} \right) N - 1 \right), \quad 0 < A < N < K$$

Let  $a = -1/AK$ ,  $b = 1/A + 1/K$  and  $c = -1$ . It is clear that the second feasibility condition is satisfied as  $ab < 0$ ,  $ac > 0$  and  $b^2 - 4ac = (A - K)^2 / (A^2 K^2) > 0$ .

### 4.3 Two-Dimensional Systems (2 species)

Let us consider the following dynamical system with two species as shown below

$$\begin{aligned}\frac{dN_1}{dt} &= \frac{N_1 f_1(N_1, N_2)}{q_1(N_1, N_2)}, \\ \frac{dN_2}{dt} &= \frac{N_2 f_2(N_1, N_2)}{q_2(N_1, N_2)}.\end{aligned}\tag{4.2}$$

where  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  are multivariate polynomial in  $N_1$  and  $N_2$  and whose coefficients are in the vector  $\Psi$ . To describe the feasibility domain analytically, the following steps are followed:

1. Let  $d_1$  and  $d_2$  equal to the largest exponent of  $N_1$  in  $f_1$  and  $f_2$  respectively. Write  $f_1(N_1, N_2) = u_{d_1} N_1^{d_1} + \dots + u_1 N_1 + u_0$  and  $f_2(N_1, N_2) = g_{d_2} N_1^{d_2} + \dots + g_1 N_1 + g_0$  where the  $u$ 's and  $g$ 's are functions of  $N_2$  and are not functions of  $N_1$ . Next, find  $T_{21}$  and  $T_{22}$  such that the resultant  $\text{Res}_{N_1}(f_1, f_2) = T_{21}f_1 + T_{22}f_2$  where  $\text{Res}_{N_1}(f_1, f_2)$  is a determinant of a square matrix of dimension  $d_1 + d_2$  as shown below.

$$\text{Res}_{N_1}(f_1, f_2) = \begin{vmatrix} u_{d_1} & u_{d_1-1} & \dots & u_1 & u_0 & 0 & \dots & 0 & N_1^{d_2-1} f_1 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & u_{d_1} & u_{d_1-1} & u_{d_1-2} & \dots & u_0 & N_1 f_1 \\ 0 & 0 & \dots & 0 & u_{d_1} & u_{d_1-1} & \dots & u_1 & f_1 \\ g_{d_2} & g_{d_2-1} & \dots & g_1 & g_0 & 0 & \dots & 0 & N_1^{d_1-1} f_2 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & g_{d_2} & g_{d_2-1} & g_{d_2-2} & \dots & g_0 & N_1 f_2 \\ 0 & 0 & \dots & 0 & g_{d_2} & g_{d_2-1} & \dots & g_1 & f_2 \end{vmatrix} = T_{21}f_1 + T_{22}f_2$$

Note that in the rows where the last entry is  $f_1$  or  $f_2$ , there are no  $u_0$  nor  $g_0$  there. To form  $\text{Res}_{N_1}(f_1, f_2)$ , it is better to start with the two rows whose the last entries are  $f_1$  and  $f_2$  then construct the matrix up. Now, if  $f_1(N_1, N_2) = N_2 N_1^2 + 2N_1 + 3N_2$  and  $f_2(N_1, N_2) = 4N_2 N_1 + 5$ , then  $d_1 = 2$ ,  $d_2 = 1$  and  $\text{Res}_{N_1}(f_1, f_2)$  is a determinant of a 3 by 3 matrix as shown below:

$$\text{Res}_{N_1}(f_1, f_2) = \begin{vmatrix} N_2 & 2 & f_1 \\ 4N_2 & 5 & N_1 f_2 \\ 0 & 4N_2 & f_2 \end{vmatrix} = \underbrace{(16N_2^2)}_{T_{21}} f_1 + \underbrace{(-3N_2 - 4N_1 N_2^2)}_{T_{22}} f_2$$

2. Let  $e_1$  and  $e_2$  equal to the largest exponent of  $N_2$  in  $f_1$  and  $f_2$  respectively. Write  $f_1(N_1, N_2) = w_{e_1} N_2^{e_1} + \dots + w_1 N_2 + w_0$  and  $f_2(N_1, N_2) = z_{e_2} N_2^{e_2} + \dots + z_1 N_2 + z_0$  where the  $w$ 's and  $z$ 's are functions of  $N_1$  and are not functions of  $N_2$ . Next, find  $T_{11}$  and  $T_{12}$  such that the resultant  $\text{Res}_{N_2}(f_1, f_2) = T_{11} f_1 + T_{12} f_2$  where  $\text{Res}_{N_2}(f_1, f_2)$  is a determinant of a square matrix of dimension  $e_1 + e_2$  as shown below.

$$\text{Res}_{N_2}(f_1, f_2) = \begin{vmatrix} w_{e_1} & w_{e_1-1} & \dots & w_1 & w_0 & 0 & \dots & 0 & N_2^{e_2-1} f_1 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & w_{e_1} & w_{e_1-1} & w_{e_1-2} & \dots & w_0 & N_2 f_1 \\ 0 & 0 & \dots & 0 & w_{e_1} & w_{e_1-1} & \dots & w_1 & f_1 \\ z_{e_2} & z_{e_2-1} & \dots & z_1 & z_0 & 0 & \dots & 0 & N_2^{e_1-1} f_2 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & z_{e_2} & z_{e_2-1} & z_{e_2-2} & \dots & z_0 & N_2 f_2 \\ 0 & 0 & \dots & 0 & z_{e_2} & z_{e_2-1} & \dots & z_1 & f_2 \end{vmatrix} = T_{11} f_1 + T_{12} f_2$$

Note that in the rows where the last entry is  $f_1$  or  $f_2$ , there are no  $w_0$  or  $z_0$  there. Again, if  $f_1(N_1, N_2) = N_2 N_1^2 + 2N_1 + 3N_2$  and  $f_2(N_1, N_2) = 4N_2 N_1 + 5$ , then  $e_1 = 1$ ,  $e_2 = 1$  and  $\text{Res}_{N_2}(f_1, f_2)$  is a determinant of a 2 by 2 matrix as shown below:

$$\text{Res}_{N_2}(f_1, f_2) = \begin{vmatrix} N_1^2 + 3 & f_1 \\ 4N_1 & f_2 \end{vmatrix} = \underbrace{(-4N_1)}_{T_{11}} f_1 + \underbrace{(N_1^2 + 3)}_{T_{12}} f_2$$

3. Evaluate the determinant of the eliminating matrix  $T(f_1, f_2)$ , whose elements  $T_{11}$ ,  $T_{12}$ ,  $T_{21}$ ,  $T_{22}$  have been obtained in the earlier two steps, as well as the determinant of the Jacobian of  $f_1$  and  $f_2$ . Note that the first row of  $T(f_1, f_2)$  corresponds to the coefficients of  $f_1$  and  $f_2$  in  $\text{Res}_{N_2}(f_1, f_2)$  while the second row corresponds to the coefficients of  $f_1$  and  $f_2$  in  $\text{Res}_{N_1}(f_1, f_2)$ .

$$T(f_1, f_2) = \begin{vmatrix} T_{11} & T_{12} \\ T_{21} & T_{22} \end{vmatrix} = T_{11}T_{22} - T_{12}T_{21}$$

$$J(f_1, f_2) = \begin{vmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{vmatrix} = \frac{\partial f_1}{\partial N_1} \frac{\partial f_2}{\partial N_2} - \frac{\partial f_1}{\partial N_2} \frac{\partial f_2}{\partial N_1}$$

4. Expand the function  $G(f_1(N_1, N_2), f_2(N_1, N_2))$  that is shown below, around  $N_1 = \infty$  and  $N_2 = \infty$  (or perform series expansion of  $G(f_1(1/x, 1/y), f_2(1/x, 1/y))$  around  $x = 0$  and  $y = 0$  which gives identical coefficients) to obtain the  $\Sigma$ 's (symmetric sums of the roots).

$$G(f_1, f_2) = \frac{T(f_1, f_2)J(f_1, f_2)}{\text{Res}_{N_1}(f_1, f_2)\text{Res}_{N_2}(f_1, f_2)}$$

$$= \frac{\Sigma_{0,0}}{N_1 N_2} + \frac{\Sigma_{1,0}}{N_1^2 N_2} + \frac{\Sigma_{0,1}}{N_1 N_2^2} + \frac{\Sigma_{1,1}}{N_1^2 N_2^2} + \frac{\Sigma_{2,0}}{N_1^3 N_2} + \frac{\Sigma_{2,1}}{N_1^3 N_2^2} + \frac{\Sigma_{0,2}}{N_1 N_2^3} + \frac{\Sigma_{1,2}}{N_1^2 N_2^3}$$

$$+ \frac{\Sigma_{3,0}}{N_1^4 N_2} + \frac{\Sigma_{3,1}}{N_1^4 N_2^2} + \frac{\Sigma_{0,3}}{N_1 N_2^4} + \frac{\Sigma_{1,3}}{N_1^2 N_2^4} + \dots$$

Note that  $f_1$  and  $f_2$  are substituted in both  $\text{Res}_{N_1}(f_1, f_2)$  and  $\text{Res}_{N_2}(f_1, f_2)$  to fully express the resultants in terms of  $N_1, N_2$  and model parameters  $\Psi$  before evaluating  $G(f_1, f_2)$  and expanding it. For the symmetric sums, denote the roots of  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  by  $\boldsymbol{\eta}_k = [\eta_{k,1}, \eta_{k,2}]^T$  for  $k = 1, \dots, \Theta$ . The symmetric sum  $\Sigma_{m,n}$  for any  $m$  and  $n$  is given by  $\Sigma_{m,n} = \sum_{k=1}^{\Theta} \eta_{k,1}^m \eta_{k,2}^n$ . In particular, note that  $\Theta = \Sigma_{0,0}$  is the number of complex roots of  $f_1$  and  $f_2$  with a general coefficients. It is important to record that number.

5. Choose a map  $m(N_1, N_2) = [1, m_1, m_2, \dots, m_{\Theta-1}]^T$  of length  $\Theta$  with independent entries that are functions of  $N_1$  and  $N_2$ . If  $\Theta = 4$ , we can let  $m(N_1, N_2) = [1, N_1, N_2, N_1 N_2]^T$ . It does not matter what the  $m$ 's are as long as no entry is a linear combination of the others and step 7 of the procedure does not fail (in step 7 we give more details). Then let  $Q(N_1, N_2) = N_1 N_2$  and compute the symmetric matrix  $S(s_1, s_2) = W \Delta W^t$  where  $W_{ij} = m_i(\eta_{j,1}, \eta_{j,2})$  and  $\Delta_{ii} = Q(\eta_{i,1} - s_1, \eta_{i,2} - s_2)$  is a diagonal matrix.
6. The next task is to evaluate the determinant of  $S(s_1, s_2)$  and write it in the form  $\det(S(s_1, s_2) - \lambda I) = (-1)^{\Theta} \lambda^{\Theta} + v_{\Theta-1}(s_1, s_2) \lambda^{\Theta-1} + \dots + v_0(s_1, s_2)$ . After that consider the sequence  $\mathbf{v} = [v_{\Theta}(s_1, s_2) = (-1)^{\Theta}, v_{\Theta-1}(s_1, s_2), \dots, v_0(s_1, s_2)]$  and let  $V(s_1, s_2)$  be

the number of consecutive sign changes in  $\mathbf{v}$ . The formula of  $V(s_1, s_2)$  is

$$V(s_1, s_2) = \sum_{i=0}^{\Theta-1} \frac{1 - \text{sign}(v_i(s_1, s_2)v_{i+1}(s_1, s_2))}{2}.$$

7. For any interval  $(a, b] \times (c, d]$ , the number of real roots of  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  in  $(a, b] \times (c, d]$  is exactly  $[V(a, c) - V(a, b) + V(b, d) - V(b, c)]/2$ . For the feasibility domain, note that the points  $\{(0, 0), (0, \infty), (\infty, 0), (\infty, \infty)\}$  are the vertices of the "box" that bound it. Hence, the expression of  $F(\Psi)$  is simply  $F(\Psi) = [V(0, 0) - V(0, \infty) - V(\infty, 0) + V(\infty, \infty)]/2$ . Here,  $\infty$  is a limit; therefore, 0 is evaluated first before the limit is taken at infinity. For  $V(\infty, \infty)$  where the limit of two quantities approach infinity, the limit is unique. Therefore, it does not matter along which direction the limit is taken. To evaluate those  $V$ 's we need to evaluate the  $v$ 's at those limits. Note that for any function  $p$ ,  $\text{sign}(p(S(0, 0))) = \text{sign}$  of the constant term in  $p(S(s_1, s_2))$ . For the other cases, note that

- $\text{sign}(p(S(0, \infty))) = \text{sign}$  of the coefficient of the term associated with the highest power of  $s_2$  in  $p(S(s_1, s_2)) = \text{sign}$  of the constant term of the common numerator of  $p(S(0, 1/y)) = \text{sign}$  of the numerator of  $p(S(0, 1/y))$  evaluated at  $y = 0$
- $\text{sign}(p(S(\infty, 0))) = \text{sign}$  of the coefficient of the term associated with the highest power of  $s_1$  in  $p(S(s_1, s_2)) = \text{sign}$  of the constant term of the common numerator of  $p(S(1/x, 0)) = \text{sign}$  of the numerator of  $p(S(1/x, 0))$  evaluated at  $x = 0$
- $\text{sign}(p(S(\infty, \infty))) = \text{sign}$  of the coefficient of the term associated with the highest power of  $s_1 s_2$  in  $p(S(s_1, s_2)) = \text{sign}$  of the constant term of the common numerator of  $p(S(1/x, 1/y)) = \text{sign}$  of the numerator of  $p(S(1/x, 1/y))$  evaluated at  $x, y = 0$

After evaluating the  $v$ 's, we assemble  $F(\Psi)$ . If  $F(\Psi)$  or any of the  $V$ 's is not a non-negative integer, even for a single case where  $\Psi$  is randomly chosen, or the vector  $\mathbf{v}$  contains zeros, then the map  $m(N_1, N_2)$  must be changed. One remedy to rectify this is increasing the order of one of the components of  $m$ . For example, if  $m(N_1, N_2) = [1, N_1, N_2, N_1 N_2]$  fails, then one can try  $m(N_1, N_2) = [1, N_1^2, N_2, N_1 N_2]$ .



8. As in the univariate case, call  $v_0(0,0), \dots, v_{\Theta-1}(0,0), v_0(0,\infty), \dots, v_{\Theta-1}(0,\infty), v_0(\infty,\infty), \dots, v_{\Theta-1}(\infty,\infty), v_0(\infty,0), \dots, v_{\Theta-1}(\infty,0)$  the feasibility basis which involves  $4\Theta$  quantities as feasibility conditions are only dependent on those quantities. Since there are  $4\Theta$  quantities and each can take a positive or a negative sign, then there are  $2^{4\Theta}$  sign combinations. Many of those combinations are impossible to occur (empty) for any choice of real  $\Psi$ . To detect the non-empty sign combinations, we compute the signs of all the  $c$ 's (the feasibility basis) as well as  $F(\Psi)$  for a range of parameters  $\Psi$ , where each component of  $\Psi$  varies independently in a large domain (say uniformly between  $-100$  and  $100$  or in any suitable domain). This operation is cheaply computed as it is evaluation a few functions and not solving systems of equations. After that, we extract unique sign combinations of the  $v$ 's which yield  $F(\Psi) \geq 1$  and put them in a feasibility table whose rows are the signs of the  $c$ 's and columns are the individual feasibility conditions.

9. After we obtain the feasibility table, we perform minimization to it. If two columns differ by a single sign (in one row), the two columns are combined into one and an X is placed in the row where there is a single sign difference. We repeat the same process until no two columns differ by a single sign. After that we go through a single column at a time and iterate through each quantity in the basis then compute the conditional probabilities that the quantity takes its correspondent sign given that all remaining quantities have their correspondent signs. If one or more conditional probabilities are 1, the sign of one of those quantities may be replaced by **X** in the table. We then repeat computing the same conditional probabilities which were 1 but without the **X**'ed quantity being part of the calculation. If any conditional probability is 1 we repeat the process until it terminates. Plotting the signs of the feasibility basis against  $F(\Psi)$  may reveal extra minimization information (see application section).

### 4.3.1 Illustrative Example

Consider the following LV system with a simple higher-order term  $N_1N_2$

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(r_1 + a_{11}N_1 + a_{12}N_2 + b_1N_1N_2) \\ \frac{dN_2}{dt} &= N_2(r_2 + a_{21}N_1 + a_{22}N_2 + b_2N_1N_2)\end{aligned}$$

Let  $f_1(N_1, N_2) = r_1 + a_{11}N_1 + a_{12}N_2 + b_1N_1N_2$  and  $f_2(N_1, N_2) = r_2 + a_{21}N_1 + a_{22}N_2 + b_2N_1N_2$  with  $\Psi = (r_1, r_2, a_{11}, a_{12}, a_{21}, a_{22}, b_1, b_2)$  being the vector of model parameters. The first task is evaluating the resultants as follows:

$$\begin{aligned} \text{Res}_{N_1}(f_1, f_2) &= \begin{vmatrix} a_{11} + b_1N_2 & f_1 \\ a_{21} + b_2N_2 & f_2 \end{vmatrix} = \underbrace{-(a_{21} + b_2N_2)}_{T_{21}} f_1 + \underbrace{(a_{11} + b_1N_2)}_{T_{22}} f_2 \\ &= (a_{22}b_1 - a_{12}b_2)N_2^2 + (a_{11}a_{22} - a_{12}a_{21} + b_1r_2 - b_2r_1)N_2 + (a_{11}r_2 - a_{21}r_1) \\ \text{Res}_{N_2}(f_1, f_2) &= \begin{vmatrix} a_{12} + b_1N_1 & f_1 \\ a_{22} + b_2N_1 & f_2 \end{vmatrix} = \underbrace{-(a_{22} + b_2N_1)}_{T_{11}} f_1 + \underbrace{(a_{12} + b_1N_1)}_{T_{12}} f_2 \\ &= (a_{21}b_1 - a_{11}b_2)N_1^2 + (-a_{11}a_{22} + a_{12}a_{21} + b_1r_2 - b_2r_1)N_1 + (a_{12}r_2 - a_{22}r_1) \end{aligned}$$

From above, the entries of the eliminating matrix  $T(f_1, f_2)$  are  $T_{11} = -(a_{22} + b_2N_1)$ ,  $T_{12} = (a_{12} + b_1N_1)$ ,  $T_{21} = -(a_{21} + b_2N_2)$  and  $T_{22} = (a_{11} + b_1N_2)$ . After that we evaluate the determinant of both eliminating matrix  $T(f_1, f_2)$  and the Jacobian of  $f_1$  and  $f_2$  as following.

$$\begin{aligned} T(f_1, f_2) &= \begin{vmatrix} -(a_{22} + b_2N_1) & a_{12} + b_1N_1 \\ -(a_{21} + b_2N_2) & a_{11} + b_1N_2 \end{vmatrix} \\ &= a_{12}a_{21} - a_{11}a_{22} + (a_{21}b_1 - a_{11}b_2)N_1 + (a_{12}b_2 - a_{22}b_1)N_2 \\ J(f_1, f_2) &= \begin{vmatrix} a_{11} + b_1N_2 & a_{12} + b_1N_1 \\ a_{21} + b_2N_2 & a_{22} + b_2N_1 \end{vmatrix} \\ &= (a_{11}a_{22} - a_{12}a_{21}) + (a_{11}b_2 - a_{21}b_1)N_1 + (a_{22}b_1 - a_{12}b_2)N_2 \end{aligned}$$

Now, we need to expand the generating function  $G(f_1(N_1, N_2), f_2(N_1, N_2))$  around  $N_1 = \infty$  and  $N_2 = \infty$  to obtain

$$\begin{aligned} G(f_1, f_2) &= \frac{T(f_1, f_2)J(f_1, f_2)}{\text{Res}_{N_1}(f_1, f_2)\text{Res}_{N_2}(f_1, f_2)} \\ &= \frac{\Sigma_{0,0}}{N_1N_2} + \frac{\Sigma_{1,0}}{N_1^2N_2} + \frac{\Sigma_{0,1}}{N_1N_2^2} + \frac{\Sigma_{1,1}}{N_1^2N_2^2} + \frac{\Sigma_{2,0}}{N_1^3N_2} + \frac{\Sigma_{2,1}}{N_1^3N_2^2} + \frac{\Sigma_{0,2}}{N_1N_2^3} + \frac{\Sigma_{1,2}}{N_1^2N_2^3} \\ &+ \frac{\Sigma_{3,0}}{N_1^4N_2} + \frac{\Sigma_{3,1}}{N_1^4N_2^2} + \frac{\Sigma_{0,3}}{N_1N_2^4} + \frac{\Sigma_{1,3}}{N_1^2N_2^4} + \dots \end{aligned}$$

The expression for each of the  $\Sigma$ 's (symmetric power sums of the roots) are shown below where  $\Sigma_{i,j} = \Sigma_{i,j}^U / \Sigma_{i,j}^D$  is written as a fraction of two polynomials.

$$\begin{aligned}\Sigma_{0,0}^U &= 2 \\ \Sigma_{0,0}^D &= 1\end{aligned}$$

$$\begin{aligned}\Sigma_{1,0}^U &= a_{12}a_{21} - a_{11}a_{22} + b_1r_2 - b_2r_1 \\ \Sigma_{1,0}^D &= (a_{11}b_2 - a_{21}b_1)\end{aligned}$$

$$\begin{aligned}\Sigma_{0,1}^U &= a_{11}a_{22} - a_{12}a_{21} + b_1r_2 - b_2r_1 \\ \Sigma_{0,1}^D &= (a_{12}b_2 - a_{22}b_1)\end{aligned}$$

$$\begin{aligned}\Sigma_{2,0}^U &= a_{11}^2a_{22}^2 - 2a_{11}a_{12}a_{21}a_{22} + 2a_{11}a_{12}b_2r_2 - 2a_{11}a_{22}b_1r_2 + a_{12}^2a_{21}^2 - 2a_{12}a_{21}b_2r_1 \\ &\quad + 2a_{21}a_{22}b_1r_1 + b_1^2r_2^2 - 2b_1b_2r_1r_2 + b_2^2r_1^2 \\ \Sigma_{2,0}^D &= (a_{11}b_2 - a_{21}b_1)^2\end{aligned}$$

$$\begin{aligned}\Sigma_{0,2}^U &= a_{11}^2a_{22}^2 - 2a_{11}a_{12}a_{21}a_{22} + 2a_{11}a_{12}b_2r_2 - 2a_{11}a_{22}b_2r_1 + a_{12}^2a_{21}^2 - 2a_{12}a_{21}b_1r_2 \\ &\quad + 2a_{21}a_{22}b_1r_1 + b_1^2r_2^2 - 2b_1b_2r_1r_2 + b_2^2r_1^2 \\ \Sigma_{0,2}^D &= (a_{12}b_2 - a_{22}b_1)^2\end{aligned}$$

$$\begin{aligned}\Sigma_{1,1}^U &= 2a_{11}a_{12}a_{21}a_{22} - a_{12}^2a_{21}^2 - a_{11}^2a_{22}^2 - 2a_{11}a_{12}b_2r_2 + a_{11}a_{22}b_1r_2 + a_{11}a_{22}b_2r_1 \\ &\quad + a_{12}a_{21}b_1r_2 + a_{12}a_{21}b_2r_1 - 2a_{21}a_{22}b_1r_1 \\ \Sigma_{1,1}^D &= (a_{11}b_2 - a_{21}b_1)(a_{12}b_2 - a_{22}b_1)\end{aligned}$$

$$\begin{aligned}\Sigma_{2,1}^U &= a_{11}^3a_{22}^3 - 3a_{11}^2a_{12}a_{21}a_{22}^2 + 3a_{11}^2a_{12}a_{22}b_2r_2 - 2a_{11}^2a_{22}^2b_1r_2 - a_{11}^2a_{22}^2b_2r_1 \\ &\quad + 3a_{11}a_{12}^2a_{21}^2a_{22} - 3a_{11}a_{12}^2a_{21}b_2r_2 + a_{11}a_{12}a_{21}a_{22}b_1r_2 - a_{11}a_{12}a_{21}a_{22}b_2r_1 \\ &\quad - a_{11}a_{12}b_1b_2r_2^2 + a_{11}a_{12}b_2^2r_1r_2 + 3a_{11}a_{21}a_{22}^2b_1r_1 + a_{11}a_{22}b_1^2r_2^2 - a_{11}a_{22}b_1b_2r_1r_2 \\ &\quad - a_{12}^3a_{21}^3 + a_{12}^2a_{21}^2b_1r_2 + 2a_{12}^2a_{21}^2b_2r_1 - 3a_{12}a_{21}^2a_{22}b_1r_1 + a_{12}a_{21}b_1b_2r_1r_2 \\ &\quad - a_{12}a_{21}b_2^2r_1^2 - a_{21}a_{22}b_1^2r_1r_2 + a_{21}a_{22}b_1b_2r_1^2 \\ \Sigma_{2,1}^D &= (a_{11}b_2 - a_{21}b_1)^2(a_{12}b_2 - a_{22}b_1)\end{aligned}$$

$$\begin{aligned}\Sigma_{1,2}^U &= -a_{11}^3a_{22}^3 + 3a_{11}^2a_{12}a_{21}a_{22}^2 - 3a_{11}^2a_{12}a_{22}b_2r_2 + a_{11}^2a_{22}^2b_1r_2 + 2a_{11}^2a_{22}^2b_2r_1 \\ &\quad - 3a_{11}a_{12}^2a_{21}^2a_{22} + 3a_{11}a_{12}^2a_{21}b_2r_2 + a_{11}a_{12}a_{21}a_{22}b_1r_2 - a_{11}a_{12}a_{21}a_{22}b_2r_1 \\ &\quad - a_{11}a_{12}b_1b_2r_2^2 + a_{11}a_{12}b_2^2r_1r_2 - 3a_{11}a_{21}a_{22}^2b_1r_1 + a_{11}a_{22}b_1b_2r_1r_2 - a_{11}a_{22}b_2^2r_1^2 \\ &\quad + a_{12}^3a_{21}^3 - 2a_{12}^2a_{21}^2b_1r_2 - a_{12}^2a_{21}^2b_2r_1 + 3a_{12}a_{21}^2a_{22}b_1r_1 + a_{12}a_{21}b_1^2r_2^2 \\ &\quad - a_{12}a_{21}b_1b_2r_1r_2 - a_{21}a_{22}b_1^2r_1r_2 + a_{21}a_{22}b_1b_2r_1^2 \\ \Sigma_{1,2}^D &= (a_{11}b_2 - a_{21}b_1)(a_{12}b_2 - a_{22}b_1)^2\end{aligned}$$

$$\begin{aligned}
\Sigma_{3,0}^U &= -a_{11}^3 a_{22}^3 + 3a_{11}^2 a_{12} a_{21} a_{22}^2 - 3a_{11}^2 a_{12} a_{22} b_2 r_2 + 3a_{11}^2 a_{22}^2 b_1 r_2 - 3a_{11} a_{12}^2 a_{21}^2 a_{22} \\
&\quad + 3a_{11} a_{12}^2 a_{21} b_2 r_2 - 3a_{11} a_{12} a_{21} a_{22} b_1 r_2 + 3a_{11} a_{12} a_{21} a_{22} b_2 r_1 + 3a_{11} a_{12} b_1 b_2 r_2^2 \\
&\quad - 3a_{11} a_{12} b_2^2 r_1 r_2 - 3a_{11} a_{21} a_{22}^2 b_1 r_1 - 3a_{11} a_{22} b_1^2 r_2^2 + 3a_{11} a_{22} b_1 b_2 r_1 r_2 \\
&\quad + a_{12}^3 a_{21}^3 - 3a_{12}^2 a_{21}^2 b_2 r_1 + 3a_{12} a_{21}^2 a_{22} b_1 r_1 - 3a_{12} a_{21} b_1 b_2 r_1 r_2 + 3a_{12} a_{21} b_2^2 r_1^2 \\
&\quad + 3a_{21} a_{22} b_1^2 r_1 r_2 - 3a_{21} a_{22} b_1 b_2 r_1^2 + b_1^3 r_2^3 - 3b_1^2 b_2 r_1 r_2^2 + 3b_1 b_2^2 r_1^2 r_2 - b_2^3 r_1^3 \\
\Sigma_{3,0}^D &= (a_{11} b_2 - a_{21} b_1)^3
\end{aligned}$$

$$\begin{aligned}
\Sigma_{0,3}^U &= a_{11}^3 a_{22}^3 - 3a_{11}^2 a_{12} a_{21} a_{22}^2 + 3a_{11}^2 a_{12} a_{22} b_2 r_2 - 3a_{11}^2 a_{22}^2 b_2 r_1 + 3a_{11} a_{12}^2 a_{21}^2 a_{22} \\
&\quad - 3a_{11} a_{12}^2 a_{21} b_2 r_2 - 3a_{11} a_{12} a_{21} a_{22} b_1 r_2 + 3a_{11} a_{12} a_{21} a_{22} b_2 r_1 + 3a_{11} a_{12} b_1 b_2 r_2^2 \\
&\quad - 3a_{11} a_{12} b_2^2 r_1 r_2 + 3a_{11} a_{21} a_{22}^2 b_1 r_1 - 3a_{11} a_{22} b_1 b_2 r_1 r_2 + 3a_{11} a_{22} b_2^2 r_1^2 \\
&\quad - a_{12}^3 a_{21}^3 + 3a_{12}^2 a_{21}^2 b_1 r_2 - 3a_{12} a_{21}^2 a_{22} b_1 r_1 - 3a_{12} a_{21} b_1^2 r_2^2 + 3a_{12} a_{21} b_1 b_2 r_1 r_2 \\
&\quad + 3a_{21} a_{22} b_1^2 r_1 r_2 - 3a_{21} a_{22} b_1 b_2 r_1^2 + b_1^3 r_2^3 - 3b_1^2 b_2 r_1 r_2^2 + 3b_1 b_2^2 r_1^2 r_2 - b_2^3 r_1^3 \\
\Sigma_{0,3}^D &= (a_{12} b_2 - a_{22} b_1)^3
\end{aligned}$$

$$\begin{aligned}
\Sigma_{3,1}^U &= -a_{11}^4 a_{22}^4 + 4a_{11}^3 a_{12} a_{21} a_{22}^3 - 4a_{11}^3 a_{12} a_{22}^2 b_2 r_2 + 3a_{11}^3 a_{22}^3 b_1 r_2 + a_{11}^3 a_{22}^3 b_2 r_1 \\
&\quad - 6a_{11}^2 a_{12}^2 a_{21}^2 a_{22}^2 + 8a_{11}^2 a_{12}^2 a_{21} a_{22} b_2 r_2 - 2a_{11}^2 a_{12}^2 b_2^2 r_2^2 - 5a_{11}^2 a_{12} a_{21} a_{22}^2 b_1 r_2 \\
&\quad + a_{11}^2 a_{12} a_{21} a_{22}^2 b_2 r_1 + 5a_{11}^2 a_{12} a_{22} b_1 b_2 r_2^2 - a_{11}^2 a_{12} a_{22} b_2^2 r_1 r_2 - 4a_{11}^2 a_{21} a_{22}^3 b_1 r_1 \\
&\quad - 3a_{11}^2 a_{22}^2 b_1^2 r_2^2 + a_{11}^2 a_{22}^2 b_1 b_2 r_1 r_2 + 4a_{11} a_{12}^3 a_{21}^3 a_{22} - 4a_{11} a_{12}^3 a_{21}^2 b_2 r_2 \\
&\quad + a_{11} a_{12}^2 a_{21}^2 a_{22} b_1 r_2 - 5a_{11} a_{12}^2 a_{21}^2 a_{22} b_2 r_1 - a_{11} a_{12}^2 a_{21} b_1 b_2 r_2^2 + 5a_{11} a_{12}^2 a_{21} b_2^2 r_1 r_2 \\
&\quad + 8a_{11} a_{12} a_{21}^2 a_{22}^2 b_1 r_1 + a_{11} a_{12} a_{21} a_{22} b_1^2 r_2^2 - 10a_{11} a_{12} a_{21} a_{22} b_1 b_2 r_1 r_2 + a_{11} a_{12} a_{21} a_{22} b_2^2 r_1^2 \\
&\quad - a_{11} a_{12} b_1^2 b_2 r_2^3 + 2a_{11} a_{12} b_1 b_2^2 r_1 r_2^2 - a_{11} a_{12} b_2^3 r_1^2 r_2 + 5a_{11} a_{21} a_{22}^2 b_1^2 r_1 r_2 \\
&\quad - a_{11} a_{21} a_{22}^2 b_1 b_2 r_1^2 + a_{11} a_{22} b_1^3 r_2^3 - 2a_{11} a_{22} b_1^2 b_2 r_1 r_2^2 + a_{11} a_{22} b_1 b_2^2 r_1^2 r_2 - a_{12}^4 a_{21}^4 \\
&\quad + a_{12}^3 a_{21}^3 b_1 r_2 + 3a_{12}^3 a_{21}^3 b_2 r_1 - 4a_{12}^2 a_{21}^3 a_{22} b_1 r_1 + a_{12}^2 a_{21}^2 b_1 b_2 r_1 r_2 - 3a_{12}^2 a_{21}^2 b_2^2 r_1^2 \\
&\quad - a_{12} a_{21}^2 a_{22} b_1^2 r_1 r_2 + 5a_{12} a_{21}^2 a_{22} b_1 b_2 r_1^2 + a_{12} a_{21} b_1^2 b_2 r_1 r_2^2 - 2a_{12} a_{21} b_1 b_2^2 r_1^2 r_2 \\
&\quad + a_{12} a_{21} b_2^3 r_1^3 - 2a_{21}^2 a_{22}^2 b_1^2 r_1^2 - a_{21} a_{22} b_1^3 r_1 r_2^2 + 2a_{21} a_{22} b_1^2 b_2 r_1^2 r_2 - a_{21} a_{22} b_1 b_2^2 r_1^3 \\
\Sigma_{3,1}^D &= (a_{11} b_2 - a_{21} b_1)^3 (a_{12} b_2 - a_{22} b_1)
\end{aligned}$$

$$\begin{aligned}
\Sigma_{1,3}^U &= -a_{11}^4 a_{22}^4 + 4a_{11}^3 a_{12} a_{21} a_{22}^3 - 4a_{11}^3 a_{12} a_{22}^2 b_2 r_2 + a_{11}^3 a_{22}^3 b_1 r_2 + 3a_{11}^3 a_{22}^3 b_2 r_1 \\
&\quad - 6a_{11}^2 a_{12}^2 a_{21}^2 a_{22}^2 + 8a_{11}^2 a_{12}^2 a_{21} a_{22} b_2 r_2 - 2a_{11}^2 a_{12}^2 b_2^2 r_2^2 + a_{11}^2 a_{12} a_{21} a_{22}^2 b_1 r_2 \\
&\quad - 5a_{11}^2 a_{12} a_{21} a_{22}^2 b_2 r_1 - a_{11}^2 a_{12} a_{22} b_1 b_2 r_2^2 + 5a_{11}^2 a_{12} a_{22} b_2^2 r_1 r_2 - 4a_{11}^2 a_{21} a_{22}^3 b_1 r_1 \\
&\quad + a_{11}^2 a_{22}^2 b_1 b_2 r_1 r_2 - 3a_{11}^2 a_{22}^2 b_2^2 r_1^2 + 4a_{11} a_{12}^3 a_{21}^3 a_{22} - 4a_{11} a_{12}^3 a_{21}^2 b_2 r_2 \\
&\quad - 5a_{11} a_{12}^2 a_{21}^2 a_{22} b_1 r_2 + a_{11} a_{12}^2 a_{21}^2 a_{22} b_2 r_1 + 5a_{11} a_{12}^2 a_{21} b_1 b_2 r_2^2 - a_{11} a_{12}^2 a_{21} b_2^2 r_1 r_2 \\
&\quad + 8a_{11} a_{12} a_{21}^2 a_{22}^2 b_1 r_1 + a_{11} a_{12} a_{21} a_{22} b_1^2 r_2^2 - 10a_{11} a_{12} a_{21} a_{22} b_1 b_2 r_1 r_2 + a_{11} a_{12} a_{21} a_{22} b_2^2 r_1^2 \\
&\quad - a_{11} a_{12} b_1^2 b_2 r_2^3 + 2a_{11} a_{12} b_1 b_2^2 r_1 r_2^2 - a_{11} a_{12} b_2^3 r_1^2 r_2 - a_{11} a_{21} a_{22}^2 b_1^2 r_1 r_2 \\
&\quad + 5a_{11} a_{21} a_{22}^2 b_1 b_2 r_1^2 + a_{11} a_{22} b_1^2 b_2 r_1 r_2^2 - 2a_{11} a_{22} b_1 b_2^2 r_1^2 r_2 + a_{11} a_{22} b_2^3 r_1^3 - a_{12}^4 a_{21}^4 \\
&\quad + 3a_{12}^3 a_{21}^3 b_1 r_2 + a_{12}^3 a_{21}^3 b_2 r_1 - 4a_{12}^2 a_{21}^3 a_{22} b_1 r_1 - 3a_{12}^2 a_{21}^2 b_1^2 r_2^2 + a_{12}^2 a_{21}^2 b_1 b_2 r_1 r_2 \\
&\quad + 5a_{12} a_{21}^2 a_{22} b_1^2 r_1 r_2 - a_{12} a_{21}^2 a_{22} b_1 b_2 r_1^2 + a_{12} a_{21} b_1^3 r_2^3 - 2a_{12} a_{21} b_1^2 b_2 r_1 r_2^2 \\
&\quad + a_{12} a_{21} b_1 b_2^2 r_1^2 r_2 - 2a_{21}^2 a_{22}^2 b_1^2 r_1^2 - a_{21} a_{22} b_1^3 r_1 r_2^2 + 2a_{21} a_{22} b_1^2 b_2 r_1^2 r_2 - a_{21} a_{22} b_1 b_2^2 r_1^3 \\
\Sigma_{1,3}^D &= (a_{11} b_2 - a_{21} b_1) (a_{12} b_2 - a_{22} b_1)^3
\end{aligned}$$

$$\begin{aligned}
\Sigma_{2,2}^U = & a_{11}^4 a_{22}^4 - 4a_{11}^3 a_{12} a_{21} a_{22}^3 + 4a_{11}^3 a_{12} a_{22}^2 b_2 r_2 - 2a_{11}^3 a_{22}^3 b_1 r_2 - 2a_{11}^3 a_{22}^3 b_2 r_1 \\
& + 6a_{11}^2 a_{12}^2 a_{21}^2 a_{22}^2 - 8a_{11}^2 a_{12}^2 a_{21} a_{22} b_2 r_2 + 2a_{11}^2 a_{12}^2 b_2^2 r_2^2 + 2a_{11}^2 a_{12} a_{21} a_{22}^2 b_1 r_2 \\
& + 2a_{11}^2 a_{12} a_{21} a_{22}^2 b_2 r_1 - 2a_{11}^2 a_{12} a_{22} b_1 b_2 r_2^2 - 2a_{11}^2 a_{12} a_{22} b_2^2 r_1 r_2 + 4a_{11}^2 a_{21} a_{22}^3 b_1 r_1 \\
& + a_{11}^2 a_{22}^2 b_1^2 r_2^2 + a_{11}^2 a_{22}^2 b_2^2 r_1^2 - 4a_{11} a_{12}^3 a_{21}^3 a_{22} + 4a_{11} a_{12}^3 a_{21}^2 b_2 r_2 + 2a_{11} a_{12}^2 a_{21}^2 a_{22} b_1 r_2 \\
& + 2a_{11} a_{12}^2 a_{21}^2 a_{22} b_2 r_1 - 2a_{11} a_{12}^2 a_{21} b_1 b_2 r_2^2 - 2a_{11} a_{12}^2 a_{21} b_2^2 r_1 r_2 - 8a_{11} a_{12} a_{21}^2 a_{22}^2 b_1 r_1 \\
& + 8a_{11} a_{12} a_{21} a_{22} b_1 b_2 r_1 r_2 - 2a_{11} a_{21} a_{22}^2 b_1^2 r_1 r_2 - 2a_{11} a_{21} a_{22}^2 b_1 b_2 r_1^2 + a_{12}^4 a_{21}^4 \\
& - 2a_{12}^3 a_{21}^3 b_1 r_2 - 2a_{12}^3 a_{21}^3 b_2 r_1 + 4a_{12}^2 a_{21}^3 a_{22} b_1 r_1 + a_{12}^2 a_{21}^2 b_1^2 r_2^2 + a_{12}^2 a_{21}^2 b_2^2 r_1^2 \\
& - 2a_{12} a_{21}^2 a_{22} b_1^2 r_1 r_2 - 2a_{12} a_{21}^2 a_{22} b_1 b_2 r_1^2 + 2a_{21}^2 a_{22}^2 b_1^2 r_1^2 \\
\Sigma_{2,2}^D = & (a_{11} b_2 - a_{21} b_1)^2 (a_{12} b_2 - a_{22} b_1)^2
\end{aligned}$$

Denote the roots of  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  by  $\boldsymbol{\eta}_1 = [\eta_{1,1}, \eta_{1,2}]^T$  and  $\boldsymbol{\eta}_2 = [\eta_{2,1}, \eta_{2,2}]^T$ . Choose a monomial map  $m(N_1, N_2) = [1, c_1 N_1 + c_2 N_2]^T$  for some constants  $c_1$  and  $c_2$ . Then, let  $Q(N_1, N_2) = N_1 N_2$  and compute  $S(s_1, s_2) = W \Delta W^t$  where  $W_{ij} = m_i(\eta_{1,j}, \eta_{2,j})$  and  $\Delta_{ii} = Q(\eta_{1,i} - s_1, \eta_{2,i} - s_2)$  is a diagonal matrix as follows.

$$\begin{aligned}
W &= \begin{bmatrix} 1 & 1 \\ c_1 \eta_{1,1} + c_2 \eta_{2,1} & c_1 \eta_{1,2} + c_2 \eta_{2,2} \end{bmatrix} \\
\Delta &= \begin{bmatrix} (\eta_{1,1} - s_1)(\eta_{2,1} - s_2) & 0 \\ 0 & (\eta_{1,2} - s_1)(\eta_{2,2} - s_2) \end{bmatrix} \\
S(s_1, s_2) &= W \Delta W^t
\end{aligned}$$

Since the symmetric sums of the roots  $\eta_{1,1}^k \eta_{2,1}^m + \eta_{1,2}^k \eta_{2,2}^m$  equal  $\Sigma_{k,m}$  for  $k, m = 0, 1, 2, \dots$ , then the components of the symmetric 2x2 matrix  $S$  are shown below:

$$\begin{aligned}
S_{1,1}(s_1, s_2) &= 2s_1 s_2 - \Sigma_{0,1} s_1 - \Sigma_{1,0} s_2 + \Sigma_{1,1} \\
S_{1,2}(s_1, s_2) &= c_1 (\Sigma_{1,0} s_1 s_2 - \Sigma_{1,1} s_1 - \Sigma_{2,0} s_2 + \Sigma_{2,1}) \\
&\quad + c_2 (\Sigma_{0,1} s_1 s_2 - \Sigma_{1,1} s_2 - \Sigma_{0,2} s_1 + \Sigma_{1,2}) = S_{2,1}(s_1, s_2) \\
S_{2,2}(s_1, s_2) &= c_1^2 (\Sigma_{2,0} s_1 s_2 - \Sigma_{2,1} s_1 - \Sigma_{3,0} s_2 + \Sigma_{3,1}) \\
&\quad + 2c_1 c_2 (\Sigma_{1,1} s_1 s_2 - \Sigma_{1,2} s_1 - \Sigma_{2,1} s_2 + \Sigma_{2,2}) \\
&\quad + c_2^2 (\Sigma_{0,2} s_1 s_2 - \Sigma_{1,2} s_2 - \Sigma_{0,3} s_1 + \Sigma_{1,3})
\end{aligned}$$

The characteristic equation of the matrix  $S$  is simply  $\lambda^2 - \text{Tr}(S(s_1, s_2))\lambda + \det(S(s_1, s_2))$  whose coefficients are given by  $\mathbf{v} = [1, -\text{Tr}(S(s_1, s_2)), \det(S(s_1, s_2))]$ . Hence, the quantities of interest are  $-\text{Tr}(S(s_1, s_2))$  and  $\det(S(s_1, s_2))$  which are shown next.

$$-\text{Tr}(S(s_1, s_2)) = (-\Sigma_{20}c_1^2 - 2\Sigma_{11}c_1c_2 - \Sigma_{02}c_2^2 - 2)s_1s_2 + (\Sigma_{21}c_1^2 + 2\Sigma_{12}c_1c_2 + \Sigma_{03}c_2^2 + \Sigma_{01})s_1 \\ + (\Sigma_{30}c_1^2 + 2\Sigma_{21}c_1c_2 + \Sigma_{12}c_2^2 + \Sigma_{10})s_2 + (-\Sigma_{31}c_1^2 - 2\Sigma_{22}c_1c_2 - \Sigma_{13}c_2^2 - \Sigma_{11})$$

$$\det(S(s_1, s_2)) = (-\Sigma_{01}^2c_2^2 - 2\Sigma_{01}\Sigma_{10}c_1c_2 - \Sigma_{10}^2c_1^2 + 2\Sigma_{20}c_1^2 + 4\Sigma_{11}c_1c_2 + 2\Sigma_{02}c_2^2)s_1^2s_2^2 \\ + (\Sigma_{01}\Sigma_{02}c_2^2 - 2\Sigma_{21}c_1^2 - 4\Sigma_{12}c_1c_2 - 2\Sigma_{03}c_2^2 - \Sigma_{01}\Sigma_{20}c_1^2 + 2\Sigma_{10}\Sigma_{11}c_1^2 \\ + 2\Sigma_{02}\Sigma_{10}c_1c_2)s_1^2s_2 + (-\Sigma_{02}^2c_2^2 - 2\Sigma_{02}\Sigma_{11}c_1c_2 - \Sigma_{11}^2c_1^2 + \Sigma_{01}\Sigma_{21}c_1^2 \\ + 2\Sigma_{01}\Sigma_{12}c_1c_2 + \Sigma_{01}\Sigma_{03}c_2^2)s_1^2 + (2\Sigma_{01}\Sigma_{11}c_2^2 - 2\Sigma_{30}c_1^2 - 4\Sigma_{21}c_1c_2 - 2\Sigma_{12}c_2^2 \\ - \Sigma_{02}\Sigma_{10}c_2^2 + \Sigma_{10}\Sigma_{20}c_1^2 + 2\Sigma_{01}\Sigma_{20}c_1c_2)s_1s_2^2 + (2\Sigma_{13}c_2^2 + 2\Sigma_{31}c_1^2 + 4\Sigma_{22}c_1c_2 \\ - \Sigma_{01}\Sigma_{12}c_2^2 - \Sigma_{02}\Sigma_{11}c_2^2 + \Sigma_{03}\Sigma_{10}c_2^2 + \Sigma_{01}\Sigma_{30}c_1^2 - \Sigma_{10}\Sigma_{21}c_1^2 - \Sigma_{11}\Sigma_{20}c_1^2 \\ - 2\Sigma_{02}\Sigma_{20}c_1c_2)s_1s_2 + (2\Sigma_{02}\Sigma_{12}c_2^2 - \Sigma_{01}\Sigma_{13}c_2^2 - \Sigma_{03}\Sigma_{11}c_2^2 - \Sigma_{01}\Sigma_{31}c_1^2 \\ + \Sigma_{11}\Sigma_{21}c_1^2 - 2\Sigma_{01}\Sigma_{22}c_1c_2 + 2\Sigma_{02}\Sigma_{21}c_1c_2)s_1 + (-\Sigma_{11}^2c_2^2 - 2\Sigma_{11}\Sigma_{20}c_1c_2 \\ - \Sigma_{20}^2c_1^2 + \Sigma_{10}\Sigma_{30}c_1^2 + 2\Sigma_{10}\Sigma_{21}c_1c_2 + \Sigma_{10}\Sigma_{12}c_2^2)s_2^2 + (\Sigma_{11}\Sigma_{12}c_2^2 - \Sigma_{10}\Sigma_{13}c_2^2 \\ - \Sigma_{10}\Sigma_{31}c_1^2 - \Sigma_{11}\Sigma_{30}c_1^2 + 2\Sigma_{20}\Sigma_{21}c_1^2 - 2\Sigma_{10}\Sigma_{22}c_1c_2 + 2\Sigma_{12}\Sigma_{20}c_1c_2)s_2 \\ + (-\Sigma_{12}^2c_2^2 - 2\Sigma_{12}\Sigma_{21}c_1c_2 - \Sigma_{21}^2c_1^2 + \Sigma_{11}\Sigma_{31}c_1^2 + 2\Sigma_{11}\Sigma_{22}c_1c_2 + \Sigma_{11}\Sigma_{13}c_2^2)$$

Let  $V(s_1, s_2)$  be the number of consecutive sign changes in  $\mathbf{v}$ . Since we are interested in the feasibility domain, note that the points  $\{(0, 0), (0, \infty), (\infty, 0), (\infty, \infty)\}$  are the vertices of the "box" that bound the feasibility domain. Hence, the expression of  $F(\Psi)$  is simply  $F(\Psi) = [V(0, 0) - V(0, \infty) - V(\infty, 0) + V(\infty, \infty)]/2$ . Here,  $\infty$  is a limit; therefore, 0 is evaluated first before the limit is taken at infinity. For  $V(\infty, \infty)$  where the limit of two quantities approach infinity, the limit is unique. Therefore, it does not matter along which direction the limit is taken. Now, we need to evaluate  $-\text{Tr}(S)$  and  $\det(S)$  at those four vertices which are the basis to construct the inequalities that describe the feasible domain.

$$\text{sign}(-\text{Tr}(S(0, 0))) = \text{sign}(-\Sigma_{31}c_1^2 - 2\Sigma_{22}c_1c_2 - \Sigma_{13}c_2^2 - \Sigma_{11})$$

$$\text{sign}(\det(S(0, 0))) = \text{sign}(-\Sigma_{12}^2c_2^2 - 2\Sigma_{12}\Sigma_{21}c_1c_2 - \Sigma_{21}^2c_1^2 + \Sigma_{11}\Sigma_{31}c_1^2 + 2\Sigma_{11}\Sigma_{22}c_1c_2 + \Sigma_{11}\Sigma_{13}c_2^2)$$

$$\text{sign}(-\text{Tr}(S(\infty, 0))) = \text{sign}(\Sigma_{21}c_1^2 + 2\Sigma_{12}c_1c_2 + \Sigma_{03}c_2^2 + \Sigma_{01})$$

$$\text{sign}(\det(S(\infty, 0))) = \text{sign}(-\Sigma_{02}^2c_2^2 - 2\Sigma_{02}\Sigma_{11}c_1c_2 - \Sigma_{11}^2c_1^2 + \Sigma_{01}\Sigma_{21}c_1^2 + 2\Sigma_{01}\Sigma_{12}c_1c_2 + \Sigma_{01}\Sigma_{03}c_2^2)$$

$$\text{sign}(-\text{Tr}(S(0, \infty))) = \text{sign}(\Sigma_{30}c_1^2 + 2\Sigma_{21}c_1c_2 + \Sigma_{12}c_2^2 + \Sigma_{10})$$

$$\text{sign}(\det(S(0, \infty))) = \text{sign}(-\Sigma_{11}^2c_2^2 - 2\Sigma_{11}\Sigma_{20}c_1c_2 - \Sigma_{20}^2c_1^2 + \Sigma_{10}\Sigma_{30}c_1^2 + 2\Sigma_{10}\Sigma_{21}c_1c_2 + \Sigma_{10}\Sigma_{12}c_2^2)$$

$$\text{sign}(-\text{Tr}(S(\infty, \infty))) = \text{sign}(-\Sigma_{20}c_1^2 - 2\Sigma_{11}c_1c_2 - \Sigma_{02}c_2^2 - 2)$$

$$\text{sign}(\det(S(\infty, \infty))) = \text{sign}(-\Sigma_{01}^2c_2^2 - 2\Sigma_{01}\Sigma_{10}c_1c_2 - \Sigma_{10}^2c_1^2 + 2\Sigma_{20}c_1^2 + 4\Sigma_{11}c_1c_2 + 2\Sigma_{02}c_2^2)$$

Note that the formula of  $F(\Psi)$  is completely independent of  $c_1$  and  $c_2$  and the property can be checked with our provided code. Let us set  $c_1 = 1$  and  $c_2 = 0$  for convenience. Now, the

feasible domain is the set of all inequalities so that  $F(\Psi) \geq 1$  and found 13 non-empty ones. This was done via computing  $F(\Psi)$  for a range of parameters ( $\Psi$ , with each component is varied independently and uniformly between  $-1$  and  $1$ ). There was no more increase in the number of non-empty sets (the 13 ones) when the range of each parameter is varied independently and uniformly between  $-100$  to  $100$ . The 13 sets are shown in the columns below and satisfying any of those guarantees feasibility. The signs  $-$  and  $+$  mean that the quantity on the left-hand most in the table is less than  $0$  and greater than  $0$  respectively. In this table, we care about conditions that satisfy  $F(\Psi)$  and we will not separate them based on whether  $F$  takes a value of  $1$  or  $2$ .

		$C_1$	$C_2$	$C_3$	$C_4$	$C_5$	$C_6$	$C_7$	$C_8$	$C_9$	$C_{10}$	$C_{11}$	$C_{12}$	$C_{13}$
$-\text{Tr}(S(0,0))$	$-\Sigma_{31} - \Sigma_{11}$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$+$	$+$	$+$	$+$
$\det(S(0,0))$	$-\Sigma_{21}^2 + \Sigma_{11}\Sigma_{31}$	$-$	$-$	$-$	$-$	$+$	$+$	$+$	$+$	$+$	$-$	$-$	$-$	$-$
$-\text{Tr}(S(\infty,0))$	$\Sigma_{21} + \Sigma_{01}$	$-$	$+$	$+$	$+$	$-$	$-$	$+$	$+$	$+$	$-$	$+$	$+$	$+$
$\det(S(\infty,0))$	$-\Sigma_{11}^2 + \Sigma_{01}\Sigma_{21}$	$-$	$-$	$+$	$+$	$-$	$-$	$-$	$-$	$+$	$-$	$-$	$+$	$+$
$-\text{Tr}(S(0,\infty))$	$\Sigma_{30} + \Sigma_{10}$	$+$	$+$	$-$	$+$	$-$	$+$	$-$	$+$	$+$	$+$	$+$	$-$	$+$
$\det(S(0,\infty))$	$-\Sigma_{20}^2 + \Sigma_{10}\Sigma_{30}$	$+$	$+$	$-$	$-$	$-$	$-$	$-$	$-$	$+$	$+$	$+$	$-$	$-$
$-\text{Tr}(S(\infty,\infty))$	$-\Sigma_{20} - 2$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$	$-$
$\det(S(\infty,\infty))$	$-\Sigma_{10}^2 + 2\Sigma_{20}$	$+$	$+$	$+$	$+$	$+$	$+$	$+$	$+$	$+$	$+$	$+$	$+$	$+$

From the table,  $-\text{Tr}(S(\infty,\infty))$  is negative and  $\det(S(\infty,\infty))$  is positive for all 13 conditions. This is because the relations  $-\Sigma_{20} - 2 < 0$  always holds (minus sum of squares minus a positive number must be negative). Also, the relation  $-\Sigma_{10}^2 + 2\Sigma_{20} > 0$  always holds, which follows from the AM-GM inequality. Hence, the last two conditions are redundant and can be eliminated as they are automatically satisfied. In addition, the 13 sets can be compressed nicely into 4 as follows. Note that columns 1 and 2 (i.e,  $C_1$  and  $C_2$ ) differ in sign in the third row ( $-\text{Tr}(S(\infty,0))$ ). Hence, the two conditions can be combined into one without caring about the sign of  $-\text{Tr}(S(\infty,0))$ . The same applies to columns 3 and 4 (i.e,  $C_3$  and  $C_4$ ), 5 and 6 (i.e,  $C_5$  and  $C_6$ ), 7 and 8 (i.e,  $C_7$  and  $C_8$ ), 10 and 11 (i.e,  $C_{10}$  and  $C_{11}$ ) as well as 12 and 13 (i.e,  $C_{12}$  and  $C_{13}$ ) since these pairs of columns differ by a single sign only. The reduced table from combining columns (conditions) is shown below where X denotes to no condition:

		$C_{1+2}$	$C_{3+4}$	$C_{5+6}$	$C_{7+8}$	$C_9$	$C_{10+11}$	$C_{12+13}$
$-\text{Tr}(S(0, 0))$	$-\Sigma_{31} - \Sigma_{11}$	-	-	-	-	-	+	+
$\det(S(0, 0))$	$-\Sigma_{21}^2 + \Sigma_{11}\Sigma_{31}$	-	-	+	+	+	-	-
$-\text{Tr}(S(\infty, 0))$	$\Sigma_{21} + \Sigma_{01}$	X	+	-	+	+	X	+
$\det(S(\infty, 0))$	$-\Sigma_{11}^2 + \Sigma_{01}\Sigma_{21}$	-	+	-	-	+	-	+
$-\text{Tr}(S(0, \infty))$	$\Sigma_{30} + \Sigma_{10}$	+	X	X	X	+	+	X
$\det(S(0, \infty))$	$-\Sigma_{20}^2 + \Sigma_{10}\Sigma_{30}$	+	-	-	-	+	+	-

Furthermore, we can combine  $C_{1+2}$  with  $C_{10+11}$ ,  $C_{3+4}$  with  $C_{12+13}$  and  $C_{5+6}$  with  $C_{7+8}$  to produce the following table:

		$C_{1+2+10+11}$	$C_{3+4+12+13}$	$C_{5+6+7+8}$	$C_9$
$-\text{Tr}(S(0, 0))$	$-\Sigma_{3,1} - \Sigma_{1,1}$	X	X	-	-
$\det(S(0, 0))$	$-\Sigma_{2,1}^2 + \Sigma_{1,1}\Sigma_{3,1}$	-	-	+	+
$-\text{Tr}(S(\infty, 0))$	$\Sigma_{2,1} + \Sigma_{0,1}$	X	+	X	+
$\det(S(\infty, 0))$	$-\Sigma_{1,1}^2 + \Sigma_{0,1}\Sigma_{2,1}$	-	+	-	+
$-\text{Tr}(S(0, \infty))$	$\Sigma_{3,0} + \Sigma_{1,0}$	+	X	X	+
$\det(S(0, \infty))$	$-\Sigma_{2,0}^2 + \Sigma_{1,0}\Sigma_{3,0}$	+	-	-	+

So far, we have combined columns but have not investigated whether there are redundant signs in each column. Upon computing the conditional probability that a sign occurs given that all other signs occur in the same column and keep deleting signs until there is no conditional probability of 1, we find the following minimized table that is shown below:

		$C'_1$	$C'_2$	$C'_3$	$C'_4$
$-\text{Tr}(S(0, 0))$	$-\Sigma_{3,1} - \Sigma_{1,1}$	X	X	-	X
$\det(S(0, 0))$	$-\Sigma_{2,1}^2 + \Sigma_{1,1}\Sigma_{3,1}$	X	X	+	X
$-\text{Tr}(S(\infty, 0))$	$\Sigma_{2,1} + \Sigma_{0,1}$	X	+	X	+
$\det(S(\infty, 0))$	$-\Sigma_{1,1}^2 + \Sigma_{0,1}\Sigma_{2,1}$	-	+	-	+
$-\text{Tr}(S(0, \infty))$	$\Sigma_{3,0} + \Sigma_{1,0}$	+	X	X	+
$\det(S(0, \infty))$	$-\Sigma_{2,0}^2 + \Sigma_{1,0}\Sigma_{3,0}$	+	-	X	+

Let  $Q_i$  be the basis quantity in row  $i$ . The minimized table above is not unique. For column  $C'_1$ , the user may eliminate either  $Q_2 < 0$  or  $Q_4 < 0$  in that column but not both. This is because  $P(Q_2 < 0 | Q_4 < 0, Q_5 > 0, Q_6 > 0) = 1$  and  $P(Q_4 < 0 | Q_2 < 0, Q_5 > 0, Q_6 > 0) = 1$  but upon deleting either  $Q_2 < 0$  or  $Q_4 < 0$  from these conditional probabilities, we find  $P(Q_2 < 0 | Q_5 > 0, Q_6 > 0) \neq 1$  and  $P(Q_4 < 0 | Q_5 > 0, Q_6 > 0) \neq 1$  meaning that the inequalities  $Q_2 < 0$  and  $Q_4 < 0$  imply one another given that  $Q_5 > 0$  and  $Q_6 > 0$ .



### 4.3.2 Application: 2-Species with Type III Functional Responses

Consider the simplest 2-species LV model with type III functional responses model that is impossible to solve for the location of the equilibrium points analytically.

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(r_1 + a_{11}N_1 + a_{12}\frac{N_1N_2}{1 + hN_1^2}) \\ \frac{dN_2}{dt} &= N_2(r_2 + a_{21}\frac{N_1^2}{1 + hN_1^2} + a_{22}N_2)\end{aligned}$$

Let  $\Psi = (r_1, r_2, a_{11}, a_{12}, a_{21}, a_{22}, h)$  be the vector of model parameters. The common numerators of the RHS of the system above, after deleting  $N_1$  and  $N_2$  outside the brackets, are given by  $f_1(N_1, N_2) = r_1 + a_{11}N_1 + a_{12}N_1N_2 + r_1hN_1^2 + a_{11}hN_1^3$  and  $f_2(N_1, N_2) = r_2 + a_{22}N_2 + (a_{21} + r_2h)N_1^2 + a_{22}hN_1^2N_2$  for lines 1 and 2 respectively. Upon eliminating  $N_1$  from both  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  we obtain  $\text{Res}_{N_1}(f_1, f_2)$  which is a polynomial of degree 5 in  $N_2$  which cannot be solved analytically in closed-form. Similarly, upon eliminating  $N_2$  from both  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  we obtain  $\text{Res}_{N_2}(f_1, f_2)$  which is a polynomial of degree 5 in  $N_1$ . The two resultants, each written in two forms (i.e, polynomial combination of  $f_1$  and  $f_2$  or in terms of  $N$ 's) are shown below:

$$\begin{aligned}\text{Res}_{N_1}(f_1, f_2) &= \begin{vmatrix} a_{11}h & r_1h & a_{11} + a_{12}N_2 & r_1 & N_1f_1 \\ 0 & a_{11}h & r_1h & a_{11} + a_{12}N_2 & f_1 \\ a_{21} + r_2h + a_{22}hN_2 & 0 & r_2 + a_{22}N_2 & 0 & N_1^2f_2 \\ 0 & a_{21} + r_2h + a_{22}hN_2 & 0 & r_2 + a_{22}N_2 & N_1f_2 \\ 0 & 0 & a_{21} + r_2h + a_{22}hN_2 & 0 & f_2 \end{vmatrix} \\ &= T_{21}f_1 + T_{22}f_2 = \sum_{l_2=0}^5 h_{(2,l_2)}N_2^{l_2}, \text{ where} \end{aligned}$$

$$\begin{aligned}T_{21} &= (a_{21} + hr_2 + N_2a_{22}h)^2(a_{21}r_1 - N_1a_{11}a_{21} - N_1N_2a_{12}a_{21} - N_1N_2a_{12}hr_2 - N_1N_2^2a_{12}a_{22}h) \\ T_{22} &= N_1^2N_2^3a_{11}a_{12}a_{22}^2h^3 + 2N_1^2N_2^2a_{11}a_{12}a_{21}a_{22}h^2 + 2N_1^2N_2^2a_{11}a_{12}a_{22}h^3r_2 + N_1^2N_2a_{11}^2a_{21}a_{22}h^2 \\ &\quad + N_1^2N_2a_{11}a_{12}a_{21}^2h + 2N_1^2N_2a_{11}a_{12}a_{21}h^2r_2 + N_1^2N_2a_{11}a_{12}h^3r_2^2 + N_1^2a_{11}^2a_{21}^2h + N_1^2a_{11}^2a_{21}h^2r_2 \\ &\quad + N_1N_2^3a_{12}a_{22}^2h^3r_1 + 2N_1N_2^2a_{12}a_{21}a_{22}h^2r_1 + 2N_1N_2^2a_{12}a_{22}h^3r_1r_2 + N_1N_2a_{12}a_{21}^2hr_1 \\ &\quad + 2N_1N_2a_{12}a_{21}h^2r_1r_2 + N_1N_2a_{12}h^3r_1r_2^2 + N_2^4a_{12}^2a_{22}^2h^2 + 2N_2^3a_{12}^2a_{21}a_{22}h + 2N_2^3a_{12}^2a_{22}h^2r_2 \\ &\quad + 2N_2^2a_{11}a_{12}a_{21}a_{22}h + N_2^2a_{12}^2a_{21}^2 + 2N_2^2a_{12}^2a_{21}hr_2 + N_2^2a_{12}^2h^2r_2^2 + 2N_2a_{11}a_{12}a_{21}^2 \\ &\quad + 2N_2a_{11}a_{12}a_{21}hr_2 - N_2a_{21}a_{22}h^2r_1^2 + a_{11}^2a_{21}^2 - a_{21}^2hr_1^2 - a_{21}h^2r_1^2r_2\end{aligned}$$

$$\begin{aligned}
h_{(2,5)} &= a_{12}^2 a_{22}^3 h^2 \\
h_{(2,4)} &= 3r_2 a_{12}^2 a_{22}^2 h^2 + 2a_{21} a_{12}^2 a_{22}^2 h \\
h_{(2,3)} &= a_{12}^2 a_{21}^2 a_{22} + 4a_{12}^2 a_{21} a_{22} h r_2 + 3a_{12}^2 a_{22} h^2 r_2^2 + 2a_{11} a_{12} a_{21} a_{22}^2 h \\
h_{(2,2)} &= a_{12}^2 a_{21}^2 r_2 + 2a_{12}^2 a_{21} h r_2^2 + a_{12}^2 h^2 r_2^3 + 2a_{11} a_{22} a_{12} a_{21}^2 + 4a_{11} a_{22} a_{12} a_{21} h r_2 \\
h_{(2,1)} &= a_{22} a_{11}^2 a_{21}^2 + 2a_{12} a_{11} a_{21}^2 r_2 + 2a_{12} h a_{11} a_{21} r_2^2 + a_{22} h a_{21}^2 r_1^2 \\
h_{(2,0)} &= r_2 a_{11}^2 a_{21}^2 + a_{21}^3 r_1^2 + h r_2 a_{21}^2 r_1^2
\end{aligned}$$

$$\text{Res}_{N_2}(f_1, f_2) = \begin{vmatrix} a_{12} N_1 & f_1 \\ a_{22} + a_{22} h N_1^2 & f_2 \end{vmatrix} = T_{11} f_1 + T_{12} f_2 = \sum_{l_1=0}^5 h_{(1,l_1)} N_1^{l_1}, \text{ where}$$

$$\begin{aligned}
T_{11} &= -a_{22} - a_{22} h N_1^2 \\
T_{12} &= N_1 a_{12} \\
h_{(1,5)} &= -a_{11} a_{22} h^2 \\
h_{(1,4)} &= -a_{22} h^2 r_1 \\
h_{(1,3)} &= a_{12} a_{21} - 2a_{11} a_{22} h + a_{12} h r_2 \\
h_{(1,2)} &= -2a_{22} h r_1 \\
h_{(1,1)} &= a_{12} r_2 - a_{11} a_{22} \\
h_{(1,0)} &= -a_{22} r_1
\end{aligned}$$

Observe that  $\text{Res}_{N_1}(f_1, f_2)$  contains no  $N_1$  and is a polynomial of degree 5 in  $N_2$  only. Similarly,  $\text{Res}_{N_2}(f_1, f_2)$  contains no  $N_2$  and is a polynomial of degree 5 in  $N_1$  only. This is an indication that the number of roots of  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  is 5. Note that the roots of the univariate polynomials  $\text{Res}_{N_1}(f_1, f_2)$  and  $\text{Res}_{N_2}(f_1, f_2)$ , upon appropriate pairing of roots of the first polynomial with the second, are the roots of the system  $f_1(N_1, N_2) = 0$  and  $f_2(N_1, N_2) = 0$ . From Abel's impossibility theorem, since it is impossible to solve for the roots of a quintic or higher degree polynomials in terms of radicals, then the roots of either  $\text{Res}_{N_1}(f_1, f_2)$  or  $\text{Res}_{N_2}(f_1, f_2)$  are unattainable analytically which implies that the system  $f_1(N_1, N_2) = 0$  and  $f_2(N_1, N_2) = 0$  cannot be solved. After finding the resultants in both forms, we evaluate the determinant of the eliminating matrix, which is  $T(f_1, f_2) = T_{11}T_{22} - T_{12}T_{21}$  and the determinant of the Jacobian of  $f_1$  and  $f_2$  as following

$$\begin{aligned}
J(f_1, f_2) &= \begin{vmatrix} 3a_{11} h N_1^2 + 2h r_1 N_1 + a_{11} + N_2 a_{12} & N_1 a_{12} \\ 2N_1 a_{21} + 2N_1 h r_2 + 2N_1 N_2 a_{22} h & a_{22} h N_1^2 + a_{22} \end{vmatrix} = a_{11} a_{22} + N_2 a_{12} a_{22} - 2N_1^2 a_{12} a_{21} \\
&\quad + 4N_1^2 a_{11} a_{22} h - 2N_1^2 a_{12} h r_2 + 3N_1^4 a_{11} a_{22} h^2 + 2N_1^3 a_{22} h^2 r_1 + 2N_1 a_{22} h r_1 - N_1^2 N_2 a_{12} a_{22} h
\end{aligned}$$

Now, we need to expand the generating function  $G(f_1(N_1, N_2), f_2(N_1, N_2))$  around  $N_1 = \infty$  and  $N_2 = \infty$  (no need to perform a two-variable series expansion). Since  $\text{Res}_{N_1}(f_1, f_2)$  and  $\text{Res}_{N_2}(f_1, f_2)$  are univariate polynomials, we expand their reciprocal individually to get the series  $1/\text{Res}_{N_2}(f_1, f_2) = \sum_{m_1=1}^{\infty} p_{(1,m_1)}/N_1^{m_1+4}$  and  $1/\text{Res}_{N_1}(f_1, f_2) = \sum_{m_2=1}^{\infty} p_{(2,m_2)}/N_2^{m_2+4}$ . The coefficients can be obtained via MATLAB's 'taylor' function where  $N_1$  and  $N_2$  are substituted by  $1/x$  and  $1/y$  respectively. Alternatively, these  $p$ 's can be obtained analytically as follows. We have already written  $\text{Res}_{N_2}(f_1, f_2) = \sum_{l_1=0}^{K_1} h_{(1,l_1)}N_1^{l_1}$  and  $\text{Res}_{N_1}(f_1, f_2) = \sum_{l_2=0}^{K_2} h_{(2,l_2)}N_2^{l_2}$  where we have  $K_1 = K_2 = 5$ . After that, construct the following 2 matrices  $A_1$  and  $A_2$

$$A_i = \begin{bmatrix} 1 & 0 & 0 & 0 & \dots \\ h_{(i,K_i)} & h_{(i,K_i-1)} & h_{(i,K_i-2)} & h_{(i,K_i-3)} & \dots \\ 0 & h_{(i,K_i)} & h_{(i,K_i-1)} & h_{(i,K_i-2)} & \dots \\ 0 & 0 & h_{(i,K_i)} & h_{(i,K_i-1)} & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{bmatrix}, \quad i = 1, 2$$

Next, let  $\text{Res}_{(N_1, N_2)/N_1}(f_1, f_2) \equiv \text{Res}_{N_2}(f_1, f_2)$  and  $\text{Res}_{(N_1, N_2)/N_2}(f_1, f_2) \equiv \text{Res}_{N_1}(f_1, f_2)$ .

The reciprocal of each resultant is given by

$$\frac{1}{\text{Res}_{(N_1, N_2)/N_i}(f_1, f_2)} = \frac{1}{N_i^{K_i-1}} \sum_{m_i=1}^{\infty} \frac{p_{(i,m_i)}}{N_i^{m_i}}, \quad p_{(i,m_i)} = \frac{(-1)^{m_i+1}}{h_{(i,K_i)}^{m_i}} \det(A_i[1 : m_i, 1 : m_i]), \quad i = 1, 2$$

Here,  $A_i[1 : m_i, 1 : m_i]$  is the sub-matrix of  $A_i$  that contains its first  $m_i$  rows and columns.

After obtaining both series expansion of the resultant reciprocal, multiply the result by

$T(f_1, f_2)J(f_1, f_2)$  to obtain

$$G(f_1, f_2) = \frac{T(f_1, f_2)J(f_1, f_2)}{\text{Res}_{N_1}(f_1, f_2)\text{Res}_{N_2}(f_1, f_2)} = \frac{\Sigma_{0,0}}{N_1 N_2} + \frac{\Sigma_{1,0}}{N_1^2 N_2} + \frac{\Sigma_{0,1}}{N_1 N_2^2} + \frac{\Sigma_{1,1}}{N_1^2 N_2^2} \\ + \frac{\Sigma_{2,0}}{N_1^3 N_2} + \frac{\Sigma_{2,1}}{N_1^3 N_2^2} + \frac{\Sigma_{0,2}}{N_1 N_2^3} + \frac{\Sigma_{1,2}}{N_1^2 N_2^3} + \frac{\Sigma_{3,0}}{N_1^4 N_2} + \frac{\Sigma_{3,1}}{N_1^4 N_2^2} + \frac{\Sigma_{0,3}}{N_1 N_2^4} + \frac{\Sigma_{1,3}}{N_1^2 N_2^4} + \dots$$

The expression for each of the  $\Sigma$ 's (symmetric power sums of the roots) are shown below

where  $\Sigma_{i,j} = \Sigma_{i,j}^U / \Sigma_{i,j}^D$  is written as a fraction of two polynomials.

$$\Sigma_{0,0}^U = 5$$

$$\Sigma_{0,0}^D = 1$$

$$\Sigma_{1,0}^U = -r_1$$

$$\Sigma_{1,0}^D = a_{11}$$

$$\Sigma_{0,1}^U = -2a_{21} - 3hr_2$$

$$\Sigma_{0,1}^D = a_{22}h$$

$$\Sigma_{2,0}^U = -4a_{22}a_{11}^2h + 2a_{12}r_2a_{11}h + 2a_{12}a_{21}a_{11} + a_{22}h^2r_1^2$$

$$\Sigma_{2,0}^D = a_{11}^2a_{22}h^2$$

$$\Sigma_{1,1}^U = r_1(a_{21} + hr_2)$$

$$\Sigma_{1,1}^D = a_{11}a_{22}h$$

$$\Sigma_{0,2}^U = 2a_{12}a_{21}^2 + 4a_{12}a_{21}hr_2 - 4a_{11}a_{22}a_{21}h + 3a_{12}h^2r_2^2$$

$$\Sigma_{0,2}^D = a_{12}a_{22}^2h^2$$

$$\Sigma_{3,0}^U = -r_1(a_{22}h^2r_1^2 + 3a_{11}a_{12}r_2h + 3a_{11}a_{12}a_{21})$$

$$\Sigma_{3,0}^D = a_{11}^3a_{22}h^2$$

$$\Sigma_{2,1}^U = 6a_{22}a_{11}^2a_{21}h + 2a_{22}a_{11}^2h^2r_2 - 2a_{12}a_{11}a_{21}^2 - 4a_{12}a_{11}a_{21}hr_2 - 2a_{12}a_{11}h^2r_2^2 - a_{22}a_{21}h^2r_1^2 - a_{22}h^3r_1^2r_2$$

$$\Sigma_{2,1}^D = a_{11}^2a_{22}^2h^3$$

$$\Sigma_{1,2}^U = -r_1(a_{12}a_{21}^2 + 2a_{12}a_{21}hr_2 + 4a_{11}a_{22}a_{21}h + a_{12}h^2r_2^2)$$

$$\Sigma_{1,2}^D = a_{11}a_{12}a_{22}^2h^2$$

$$\Sigma_{0,3}^U = -2a_{12}a_{21}^3 - 6a_{12}a_{21}^2hr_2 + 6a_{11}a_{22}a_{21}^2h - 6a_{12}a_{21}h^2r_2^2 + 6a_{11}a_{22}a_{21}h^2r_2 - 3a_{12}h^3r_2^3$$

$$\Sigma_{0,3}^D = a_{12}a_{22}^3h^3$$

$$\Sigma_{4,0}^U = 4a_{11}^4a_{22}^2h^2 - 8a_{11}^3a_{12}a_{21}a_{22}h - 4a_{11}^3a_{12}a_{22}h^2r_2 + 2a_{11}^2a_{12}^2a_{21}^2 + 4a_{11}^2a_{12}^2a_{21}hr_2 + 2a_{11}^2a_{12}^2h^2r_2^2 + 4a_{11}a_{12}a_{21}a_{22}h^2r_1^2 + 4a_{11}a_{12}a_{22}h^3r_1^2r_2 + a_{22}^2h^4r_1^4$$

$$\Sigma_{4,0}^D = a_{11}^4a_{22}^2h^4$$

$$\Sigma_{3,1}^U = r_1(-a_{22}a_{11}^2a_{21}h + 3a_{12}a_{11}a_{21}^2 + 6a_{12}a_{11}a_{21}hr_2 + 3a_{12}a_{11}h^2r_2^2 + a_{22}a_{21}h^2r_1^2 + a_{22}h^3r_1^2r_2)$$

$$\Sigma_{3,1}^D = a_{11}^3a_{22}^2h^3$$

$$\begin{aligned}\Sigma_{2,2}^U &= 4a_{11}^3 a_{21} a_{22}^2 h^2 - 8a_{11}^2 a_{12} a_{21}^2 a_{22} h - 10a_{11}^2 a_{12} a_{21} a_{22} h^2 r_2 - 2a_{11}^2 a_{12} a_{22} h^3 r_2^2 + 2a_{11} a_{12}^2 a_{21}^3 \\ &\quad + 6a_{11} a_{12}^2 a_{21}^2 h r_2 + 6a_{11} a_{12}^2 a_{21} h^2 r_2^2 + 2a_{11} a_{12}^2 h^3 r_2^3 + a_{12} a_{21}^2 a_{22} h^2 r_1^2 + 2a_{12} a_{21} a_{22} h^3 r_1^2 r_2 \\ &\quad + a_{12} a_{22} h^4 r_1^2 r_2^2\end{aligned}$$

$$\Sigma_{2,2}^D = a_{11}^2 a_{12} a_{22}^3 h^4$$

$$\Sigma_{1,3}^U = r_1 (a_{12} a_{21}^3 + 3a_{12} a_{21}^2 h r_2 + 5a_{11} a_{22} a_{21}^2 h + 3a_{12} a_{21} h^2 r_2^2 + 6a_{11} a_{22} a_{21} h^2 r_2 + a_{12} h^3 r_2^3)$$

$$\Sigma_{1,3}^D = a_{11} a_{12} a_{22}^3 h^3$$

$$\begin{aligned}\Sigma_{0,4}^U &= 4a_{11}^2 a_{21}^2 a_{22}^2 h^2 - 8a_{11} a_{12} a_{21}^3 a_{22} h - 16a_{11} a_{12} a_{21}^2 a_{22} h^2 r_2 - 8a_{11} a_{12} a_{21} a_{22} h^3 r_2^2 + 2a_{12}^2 a_{21}^4 \\ &\quad + 8a_{12}^2 a_{21}^3 h r_2 + 12a_{12}^2 a_{21}^2 h^2 r_2^2 + 8a_{12}^2 a_{21} h^3 r_2^3 + 3a_{12}^2 h^4 r_2^4 - 4a_{21}^2 a_{22}^2 h^3 r_1^2\end{aligned}$$

$$\Sigma_{0,4}^D = a_{12}^2 a_{22}^4 h^4$$

$$\begin{aligned}\Sigma_{5,0}^U &= -r_1 (-10a_{11}^3 a_{12} a_{21} a_{22} h - 5a_{11}^3 a_{12} a_{22} h^2 r_2 + 5a_{11}^2 a_{12}^2 a_{21}^2 + 10a_{11}^2 a_{12}^2 a_{21} h r_2 + 5a_{11}^2 a_{12}^2 h^2 r_2^2 \\ &\quad + 5a_{11} a_{12} a_{21} a_{22} h^2 r_1^2 + 5a_{11} a_{12} a_{22} h^3 r_1^2 r_2 + a_{22}^2 h^4 r_1^4)\end{aligned}$$

$$\Sigma_{5,0}^D = a_{11}^5 a_{22}^2 h^4$$

$$\begin{aligned}\Sigma_{4,1}^U &= -10a_{11}^4 a_{21} a_{22}^2 h^2 - 2a_{11}^4 a_{22}^2 h^3 r_2 + 10a_{11}^3 a_{12} a_{21}^2 a_{22} h + 14a_{11}^3 a_{12} a_{21} a_{22} h^2 r_2 - 2a_{11}^2 a_{12}^2 a_{21}^3 \\ &\quad + 4a_{11}^3 a_{12} a_{22} h^3 r_2^2 - 6a_{11}^2 a_{12}^2 a_{21}^2 h r_2 - 6a_{11}^2 a_{12}^2 a_{21} h^2 r_2^2 - 2a_{11}^2 a_{12}^2 h^3 r_2^3 - 8a_{11} a_{12} a_{21} a_{22} h^3 r_1^2 r_2 \\ &\quad - a_{21} a_{22}^2 h^4 r_1^4 - a_{22}^2 h^5 r_1^4 r_2 + a_{11}^2 a_{21} a_{22}^2 h^3 r_1^2 - 4a_{11} a_{12} a_{21}^2 a_{22} h^2 r_1^2 - 4a_{11} a_{12} a_{22} h^4 r_1^2 r_2^2\end{aligned}$$

$$\Sigma_{4,1}^D = a_{11}^4 a_{22}^3 h^5$$

$$\begin{aligned}\Sigma_{3,2}^U &= -r_1 (-4a_{11}^3 a_{21} a_{22}^2 h^2 - 2a_{11}^2 a_{12} a_{21}^2 a_{22} h - 2a_{11}^2 a_{12} a_{21} a_{22} h^2 r_2 + 3a_{11} a_{12}^2 a_{21}^3 + 9a_{11} a_{12}^2 a_{21}^2 h r_2 \\ &\quad + 9a_{11} a_{12}^2 a_{21} h^2 r_2^2 + 3a_{11} a_{12}^2 h^3 r_2^3 + a_{12} a_{21}^2 a_{22} h^2 r_1^2 + 2a_{12} a_{21} a_{22} h^3 r_1^2 r_2 + a_{12} a_{22} h^4 r_1^2 r_2^2)\end{aligned}$$

$$\Sigma_{3,2}^D = a_{11}^3 a_{12} a_{22}^3 h^4$$

$$\begin{aligned}\Sigma_{2,3}^U &= -10a_{11}^3 a_{21}^2 a_{22}^2 h^2 - 6a_{11}^3 a_{21} a_{22}^2 h^3 r_2 + 10a_{11}^2 a_{12} a_{21}^3 a_{22} h + 22a_{11}^2 a_{12} a_{21}^2 a_{22} h^2 r_2 - 2a_{11} a_{12}^2 a_{21}^4 \\ &\quad + 14a_{11}^2 a_{12} a_{21} a_{22} h^3 r_2^2 + 2a_{11}^2 a_{12} a_{22} h^4 r_2^3 - 8a_{11} a_{12}^2 a_{21}^3 h r_2 - 12a_{11} a_{12}^2 a_{21}^2 h^2 r_2^2 - 8a_{11} a_{12}^2 a_{21} h^3 r_2^3 \\ &\quad - 2a_{11} a_{12}^2 h^4 r_2^4 - a_{12} a_{21}^3 a_{22} h^2 r_1^2 - 3a_{12} a_{21}^2 a_{22} h^3 r_1^2 r_2 - 3a_{12} a_{21} a_{22} h^4 r_1^2 r_2^2 - a_{12} a_{22} h^5 r_1^2 r_2^3\end{aligned}$$

$$\Sigma_{2,3}^D = a_{11}^2 a_{12} a_{22}^4 h^5$$

$$\begin{aligned}\Sigma_{1,4}^U &= -r_1 (-8a_{11}^2 a_{21}^2 a_{22}^2 h^2 + 6a_{11} a_{12} a_{21}^3 a_{22} h + 13a_{11} a_{12} a_{21}^2 a_{22} h^2 r_2 + 8a_{11} a_{12} a_{21} a_{22} h^3 r_2^2 + a_{12}^2 a_{21}^4 \\ &\quad + 4a_{12}^2 a_{21}^3 h r_2 + 6a_{12}^2 a_{21}^2 h^2 r_2^2 + 4a_{12}^2 a_{21} h^3 r_2^3 + a_{12}^2 h^4 r_2^4)\end{aligned}$$

$$\Sigma_{1,4}^D = a_{11} a_{12}^2 a_{22}^4 h^4$$

$$\begin{aligned}\Sigma_{0,5}^U &= -10a_{11}^2 a_{21}^3 a_{22}^2 h^2 - 10a_{11}^2 a_{21}^2 a_{22}^2 h^3 r_2 + 10a_{11} a_{12} a_{21}^4 a_{22} h + 30a_{11} a_{12} a_{21}^3 a_{22} h^2 r_2 - 2a_{12}^2 a_{21}^5 \\ &\quad + 30a_{11} a_{12} a_{21}^2 a_{22} h^3 r_2^2 + 10a_{11} a_{12} a_{21} a_{22} h^4 r_2^3 - 10a_{12}^2 a_{21}^4 h r_2 - 20a_{12}^2 a_{21}^3 h^2 r_2^2 - 20a_{12}^2 a_{21}^2 h^3 r_2^3 \\ &\quad - 10a_{12}^2 a_{21} h^4 r_2^4 - 3a_{12}^2 h^5 r_2^5 + 5a_{21}^3 a_{22}^2 h^3 r_1^2 + 10a_{21}^2 a_{22}^2 h^4 r_1^2 r_2\end{aligned}$$

$$\Sigma_{0,5}^D = a_{12}^2 a_{22}^5 h^5$$

$$\begin{aligned}\Sigma_{5,1}^U &= r_1(a_{11}^4 a_{21} a_{22}^2 h^2 - 13a_{11}^3 a_{12} a_{21}^2 a_{22} h - 18a_{11}^3 a_{12} a_{21} a_{22} h^2 r_2 - 5a_{11}^3 a_{12} a_{22} h^3 r_2^2 + 5a_{11}^2 a_{12}^2 a_{21}^3 \\ &\quad + 15a_{11}^2 a_{12}^2 a_{21}^2 h r_2 + 15a_{11}^2 a_{12}^2 a_{21} h^2 r_2^2 + 5a_{11}^2 a_{12}^2 h^3 r_2^3 - a_{11}^2 a_{21} a_{22}^2 h^3 r_1^2 + 5a_{11} a_{12} a_{21}^2 a_{22} h^2 r_1^2 \\ &\quad + 10a_{11} a_{12} a_{21} a_{22} h^3 r_1^2 r_2 + 5a_{11} a_{12} a_{22} h^4 r_1^2 r_2^2 + a_{21} a_{22}^2 h^4 r_1^4 + a_{22}^2 h^5 r_1^4 r_2)\end{aligned}$$

$$\Sigma_{5,1}^D = a_{11}^5 a_{22}^3 h^5$$

$$\begin{aligned}\Sigma_{4,2}^U &= -4a_{11}^5 a_{21} a_{22}^3 h^3 + 18a_{11}^4 a_{12} a_{21}^2 a_{22}^2 h^2 + 16a_{11}^4 a_{12} a_{21} a_{22}^2 h^3 r_2 + 2a_{11}^4 a_{12} a_{22}^2 h^4 r_2^2 + 2a_{11}^2 a_{12}^3 a_{21}^4 \\ &\quad - 12a_{11}^3 a_{12}^2 a_{21}^3 a_{22} h - 28a_{11}^3 a_{12}^2 a_{21}^2 a_{22} h^2 r_2 - 4a_{11}^3 a_{12}^2 a_{22} h^4 r_2^3 + 8a_{11}^2 a_{12}^3 a_{21}^3 h r_2 + 2a_{11}^2 a_{12}^3 h^4 r_2^4 \\ &\quad - 20a_{11}^3 a_{12}^2 a_{21} a_{22} h^3 r_2^2 + 12a_{11}^2 a_{12}^3 a_{21}^2 h^2 r_2^2 + 8a_{11}^2 a_{12}^3 a_{21} h^3 r_2^3 - 2a_{11}^2 a_{12} a_{21}^2 a_{22} h^3 r_1^2 + a_{12} a_{22}^2 h^6 r_1^4 r_2^2 \\ &\quad - 2a_{11}^2 a_{12} a_{21} a_{22}^2 h^4 r_1^2 r_2 + 4a_{11} a_{12}^2 a_{21}^3 a_{22} h^2 r_1^2 + 12a_{11} a_{12}^2 a_{21}^2 a_{22} h^3 r_1^2 r_2 + 12a_{11} a_{12}^2 a_{21} a_{22} h^4 r_1^2 r_2^2 \\ &\quad + 4a_{11} a_{12}^2 a_{22} h^5 r_1^2 r_2^3 + a_{12} a_{21}^2 a_{22}^2 h^4 r_1^4 + 2a_{12} a_{21} a_{22}^2 h^5 r_1^4 r_2\end{aligned}$$

$$\Sigma_{4,2}^D = a_{11}^4 a_{12} a_{22}^4 h^6$$

$$\begin{aligned}\Sigma_{3,3}^U &= r_1(-9a_{11}^3 a_{21}^2 a_{22}^2 h^2 - 6a_{11}^3 a_{21} a_{22}^2 h^3 r_2 - 3a_{11}^2 a_{12} a_{21}^3 a_{22} h - 6a_{11}^2 a_{12} a_{21}^2 a_{22} h^2 r_2 + a_{12} a_{22} h^5 r_1^2 r_2^3 \\ &\quad - 3a_{11}^2 a_{12} a_{21} a_{22} h^3 r_2^2 + 3a_{11} a_{12}^2 a_{21}^4 + 12a_{11} a_{12}^2 a_{21}^3 h r_2 + 18a_{11} a_{12}^2 a_{21}^2 h^2 r_2^2 + 12a_{11} a_{12}^2 a_{21} h^3 r_2^3 \\ &\quad + 3a_{11} a_{12}^2 h^4 r_2^4 + a_{12} a_{21}^3 a_{22} h^2 r_1^2 + 3a_{12} a_{21}^2 a_{22} h^3 r_1^2 r_2 + 3a_{12} a_{21} a_{22} h^4 r_1^2 r_2^2)\end{aligned}$$

$$\Sigma_{3,3}^D = a_{11}^3 a_{12} a_{22}^4 h^5$$

$$\begin{aligned}\Sigma_{2,4}^U &= 2a_{11} a_{12}^3 a_{21}^5 - 4a_{11}^4 a_{21}^2 a_{22}^3 h^3 + 18a_{11}^3 a_{12} a_{21}^3 a_{22}^2 h^2 + 26a_{11}^3 a_{12} a_{21}^2 a_{22}^2 h^3 r_2 + 8a_{11}^3 a_{12} a_{21} a_{22}^2 h^4 r_2^2 \\ &\quad - 12a_{11}^2 a_{12}^2 a_{21}^4 a_{22} h + 2a_{11} a_{12}^3 h^5 r_2^5 + a_{12}^2 a_{21}^4 a_{22} h^2 r_1^2 - 38a_{11}^2 a_{12}^2 a_{21}^3 a_{22} h^2 r_2 - 42a_{11}^2 a_{12}^2 a_{21}^2 a_{22} h^3 r_2^2 \\ &\quad - 18a_{11}^2 a_{12}^2 a_{21} a_{22} h^4 r_2^3 - 2a_{11}^2 a_{12}^2 a_{22} h^5 r_2^4 + 4a_{11}^2 a_{21}^2 a_{22}^2 h^4 r_1^2 + 10a_{11} a_{12}^3 a_{21}^4 h r_2 + 20a_{11} a_{12}^3 a_{21}^3 h^2 r_2^2 \\ &\quad + 20a_{11} a_{12}^3 a_{21}^2 h^3 r_2^3 + 10a_{11} a_{12}^3 a_{21} h^4 r_2^4 + 4a_{12}^2 a_{21}^3 a_{22} h^3 r_1^2 r_2 + 6a_{12}^2 a_{21}^2 a_{22} h^4 r_1^2 r_2^2 + a_{12}^2 a_{22} h^6 r_1^2 r_2^4 \\ &\quad + 4a_{12}^2 a_{21} a_{22} h^5 r_1^2 r_2^3\end{aligned}$$

$$\Sigma_{2,4}^D = a_{11}^2 a_{12}^2 a_{22}^5 h^6$$

$$\begin{aligned}\Sigma_{1,5}^U &= r_1(-19a_{11}^2 a_{21}^3 a_{22}^2 h^2 - 20a_{11}^2 a_{21}^2 a_{22}^2 h^3 r_2 + 7a_{11} a_{12} a_{21}^4 a_{22} h + 22a_{11} a_{12} a_{21}^3 a_{22} h^2 r_2 + a_{12}^2 a_{21}^5 \\ &\quad + 24a_{11} a_{12} a_{21}^2 a_{22} h^3 r_2^2 + 10a_{11} a_{12} a_{21} a_{22} h^4 r_2^3 + 5a_{12}^2 a_{21}^4 h r_2 + 10a_{12}^2 a_{21}^3 h^2 r_2^2 + 10a_{12}^2 a_{21}^2 h^3 r_2^3 \\ &\quad + 5a_{12}^2 a_{21} h^4 r_2^4 + a_{12}^2 h^5 r_2^5)\end{aligned}$$

$$\Sigma_{1,5}^D = a_{11} a_{12}^2 a_{22}^5 h^5$$

Note that if any of the parameters  $a_{11}, a_{12}, a_{22}, h$  is zero, the  $\Sigma$ 's will blow up. If one needs to consider cases where any of the latter parameters is zero, that zero should be first substituted in  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  before carrying on with what we have shown already. Next, denote the roots of  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  by  $\boldsymbol{\eta}_1 = [\eta_{1,1}, \eta_{1,2}, \dots, \eta_{1,5}]^T$  and  $\boldsymbol{\eta}_2 = [\eta_{2,1}, \eta_{2,2}, \dots, \eta_{2,5}]^T$ . Choose a monomial map  $m(N_1, N_2) = [1, N_1, N_2, N_1 N_2, N_1^2]^T$  then, let  $Q(N_1, N_2) = N_1 N_2$  and compute  $S(s_1, s_2) = W \Delta W^t$  where  $W_{ij} = m_i(\eta_{1,j}, \eta_{2,j})$  and  $\Delta_{ii} = Q(\eta_{1,i} - s_1, \eta_{2,i} - s_2)$  is a diagonal matrix as follows.

$$W = \begin{bmatrix} 1 & 1 & 1 & 1 & 1 \\ \eta_{1,1} & \eta_{1,2} & \eta_{1,3} & \eta_{1,4} & \eta_{1,5} \\ \eta_{2,1} & \eta_{2,2} & \eta_{2,3} & \eta_{2,4} & \eta_{2,5} \\ \eta_{1,1}\eta_{2,1} & \eta_{1,2}\eta_{2,2} & \eta_{1,3}\eta_{2,3} & \eta_{1,4}\eta_{2,4} & \eta_{1,5}\eta_{2,5} \\ \eta_{1,1}^2 & \eta_{1,2}^2 & \eta_{1,3}^2 & \eta_{1,4}^2 & \eta_{1,5}^2 \end{bmatrix}$$

$$\Delta = \text{diag}[(\eta_{1,1} - s_1)(\eta_{2,1} - s_2), (\eta_{1,2} - s_1)(\eta_{2,2} - s_2), (\eta_{1,3} - s_1)(\eta_{2,3} - s_2),$$

$$(\eta_{1,4} - s_1)(\eta_{2,4} - s_2), (\eta_{1,5} - s_1)(\eta_{2,5} - s_2)]$$

$$S(s_1, s_2) = W\Delta W^t$$

Note that  $\Sigma_{k,m} = \eta_{1,1}^k \eta_{2,1}^m + \eta_{1,2}^k \eta_{2,2}^m + \dots + \eta_{1,5}^k \eta_{2,5}^m$  for  $k, m = 0, 1, 2, \dots$ . Therefore, the components of the symmetric 5x5 matrix  $S$  are shown below:

$$S_{1,1}(s_1, s_2) = \Sigma_{1,1} - \Sigma_{0,1}s_1 - \Sigma_{1,0}s_2 + 5s_1s_2$$

$$S_{1,2}(s_1, s_2) = \Sigma_{2,1} - \Sigma_{1,1}s_1 - \Sigma_{2,0}s_2 + \Sigma_{1,0}s_1s_2 = S_{2,1}(s_1, s_2)$$

$$S_{1,3}(s_1, s_2) = \Sigma_{1,2} - \Sigma_{0,2}s_1 - \Sigma_{1,1}s_2 + \Sigma_{0,1}s_1s_2 = S_{3,1}(s_1, s_2)$$

$$S_{1,4}(s_1, s_2) = \Sigma_{2,2} - \Sigma_{1,2}s_1 - \Sigma_{2,1}s_2 + \Sigma_{1,1}s_1s_2 = S_{4,1}(s_1, s_2)$$

$$S_{1,5}(s_1, s_2) = \Sigma_{3,1} - \Sigma_{2,1}s_1 - \Sigma_{3,0}s_2 + \Sigma_{2,0}s_1s_2 = S_{5,1}(s_1, s_2)$$

$$S_{2,2}(s_1, s_2) = \Sigma_{3,1} - \Sigma_{2,1}s_1 - \Sigma_{3,0}s_2 + \Sigma_{2,0}s_1s_2$$

$$S_{2,3}(s_1, s_2) = \Sigma_{2,2} - \Sigma_{1,2}s_1 - \Sigma_{2,1}s_2 + \Sigma_{1,1}s_1s_2 = S_{3,2}(s_1, s_2)$$

$$S_{2,4}(s_1, s_2) = \Sigma_{3,2} - \Sigma_{2,2}s_1 - \Sigma_{3,1}s_2 + \Sigma_{2,1}s_1s_2 = S_{4,2}(s_1, s_2)$$

$$S_{2,5}(s_1, s_2) = \Sigma_{4,1} - \Sigma_{3,1}s_1 - \Sigma_{4,0}s_2 + \Sigma_{3,0}s_1s_2 = S_{5,2}(s_1, s_2)$$

$$S_{3,3}(s_1, s_2) = \Sigma_{1,3} - \Sigma_{0,3}s_1 - \Sigma_{1,2}s_2 + \Sigma_{0,2}s_1s_2$$

$$S_{3,4}(s_1, s_2) = \Sigma_{2,3} - \Sigma_{1,3}s_1 - \Sigma_{2,2}s_2 + \Sigma_{1,2}s_1s_2 = S_{4,3}(s_1, s_2)$$

$$S_{3,5}(s_1, s_2) = \Sigma_{3,2} - \Sigma_{2,2}s_1 - \Sigma_{3,1}s_2 + \Sigma_{2,1}s_1s_2 = S_{5,3}(s_1, s_2)$$

$$S_{4,4}(s_1, s_2) = \Sigma_{3,3} - \Sigma_{2,3}s_1 - \Sigma_{3,2}s_2 + \Sigma_{2,2}s_1s_2$$

$$S_{4,5}(s_1, s_2) = \Sigma_{4,2} - \Sigma_{3,2}s_1 - \Sigma_{4,1}s_2 + \Sigma_{3,1}s_1s_2 = S_{5,4}(s_1, s_2)$$

$$S_{5,5}(s_1, s_2) = \Sigma_{5,1} - \Sigma_{4,1}s_1 - \Sigma_{5,0}s_2 + \Sigma_{4,0}s_1s_2$$

The characteristic equation of the matrix  $S$  is simply  $\det(S(s_1, s_2)) = \lambda^5 + v_4(s_1, s_2)\lambda^4 + v_3(s_1, s_2)\lambda^3 + v_2(s_1, s_2)\lambda^2 + v_1(s_1, s_2)\lambda + v_0(s_1, s_2)$ . The coefficients of the characteristic equation evaluated at  $(s_1, s_2) = \{(0, 0), (\infty, 0), (0, \infty), (\infty, \infty)\}$  are shown in the following pages. Note that  $v_i(0, 0), v_i(\infty, 0), v_i(0, \infty)$  and  $v_i(\infty, \infty)$  are the coefficients of  $(s_1s_2)^0, s_1^{5-i}s_2^0, s_1^0s_2^{5-i}$  and  $(s_1s_2)^{5-i}$  of  $v_i(s_1, s_2)$  respectively for  $i = 0, 1, \dots, 5$ .

$$v_4(0,0) = -\Sigma_{1,1} - \Sigma_{1,3} - \Sigma_{3,1} - \Sigma_{3,3} - \Sigma_{5,1}$$

$$v_3(0,0) = \Sigma_{1,1}\Sigma_{1,3} + \Sigma_{1,1}\Sigma_{3,1} + \Sigma_{1,1}\Sigma_{3,3} + \Sigma_{1,3}\Sigma_{3,1} + \Sigma_{1,3}\Sigma_{3,3} + \Sigma_{1,1}\Sigma_{5,1} + \Sigma_{1,3}\Sigma_{5,1} + \Sigma_{3,1}\Sigma_{3,3} + \Sigma_{3,1}\Sigma_{5,1} \\ + \Sigma_{3,3}\Sigma_{5,1} - \Sigma_{1,2}^2 - \Sigma_{2,1}^2 - 2\Sigma_{2,2}^2 - \Sigma_{2,3}^2 - \Sigma_{3,1}^2 - 2\Sigma_{3,2}^2 - \Sigma_{4,1}^2 - \Sigma_{4,2}^2$$

$$v_2(0,0) = \Sigma_{1,1}\Sigma_{2,2}^2 + \Sigma_{1,1}\Sigma_{2,3}^2 + \Sigma_{1,3}\Sigma_{2,1}^2 + \Sigma_{1,3}\Sigma_{2,2}^2 + 2\Sigma_{1,1}\Sigma_{3,2}^2 + \Sigma_{1,2}^2\Sigma_{3,1} + \Sigma_{1,3}\Sigma_{3,1}^2 + \Sigma_{1,3}\Sigma_{3,2}^2 + \Sigma_{1,2}^2\Sigma_{3,3} \\ + \Sigma_{1,1}\Sigma_{4,1}^2 + \Sigma_{1,1}\Sigma_{4,2}^2 + \Sigma_{2,2}^2\Sigma_{3,1} + \Sigma_{1,3}\Sigma_{4,1}^2 + \Sigma_{2,1}^2\Sigma_{3,3} + \Sigma_{2,3}^2\Sigma_{3,1} + \Sigma_{1,3}\Sigma_{4,2}^2 + \Sigma_{2,2}^2\Sigma_{3,3} + \Sigma_{3,1}\Sigma_{3,2}^2 \\ + \Sigma_{1,2}^2\Sigma_{5,1} + \Sigma_{3,1}^2\Sigma_{3,3} + \Sigma_{3,2}^2\Sigma_{3,3} + \Sigma_{2,1}^2\Sigma_{5,1} + \Sigma_{3,1}\Sigma_{4,2}^2 + 2\Sigma_{2,2}^2\Sigma_{5,1} + \Sigma_{3,3}\Sigma_{4,1}^2 + \Sigma_{2,3}^2\Sigma_{5,1} + \Sigma_{3,2}^2\Sigma_{5,1} \\ + \Sigma_{3,1}^3 - \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,1} - 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2} - \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,3} - 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{2,3} - \Sigma_{1,1}\Sigma_{1,3}\Sigma_{5,1} - \Sigma_{1,1}\Sigma_{3,1}\Sigma_{3,3} \\ - 2\Sigma_{1,2}\Sigma_{3,1}\Sigma_{3,2} - 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2} - \Sigma_{1,3}\Sigma_{3,1}\Sigma_{3,3} - 2\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,2} - \Sigma_{1,1}\Sigma_{3,1}\Sigma_{5,1} - 2\Sigma_{2,1}\Sigma_{3,1}\Sigma_{4,1} \\ - \Sigma_{1,1}\Sigma_{3,3}\Sigma_{5,1} - \Sigma_{1,3}\Sigma_{3,1}\Sigma_{5,1} - 2\Sigma_{2,2}\Sigma_{3,1}\Sigma_{4,2} - 2\Sigma_{2,2}\Sigma_{3,2}\Sigma_{4,1} - \Sigma_{1,3}\Sigma_{3,3}\Sigma_{5,1} - 2\Sigma_{2,3}\Sigma_{3,2}\Sigma_{4,2} \\ - \Sigma_{3,1}\Sigma_{3,3}\Sigma_{5,1} - 2\Sigma_{3,2}\Sigma_{4,1}\Sigma_{4,2}$$

$$v_1(0,0) = -\Sigma_{3,1}^3\Sigma_{3,3} - \Sigma_{1,3}\Sigma_{3,1}^3 + \Sigma_{3,2}^4 + \Sigma_{1,2}^2\Sigma_{3,2}^2 + \Sigma_{2,1}^2\Sigma_{2,3}^2 + \Sigma_{1,2}^2\Sigma_{4,1}^2 + \Sigma_{2,1}^2\Sigma_{3,2}^2 + \Sigma_{2,2}^2\Sigma_{3,1}^2 + \Sigma_{1,2}^2\Sigma_{4,2}^2 \\ + \Sigma_{2,2}^2\Sigma_{3,2}^2 + \Sigma_{2,2}^4 + \Sigma_{2,3}^2\Sigma_{3,1}^2 + \Sigma_{2,1}^2\Sigma_{4,2}^2 + \Sigma_{2,2}^2\Sigma_{4,1}^2 + \Sigma_{3,1}^2\Sigma_{3,2}^2 + \Sigma_{2,2}^2\Sigma_{4,2}^2 + \Sigma_{2,3}^2\Sigma_{4,1}^2 - \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,2}^2 \\ + 2\Sigma_{1,1}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,2} - \Sigma_{1,1}\Sigma_{2,3}\Sigma_{3,1} - \Sigma_{1,1}\Sigma_{1,3}\Sigma_{4,2}^2 - \Sigma_{1,1}\Sigma_{2,2}\Sigma_{3,3} - 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,2} - \Sigma_{1,3}\Sigma_{2,2}^2\Sigma_{3,1} \\ - 2\Sigma_{2,1}\Sigma_{2,2}^2\Sigma_{2,3} + 2\Sigma_{2,3}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{4,2} - \Sigma_{1,1}\Sigma_{3,1}\Sigma_{3,2}^2 + 2\Sigma_{1,2}\Sigma_{3,1}^2\Sigma_{3,2} - \Sigma_{1,1}\Sigma_{3,2}^2\Sigma_{3,3} - \Sigma_{1,2}^2\Sigma_{3,1}\Sigma_{3,3} \\ - \Sigma_{1,3}\Sigma_{3,1}^2\Sigma_{3,3} + 2\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,2}\Sigma_{5,1} - \Sigma_{1,1}\Sigma_{2,2}^2\Sigma_{5,1} - \Sigma_{1,1}\Sigma_{3,3}\Sigma_{4,1}^2 - \Sigma_{1,1}\Sigma_{2,3}^2\Sigma_{5,1} - \Sigma_{1,3}\Sigma_{2,1}^2\Sigma_{5,1} \\ - \Sigma_{1,3}\Sigma_{3,1}\Sigma_{4,2}^2 + 2\Sigma_{2,2}\Sigma_{3,2}\Sigma_{3,3}\Sigma_{4,1} - \Sigma_{1,3}\Sigma_{3,3}\Sigma_{4,1}^2 - \Sigma_{1,1}\Sigma_{3,2}^2\Sigma_{5,1} - \Sigma_{1,2}^2\Sigma_{3,1}\Sigma_{5,1} + 2\Sigma_{2,2}\Sigma_{3,1}^2\Sigma_{4,2} \\ - \Sigma_{1,3}\Sigma_{3,2}^2\Sigma_{5,1} - 2\Sigma_{2,2}\Sigma_{2,3}\Sigma_{4,1}\Sigma_{4,2} - 2\Sigma_{2,3}\Sigma_{3,2}^2\Sigma_{4,1} - \Sigma_{3,1}\Sigma_{3,2}^2\Sigma_{3,3} - \Sigma_{1,2}^2\Sigma_{3,3}\Sigma_{5,1} - \Sigma_{2,2}^2\Sigma_{3,1}\Sigma_{5,1} \\ - \Sigma_{2,1}^2\Sigma_{3,3}\Sigma_{5,1} - \Sigma_{1,1}\Sigma_{1,3}\Sigma_{4,1}^2 - \Sigma_{2,3}^2\Sigma_{3,1}\Sigma_{5,1} - \Sigma_{2,2}^2\Sigma_{3,3}\Sigma_{5,1} + \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,1}\Sigma_{3,3} + 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,3} \\ - 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,3}\Sigma_{3,2} + 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,1} + 2\Sigma_{1,3}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2} + \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,1}\Sigma_{5,1} + 2\Sigma_{1,1}\Sigma_{2,2}\Sigma_{3,2}\Sigma_{4,1} \\ + 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{5,1} - 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,2}\Sigma_{4,1} - 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{4,1} + 2\Sigma_{1,3}\Sigma_{2,1}\Sigma_{3,1}\Sigma_{4,1} - 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2} \\ + \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,3}\Sigma_{5,1} + 2\Sigma_{1,1}\Sigma_{2,3}\Sigma_{3,2}\Sigma_{4,2} + 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{5,1} - 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,2}\Sigma_{4,2} - 2\Sigma_{1,2}\Sigma_{2,3}\Sigma_{3,1}\Sigma_{4,2} \\ + 2\Sigma_{1,2}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{3,3} + 2\Sigma_{1,3}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{4,2} - 2\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,1}\Sigma_{3,2} + \Sigma_{1,1}\Sigma_{3,1}\Sigma_{3,3}\Sigma_{5,1} + 2\Sigma_{1,1}\Sigma_{3,2}\Sigma_{4,1}\Sigma_{4,2} \\ + 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2}\Sigma_{5,1} - 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{4,1}\Sigma_{4,2} - 2\Sigma_{2,1}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{4,2} + 2\Sigma_{2,1}\Sigma_{3,1}\Sigma_{3,3}\Sigma_{4,1} - 2\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{4,1} \\ + \Sigma_{1,3}\Sigma_{3,1}\Sigma_{3,3}\Sigma_{5,1} + 2\Sigma_{1,3}\Sigma_{3,2}\Sigma_{4,1}\Sigma_{4,2} - \Sigma_{1,3}\Sigma_{2,1}^2\Sigma_{3,3} - \Sigma_{1,3}\Sigma_{2,2}^2\Sigma_{5,1} - 2\Sigma_{2,2}\Sigma_{3,2}^2\Sigma_{4,2} - \Sigma_{1,1}\Sigma_{3,1}\Sigma_{4,2}^2$$

$$v_0(0,0) = -\Sigma_{1,2}^2\Sigma_{3,1}\Sigma_{4,2}^2 + \Sigma_{3,3}\Sigma_{5,1}\Sigma_{1,2}^2\Sigma_{3,1} - \Sigma_{5,1}\Sigma_{1,2}^2\Sigma_{3,2}^2 + 2\Sigma_{1,2}^2\Sigma_{3,2}\Sigma_{4,1}\Sigma_{4,2} - \Sigma_{3,3}\Sigma_{1,2}^2\Sigma_{4,1}^2 \\ + 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{4,2}^2 - 2\Sigma_{3,3}\Sigma_{5,1}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2} + 2\Sigma_{5,1}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,3}\Sigma_{3,2} - 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,3}\Sigma_{4,1}\Sigma_{4,2} \\ - 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,2}^2\Sigma_{4,2} + 2\Sigma_{3,3}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,2}\Sigma_{4,1} + 2\Sigma_{5,1}\Sigma_{1,2}\Sigma_{2,2}^2\Sigma_{3,2} - 2\Sigma_{1,2}\Sigma_{2,2}^2\Sigma_{4,1}\Sigma_{4,2} \\ - 2\Sigma_{5,1}\Sigma_{1,2}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,1} + 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{4,1}^2 + 2\Sigma_{3,3}\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{4,1} - 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,2}^2\Sigma_{4,1} \\ + 2\Sigma_{1,2}\Sigma_{2,3}\Sigma_{3,1}^2\Sigma_{4,2} - 2\Sigma_{1,2}\Sigma_{2,3}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{4,1} - 2\Sigma_{3,3}\Sigma_{1,2}\Sigma_{3,1}^2\Sigma_{3,2} + 2\Sigma_{1,2}\Sigma_{3,1}\Sigma_{3,2}^3 - \Sigma_{5,1}\Sigma_{2,1}^2\Sigma_{2,3}^2 \\ + 2\Sigma_{2,1}^2\Sigma_{2,3}\Sigma_{3,2}\Sigma_{4,2} - \Sigma_{3,3}\Sigma_{2,1}^2\Sigma_{3,2}^2 - \Sigma_{1,3}\Sigma_{2,1}^2\Sigma_{4,2}^2 + \Sigma_{1,3}\Sigma_{3,3}\Sigma_{5,1}\Sigma_{2,1}^2 + 2\Sigma_{5,1}\Sigma_{2,1}\Sigma_{2,2}^2\Sigma_{2,3} \\ - 2\Sigma_{2,1}\Sigma_{2,2}^2\Sigma_{3,2}\Sigma_{4,2} - 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,1}\Sigma_{4,2} - 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,2}\Sigma_{4,1} + 2\Sigma_{3,3}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2} \\ + 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2}^3 - 2\Sigma_{1,3}\Sigma_{5,1}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2} + 2\Sigma_{1,3}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{4,1}\Sigma_{4,2} + 2\Sigma_{2,1}\Sigma_{2,2}^2\Sigma_{3,1}\Sigma_{4,1} \\ - 2\Sigma_{2,1}\Sigma_{2,3}\Sigma_{3,1}\Sigma_{3,2}^2 + 2\Sigma_{1,3}\Sigma_{2,1}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{4,2} - 2\Sigma_{1,3}\Sigma_{3,3}\Sigma_{2,1}\Sigma_{3,1}\Sigma_{4,1} - \Sigma_{5,1}\Sigma_{4,2}^2 + 2\Sigma_{2,2}^3\Sigma_{3,1}\Sigma_{4,2} \\ + 2\Sigma_{2,2}^3\Sigma_{3,2}\Sigma_{4,1} - 2\Sigma_{2,2}^2\Sigma_{2,3}\Sigma_{3,1}\Sigma_{4,1} - \Sigma_{3,3}\Sigma_{2,2}^2\Sigma_{3,1}^2 - 3\Sigma_{2,2}^2\Sigma_{3,1}\Sigma_{3,2}^2 + \Sigma_{1,3}\Sigma_{5,1}\Sigma_{2,2}^2\Sigma_{3,1} \\ - \Sigma_{1,3}\Sigma_{2,2}^2\Sigma_{4,1}^2 - \Sigma_{1,1}\Sigma_{2,2}^2\Sigma_{4,2}^2 + \Sigma_{1,1}\Sigma_{3,3}\Sigma_{5,1}\Sigma_{2,2}^2 + 4\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,1}^2\Sigma_{3,2} - 2\Sigma_{1,1}\Sigma_{5,1}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,2} \\ + 2\Sigma_{1,1}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{4,1}\Sigma_{4,2} - 2\Sigma_{1,3}\Sigma_{2,2}\Sigma_{3,1}^2\Sigma_{4,2} + 2\Sigma_{1,3}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{4,1} + 2\Sigma_{1,1}\Sigma_{2,2}\Sigma_{3,2}^2\Sigma_{4,2} \\ - 2\Sigma_{1,1}\Sigma_{3,3}\Sigma_{2,2}\Sigma_{3,2}\Sigma_{4,1} - \Sigma_{2,3}^2\Sigma_{3,1}^3 + \Sigma_{1,1}\Sigma_{5,1}\Sigma_{2,3}^2\Sigma_{3,1} - \Sigma_{1,1}\Sigma_{2,3}^2\Sigma_{4,1}^2 - 2\Sigma_{1,1}\Sigma_{2,3}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{4,2} \\ + 2\Sigma_{1,1}\Sigma_{2,3}\Sigma_{3,2}^2\Sigma_{4,1} + \Sigma_{1,3}\Sigma_{3,3}\Sigma_{3,1}^3 - \Sigma_{1,3}\Sigma_{3,1}^2\Sigma_{3,2}^2 + \Sigma_{1,1}\Sigma_{3,3}\Sigma_{3,1}\Sigma_{3,2}^2 + \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,1}\Sigma_{4,2}^2 \\ - \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,3}\Sigma_{5,1}\Sigma_{3,1} - \Sigma_{1,1}\Sigma_{3,2}^4 + \Sigma_{1,1}\Sigma_{1,3}\Sigma_{5,1}\Sigma_{3,2}^2 - 2\Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,2}\Sigma_{4,1}\Sigma_{4,2} + \Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,3}\Sigma_{4,1}^2$$



$$v_4(\infty, 0) = \Sigma_{0,1} + \Sigma_{0,3} + \Sigma_{2,1} + \Sigma_{2,3} + \Sigma_{4,1}$$

$$v_3(\infty, 0) = \Sigma_{0,1}\Sigma_{0,3} + \Sigma_{0,1}\Sigma_{2,1} + \Sigma_{0,1}\Sigma_{2,3} + \Sigma_{0,3}\Sigma_{2,1} + \Sigma_{0,3}\Sigma_{2,3} + \Sigma_{0,1}\Sigma_{4,1} + \Sigma_{0,3}\Sigma_{4,1} + \Sigma_{2,1}\Sigma_{2,3} + \Sigma_{2,1}\Sigma_{4,1} \\ + \Sigma_{2,3}\Sigma_{4,1} - \Sigma_{0,2}^2 - \Sigma_{1,1}^2 - 2\Sigma_{1,2}^2 - \Sigma_{1,3}^2 - \Sigma_{2,1}^2 - 2\Sigma_{2,2}^2 - \Sigma_{3,1}^2 - \Sigma_{3,2}^2$$

$$v_2(\infty, 0) = -\Sigma_{0,1}\Sigma_{1,3}^2 - \Sigma_{0,3}\Sigma_{1,1}^2 - \Sigma_{0,3}\Sigma_{1,2}^2 - 2\Sigma_{0,1}\Sigma_{2,2}^2 - \Sigma_{0,2}^2\Sigma_{2,1} - \Sigma_{0,3}\Sigma_{2,1}^2 - \Sigma_{0,3}\Sigma_{2,2}^2 - \Sigma_{0,2}^2\Sigma_{2,3} - \Sigma_{0,1}\Sigma_{3,1}^2 \\ + \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,1} - \Sigma_{0,1}\Sigma_{3,2}^2 - \Sigma_{1,2}^2\Sigma_{2,1} - \Sigma_{0,3}\Sigma_{3,1}^2 - \Sigma_{1,1}^2\Sigma_{2,3} - \Sigma_{1,3}^2\Sigma_{2,1} - \Sigma_{0,3}\Sigma_{3,2}^2 - \Sigma_{1,2}^2\Sigma_{2,3} - \Sigma_{2,1}\Sigma_{2,2}^2 \\ - \Sigma_{0,2}^2\Sigma_{4,1} + \Sigma_{2,1}\Sigma_{2,3}\Sigma_{4,1} - \Sigma_{2,3}\Sigma_{3,1}^2 + 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,1} - \Sigma_{1,3}^2\Sigma_{4,1} - \Sigma_{2,2}^2\Sigma_{4,1} + 2\Sigma_{1,3}\Sigma_{2,2}\Sigma_{3,2} - 2\Sigma_{1,2}^2\Sigma_{4,1} \\ + 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{1,2} + 2\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2} + \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,3} + 2\Sigma_{0,2}\Sigma_{1,2}\Sigma_{1,3} + \Sigma_{0,1}\Sigma_{0,3}\Sigma_{4,1} + \Sigma_{0,1}\Sigma_{2,1}\Sigma_{2,3} - \Sigma_{2,2}^2\Sigma_{2,3} \\ + 2\Sigma_{0,2}\Sigma_{2,1}\Sigma_{2,2} + 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,2} + \Sigma_{0,3}\Sigma_{2,1}\Sigma_{2,3} + 2\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,2} + \Sigma_{0,3}\Sigma_{2,3}\Sigma_{4,1} + \Sigma_{0,1}\Sigma_{2,1}\Sigma_{4,1} - \Sigma_{1,1}^2\Sigma_{4,1} \\ + \Sigma_{0,1}\Sigma_{2,3}\Sigma_{4,1} + \Sigma_{0,3}\Sigma_{2,1}\Sigma_{4,1} + 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,2} + 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,1} - \Sigma_{0,1}\Sigma_{1,2}^2 - \Sigma_{2,1}^2\Sigma_{2,3} - \Sigma_{2,1}^3 - \Sigma_{2,1}\Sigma_{3,2}^2$$

$$v_1(\infty, 0) = 2\Sigma_{1,3}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2} + \Sigma_{1,1}^2\Sigma_{1,3}^2 + \Sigma_{0,2}^2\Sigma_{3,1}^2 + \Sigma_{1,1}^2\Sigma_{2,2}^2 + \Sigma_{1,2}^2\Sigma_{2,1}^2 + \Sigma_{0,2}^2\Sigma_{3,2}^2 + 2\Sigma_{1,2}\Sigma_{2,2}\Sigma_{2,3}\Sigma_{3,1} \\ + \Sigma_{1,2}^2\Sigma_{2,2}^2 + \Sigma_{1,3}^2\Sigma_{2,1}^2 + \Sigma_{1,1}^2\Sigma_{3,2}^2 + \Sigma_{1,2}^2\Sigma_{3,1}^2 + \Sigma_{2,1}^2\Sigma_{2,2}^2 + \Sigma_{1,2}^2\Sigma_{3,2}^2 + \Sigma_{1,3}^2\Sigma_{3,1}^2 - \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,2}^2 + \Sigma_{2,2}^4 \\ - \Sigma_{0,1}\Sigma_{1,3}^2\Sigma_{2,1} - \Sigma_{0,1}\Sigma_{0,3}\Sigma_{3,2}^2 - \Sigma_{0,1}\Sigma_{1,2}^2\Sigma_{2,3} - 2\Sigma_{0,2}\Sigma_{1,2}^2\Sigma_{2,2} - \Sigma_{0,3}\Sigma_{1,2}^2\Sigma_{2,1} - 2\Sigma_{1,1}\Sigma_{1,2}^2\Sigma_{1,3} + \Sigma_{4,2}^4 \\ - \Sigma_{0,1}\Sigma_{2,1}\Sigma_{2,2}^2 + 2\Sigma_{0,2}\Sigma_{2,1}^2\Sigma_{2,2} - \Sigma_{0,1}\Sigma_{2,2}^2\Sigma_{2,3} - \Sigma_{0,2}^2\Sigma_{2,1}^2\Sigma_{2,3} - \Sigma_{0,3}\Sigma_{2,1}^2\Sigma_{2,3} - \Sigma_{0,1}\Sigma_{2,1}\Sigma_{3,2}^2 - \Sigma_{2,1}^3\Sigma_{2,3} \\ - \Sigma_{0,1}\Sigma_{2,3}\Sigma_{3,1}^2 - \Sigma_{0,1}\Sigma_{1,3}^2\Sigma_{4,1} - \Sigma_{0,3}\Sigma_{1,1}^2\Sigma_{4,1} - \Sigma_{0,3}\Sigma_{2,1}\Sigma_{3,2}^2 - \Sigma_{0,3}\Sigma_{1,2}^2\Sigma_{4,1} - \Sigma_{0,3}\Sigma_{2,3}\Sigma_{3,1}^2 + \Sigma_{0,2}^2\Sigma_{2,2}^2 \\ - \Sigma_{0,2}^2\Sigma_{2,1}\Sigma_{4,1} + 2\Sigma_{1,2}\Sigma_{2,1}^2\Sigma_{3,2} - \Sigma_{0,3}\Sigma_{2,2}^2\Sigma_{4,1} - 2\Sigma_{1,2}\Sigma_{2,2}^2\Sigma_{3,2} - 2\Sigma_{1,3}\Sigma_{2,2}^2\Sigma_{3,1} - \Sigma_{2,1}\Sigma_{2,2}^2\Sigma_{2,3} - \Sigma_{0,3}\Sigma_{2,1}^3 \\ - \Sigma_{1,2}^2\Sigma_{2,1}\Sigma_{4,1} - \Sigma_{1,1}^2\Sigma_{2,3}\Sigma_{4,1} - \Sigma_{1,3}^2\Sigma_{2,1}\Sigma_{4,1} - \Sigma_{1,2}^2\Sigma_{2,3}\Sigma_{4,1} + \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,1}\Sigma_{2,3} + 2\Sigma_{0,1}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,2} \\ + 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,3} - 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{1,3}\Sigma_{2,2} + 2\Sigma_{0,2}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,1} + 2\Sigma_{0,3}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,2} + \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,1}\Sigma_{4,1} \\ + 2\Sigma_{0,1}\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,1} + 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{4,1} - 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{2,2}\Sigma_{3,1} - 2\Sigma_{0,2}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,1} + 2\Sigma_{0,3}\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,1} \\ - 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2} + \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,3}\Sigma_{4,1} + 2\Sigma_{0,1}\Sigma_{1,3}\Sigma_{2,2}\Sigma_{3,2} + 2\Sigma_{0,2}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{4,1} - 2\Sigma_{0,2}\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,2} \\ - 2\Sigma_{0,2}\Sigma_{1,3}\Sigma_{2,1}\Sigma_{3,2} + 2\Sigma_{0,2}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{2,3} + 2\Sigma_{0,3}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,2} - 2\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,1}\Sigma_{2,2} + \Sigma_{0,1}\Sigma_{2,1}\Sigma_{2,3}\Sigma_{4,1} \\ + 2\Sigma_{0,1}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2} + 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,2}\Sigma_{4,1} - 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{3,1}\Sigma_{3,2} - 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2} + 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,3}\Sigma_{3,1} \\ - 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1} + \Sigma_{0,3}\Sigma_{2,1}\Sigma_{2,3}\Sigma_{4,1} + 2\Sigma_{0,3}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2} + 2\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,2}\Sigma_{4,1} - 2\Sigma_{1,2}\Sigma_{1,3}\Sigma_{3,1}\Sigma_{3,2} \\ - \Sigma_{0,1}\Sigma_{0,3}\Sigma_{3,1}^2 - \Sigma_{0,3}\Sigma_{1,1}^2\Sigma_{2,3} - \Sigma_{0,1}\Sigma_{1,2}^2\Sigma_{4,1} - \Sigma_{0,1}\Sigma_{2,2}^2\Sigma_{4,1} - \Sigma_{0,2}^2\Sigma_{2,3}\Sigma_{4,1}$$

$$v_0(\infty, 0) = 2\Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2} + \Sigma_{4,1}\Sigma_{0,2}^2\Sigma_{2,2}^2 - 2\Sigma_{0,2}^2\Sigma_{2,2}\Sigma_{3,1}\Sigma_{3,2} + \Sigma_{2,3}\Sigma_{0,2}^2\Sigma_{3,1}^2 - 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{3,2}^2 \\ - 2\Sigma_{4,1}\Sigma_{0,2}\Sigma_{1,1}\Sigma_{1,3}\Sigma_{2,2} + 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{1,3}\Sigma_{3,1}\Sigma_{3,2} + 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{2,2}^2\Sigma_{3,2} + \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,3}\Sigma_{4,1}\Sigma_{2,1} \\ - 2\Sigma_{2,3}\Sigma_{0,2}\Sigma_{1,1}\Sigma_{2,2}\Sigma_{3,1} - 2\Sigma_{4,1}\Sigma_{0,2}\Sigma_{1,2}^2\Sigma_{2,2} + 2\Sigma_{0,2}\Sigma_{1,2}^2\Sigma_{3,1}\Sigma_{3,2} + 2\Sigma_{4,1}\Sigma_{0,2}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,1} + \Sigma_{0,1}\Sigma_{4,2}^4 \\ - 2\Sigma_{0,2}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{3,1}^2 + \Sigma_{0,2}^2\Sigma_{2,1}\Sigma_{3,2}^2 + 2\Sigma_{0,2}\Sigma_{1,2}\Sigma_{2,2}^2\Sigma_{3,1} - 2\Sigma_{0,2}\Sigma_{1,3}\Sigma_{2,1}^2\Sigma_{3,2} - \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,3}\Sigma_{3,1}^2 \\ + 2\Sigma_{0,2}\Sigma_{1,3}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1} + 2\Sigma_{2,3}\Sigma_{0,2}\Sigma_{2,1}^2\Sigma_{2,2} - \Sigma_{2,3}\Sigma_{4,1}\Sigma_{0,2}^2\Sigma_{2,1} + \Sigma_{4,1}\Sigma_{1,1}^2\Sigma_{1,3}^2 - 2\Sigma_{1,1}^2\Sigma_{1,3}\Sigma_{2,2}\Sigma_{3,2} \\ + \Sigma_{2,3}\Sigma_{1,1}^2\Sigma_{2,2}^2 - \Sigma_{0,1}\Sigma_{0,3}\Sigma_{4,1}\Sigma_{2,2}^2 - \Sigma_{0,3}\Sigma_{2,3}\Sigma_{4,1}\Sigma_{1,1}^2 - 2\Sigma_{4,1}\Sigma_{1,1}\Sigma_{1,2}^2\Sigma_{1,3} + 2\Sigma_{1,1}\Sigma_{1,2}^2\Sigma_{2,2}\Sigma_{3,2} \\ + 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,1}\Sigma_{3,2} + 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,2}\Sigma_{3,1} - 2\Sigma_{2,3}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2} - 2\Sigma_{2,3}\Sigma_{0,2}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,1} \\ + 2\Sigma_{0,3}\Sigma_{4,1}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,2} - 2\Sigma_{0,3}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{3,1}\Sigma_{3,2} - 2\Sigma_{1,1}\Sigma_{1,3}^2\Sigma_{2,1}\Sigma_{3,1} + 2\Sigma_{2,3}\Sigma_{4,1}\Sigma_{0,2}\Sigma_{1,1}\Sigma_{1,2} \\ - 2\Sigma_{0,3}\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2} + 2\Sigma_{0,3}\Sigma_{2,3}\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,1} + \Sigma_{4,1}\Sigma_{1,2}^4 - 2\Sigma_{1,2}^3\Sigma_{2,1}\Sigma_{3,2} - \Sigma_{0,1}\Sigma_{0,3}\Sigma_{2,1}\Sigma_{3,2}^2 \\ + 2\Sigma_{1,2}^2\Sigma_{1,3}\Sigma_{2,1}\Sigma_{3,1} + \Sigma_{2,3}\Sigma_{1,2}^2\Sigma_{2,1}^2 + 3\Sigma_{1,2}^2\Sigma_{2,1}\Sigma_{2,2}^2 - \Sigma_{0,3}\Sigma_{4,1}\Sigma_{1,2}^2\Sigma_{2,1} + \Sigma_{0,3}\Sigma_{1,2}^2\Sigma_{3,1}^2 + \Sigma_{0,1}\Sigma_{1,2}^2\Sigma_{2,2}^2 \\ - \Sigma_{0,1}\Sigma_{2,3}\Sigma_{4,1}\Sigma_{1,2}^2 - 4\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,1}^2\Sigma_{2,2} + \Sigma_{0,3}\Sigma_{1,1}^2\Sigma_{3,2}^2 - 2\Sigma_{0,1}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{3,1}\Sigma_{3,2} + 2\Sigma_{0,3}\Sigma_{1,2}\Sigma_{2,1}^2\Sigma_{3,2} \\ - 2\Sigma_{0,3}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1} - 2\Sigma_{0,1}\Sigma_{1,2}\Sigma_{2,2}^2\Sigma_{3,2} + 2\Sigma_{0,1}\Sigma_{2,3}\Sigma_{1,2}\Sigma_{2,2}\Sigma_{3,1} + \Sigma_{1,3}^2\Sigma_{2,1}^3 - \Sigma_{0,3}\Sigma_{4,1}\Sigma_{1,3}^2\Sigma_{2,1} \\ + \Sigma_{0,1}\Sigma_{1,3}\Sigma_{3,1}^2 - 2\Sigma_{1,2}^3\Sigma_{2,2}\Sigma_{3,1} - 2\Sigma_{0,1}\Sigma_{1,3}\Sigma_{2,2}^2\Sigma_{3,1} - \Sigma_{0,3}\Sigma_{2,3}\Sigma_{2,1}^3 + \Sigma_{0,3}\Sigma_{2,1}^2\Sigma_{2,2}^2 - \Sigma_{0,1}\Sigma_{2,3}\Sigma_{2,1}\Sigma_{2,2}^2 \\ - 2\Sigma_{0,2}\Sigma_{2,1}\Sigma_{2,2}^3 - 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,2}^3 + 2\Sigma_{1,1}\Sigma_{1,3}\Sigma_{2,1}\Sigma_{2,2}^2 + 2\Sigma_{0,1}\Sigma_{1,3}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,2} + 2\Sigma_{0,1}\Sigma_{4,1}\Sigma_{1,2}\Sigma_{1,3}\Sigma_{2,2}$$

$$v_4(0, \infty) = \Sigma_{1,0} + \Sigma_{1,2} + \Sigma_{3,0} + \Sigma_{3,2} + \Sigma_{5,0}$$

$$v_3(0, \infty) = \Sigma_{1,0}\Sigma_{1,2} + \Sigma_{1,0}\Sigma_{3,0} + \Sigma_{1,0}\Sigma_{3,2} + \Sigma_{1,2}\Sigma_{3,0} + \Sigma_{1,2}\Sigma_{3,2} + \Sigma_{1,0}\Sigma_{5,0} + \Sigma_{1,2}\Sigma_{5,0} + \Sigma_{3,0}\Sigma_{3,2} + \Sigma_{3,0}\Sigma_{5,0} \\ + \Sigma_{3,2}\Sigma_{5,0} - \Sigma_{1,1}^2 - \Sigma_{2,0}^2 - 2\Sigma_{2,1}^2 - \Sigma_{2,2}^2 - \Sigma_{3,0}^2 - 2\Sigma_{3,1}^2 - \Sigma_{4,0}^2 - \Sigma_{4,1}^2$$

$$v_2(0, \infty) = \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,0} + \Sigma_{3,0}\Sigma_{3,2}\Sigma_{5,0} - \Sigma_{1,2}\Sigma_{2,1}^2 - 2\Sigma_{1,0}\Sigma_{3,1}^2 - \Sigma_{1,1}^2\Sigma_{3,0} - \Sigma_{1,2}\Sigma_{3,0}^2 - \Sigma_{1,2}\Sigma_{3,1}^2 - \Sigma_{1,1}^2\Sigma_{3,2} \\ - \Sigma_{1,0}\Sigma_{4,0}^2 - \Sigma_{1,0}\Sigma_{4,1}^2 - \Sigma_{2,1}^2\Sigma_{3,0} - \Sigma_{1,2}\Sigma_{4,0}^2 - \Sigma_{2,0}^2\Sigma_{3,2} - \Sigma_{2,2}^2\Sigma_{3,0} - \Sigma_{1,2}\Sigma_{4,1}^2 - \Sigma_{2,1}^2\Sigma_{3,2} - \Sigma_{3,0}\Sigma_{3,1}^2 \\ - \Sigma_{1,1}^2\Sigma_{5,0} - \Sigma_{3,0}\Sigma_{3,2} - \Sigma_{3,1}^2\Sigma_{3,2} - \Sigma_{2,0}^2\Sigma_{5,0} - \Sigma_{3,0}\Sigma_{4,1}^2 - 2\Sigma_{2,1}^2\Sigma_{5,0} - \Sigma_{3,2}\Sigma_{4,0}^2 - \Sigma_{2,2}^2\Sigma_{5,0} - \Sigma_{3,1}^2\Sigma_{5,0} \\ - \Sigma_{1,0}\Sigma_{2,1}^2 + 2\Sigma_{3,1}\Sigma_{4,0}\Sigma_{4,1} + 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1} + \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,2} + 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,2} + \Sigma_{1,0}\Sigma_{1,2}\Sigma_{5,0} - \Sigma_{3,0}^3 \\ + 2\Sigma_{1,1}\Sigma_{3,0}\Sigma_{3,1} + 2\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1} + \Sigma_{1,2}\Sigma_{3,0}\Sigma_{3,2} + 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1} + \Sigma_{1,0}\Sigma_{3,0}\Sigma_{5,0} + 2\Sigma_{2,0}\Sigma_{3,0}\Sigma_{4,0} \\ + \Sigma_{1,0}\Sigma_{3,2}\Sigma_{5,0} + \Sigma_{1,2}\Sigma_{3,0}\Sigma_{5,0} + 2\Sigma_{2,1}\Sigma_{3,0}\Sigma_{4,1} + 2\Sigma_{2,1}\Sigma_{3,1}\Sigma_{4,0} + \Sigma_{1,2}\Sigma_{3,2}\Sigma_{5,0} + 2\Sigma_{2,2}\Sigma_{3,1}\Sigma_{4,1} \\ - \Sigma_{1,0}\Sigma_{2,2}^2 + \Sigma_{1,0}\Sigma_{3,0}\Sigma_{3,2} - \Sigma_{1,2}\Sigma_{2,0}^2$$

$$v_1(0, \infty) = 2\Sigma_{1,1}\Sigma_{3,0}\Sigma_{3,1} + 2\Sigma_{2,1}\Sigma_{3,0}\Sigma_{4,1} + \Sigma_{1,1}^2\Sigma_{3,1}^2 + \Sigma_{2,0}^2\Sigma_{2,2}^2 + \Sigma_{1,1}^2\Sigma_{4,0}^2 + \Sigma_{2,0}^2\Sigma_{3,1}^2 + \Sigma_{2,1}^2\Sigma_{3,0}^2 + \Sigma_{1,1}^2\Sigma_{4,1}^2 \\ + \Sigma_{2,1}^2\Sigma_{3,1}^2 + \Sigma_{2,0}^2\Sigma_{4,1}^2 + \Sigma_{2,1}^2\Sigma_{4,0}^2 + \Sigma_{3,0}^2\Sigma_{3,1}^2 + \Sigma_{2,1}^2\Sigma_{4,1}^2 + \Sigma_{2,2}^2\Sigma_{4,0}^2 + 2\Sigma_{2,2}\Sigma_{3,0}\Sigma_{3,1}\Sigma_{4,1} - \Sigma_{1,0}\Sigma_{1,2}\Sigma_{4,0}^2 \\ - \Sigma_{1,0}\Sigma_{2,2}^2\Sigma_{3,0} - \Sigma_{3,0}^3\Sigma_{3,2} - \Sigma_{1,0}\Sigma_{2,1}^2\Sigma_{3,2} - 2\Sigma_{1,1}\Sigma_{2,1}^2\Sigma_{3,1} - \Sigma_{1,2}\Sigma_{2,1}^2\Sigma_{3,0} - 2\Sigma_{2,0}\Sigma_{2,1}^2\Sigma_{2,2} - \Sigma_{1,2}\Sigma_{2,0}^2\Sigma_{3,2} \\ - \Sigma_{1,0}\Sigma_{3,0}\Sigma_{3,1}^2 + \Sigma_{2,2}^2\Sigma_{3,0}^2 - \Sigma_{1,0}\Sigma_{3,1}^2\Sigma_{3,2} - \Sigma_{1,1}^2\Sigma_{3,0}\Sigma_{3,2} - \Sigma_{1,2}\Sigma_{3,0}^2\Sigma_{3,2} - \Sigma_{1,0}\Sigma_{3,0}\Sigma_{4,1}^2 - \Sigma_{1,0}\Sigma_{2,1}^2\Sigma_{5,0} \\ - \Sigma_{1,0}\Sigma_{3,2}\Sigma_{4,0}^2 - \Sigma_{1,2}\Sigma_{3,0}^3 - \Sigma_{1,2}\Sigma_{2,0}^2\Sigma_{5,0} - \Sigma_{1,2}\Sigma_{3,0}\Sigma_{4,1}^2 - \Sigma_{1,2}\Sigma_{2,1}^2\Sigma_{5,0} - \Sigma_{1,2}\Sigma_{3,2}\Sigma_{4,0}^2 - \Sigma_{1,0}\Sigma_{3,1}^2\Sigma_{5,0} \\ - \Sigma_{1,1}^2\Sigma_{3,0}\Sigma_{5,0} + \Sigma_{2,1}^4 - \Sigma_{1,2}\Sigma_{3,1}^2\Sigma_{5,0} - 2\Sigma_{2,1}\Sigma_{3,1}^2\Sigma_{4,1} - 2\Sigma_{2,2}\Sigma_{3,1}^2\Sigma_{4,0} - \Sigma_{3,0}\Sigma_{3,1}^2\Sigma_{3,2} - \Sigma_{1,1}^2\Sigma_{3,2}\Sigma_{5,0} \\ - \Sigma_{2,1}^2\Sigma_{3,0}\Sigma_{5,0} - \Sigma_{2,0}^2\Sigma_{3,2}\Sigma_{5,0} - \Sigma_{2,2}^2\Sigma_{3,0}\Sigma_{5,0} - \Sigma_{2,1}^2\Sigma_{3,2}\Sigma_{5,0} + \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,0}\Sigma_{3,2} + 2\Sigma_{1,0}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1} \\ + 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,2} - 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,2}\Sigma_{3,1} + 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,0} + 2\Sigma_{1,2}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1} + \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,0}\Sigma_{5,0} \\ + 2\Sigma_{1,0}\Sigma_{2,1}\Sigma_{3,1}\Sigma_{4,0} + 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{5,0} - 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{3,1}\Sigma_{4,0} - 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,0}\Sigma_{4,0} + 2\Sigma_{1,2}\Sigma_{2,0}\Sigma_{3,0}\Sigma_{4,0} \\ - 2\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1} + \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,2}\Sigma_{5,0} + 2\Sigma_{1,0}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{4,1} + 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{5,0} - 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,1}\Sigma_{4,1} \\ - 2\Sigma_{1,1}\Sigma_{2,2}\Sigma_{3,0}\Sigma_{4,1} + 2\Sigma_{1,1}\Sigma_{3,0}\Sigma_{3,1}\Sigma_{3,2} + 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,0}\Sigma_{4,1} - 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,0}\Sigma_{3,1} + \Sigma_{1,0}\Sigma_{3,0}\Sigma_{3,2}\Sigma_{5,0} \\ + 2\Sigma_{1,0}\Sigma_{3,1}\Sigma_{4,0}\Sigma_{4,1} + 2\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1}\Sigma_{5,0} - 2\Sigma_{2,0}\Sigma_{2,1}\Sigma_{4,0}\Sigma_{4,1} - 2\Sigma_{2,0}\Sigma_{3,0}\Sigma_{3,1}\Sigma_{4,1} + 2\Sigma_{2,0}\Sigma_{3,0}\Sigma_{3,2}\Sigma_{4,0} \\ - 2\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1}\Sigma_{4,0} + \Sigma_{1,2}\Sigma_{3,0}\Sigma_{3,2}\Sigma_{5,0} + 2\Sigma_{1,2}\Sigma_{3,1}\Sigma_{4,0}\Sigma_{4,1} + 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{5,0} - 2\Sigma_{2,1}\Sigma_{2,2}\Sigma_{4,0}\Sigma_{4,1} \\ + 2\Sigma_{2,1}\Sigma_{3,1}\Sigma_{3,2}\Sigma_{4,0} - \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,1}^2 - \Sigma_{1,0}\Sigma_{1,2}\Sigma_{4,1}^2 + \Sigma_{3,1}^4 - \Sigma_{1,0}\Sigma_{2,2}^2\Sigma_{5,0}$$

$$v_0(0, \infty) = \Sigma_{1,1}^2\Sigma_{3,0}\Sigma_{4,1}^2 - \Sigma_{3,2}\Sigma_{5,0}\Sigma_{1,1}^2\Sigma_{3,0} + \Sigma_{5,0}\Sigma_{1,1}^2\Sigma_{3,1}^2 - 2\Sigma_{1,1}^2\Sigma_{3,1}\Sigma_{4,0}\Sigma_{4,1} - 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{4,1}^2 \\ + 2\Sigma_{3,2}\Sigma_{5,0}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1} - 2\Sigma_{5,0}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,2}\Sigma_{3,1} + 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,2}\Sigma_{4,0}\Sigma_{4,1} + 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{3,1}^2\Sigma_{4,1} \\ - 2\Sigma_{3,2}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{3,1}\Sigma_{4,0} - 2\Sigma_{5,0}\Sigma_{1,1}\Sigma_{2,1}^2\Sigma_{3,1} + 2\Sigma_{1,1}\Sigma_{2,1}^2\Sigma_{4,0}\Sigma_{4,1} + 2\Sigma_{5,0}\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,0} \\ - 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{4,0}^2 - 2\Sigma_{3,2}\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,0}\Sigma_{4,0} + 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,1}^2\Sigma_{4,0} - 2\Sigma_{1,1}\Sigma_{2,2}\Sigma_{3,0}^2\Sigma_{4,1} + \Sigma_{1,0}\Sigma_{3,1}^4 \\ + 2\Sigma_{1,1}\Sigma_{2,2}\Sigma_{3,0}\Sigma_{3,1}\Sigma_{4,0} + 2\Sigma_{3,2}\Sigma_{1,1}\Sigma_{3,0}^2\Sigma_{3,1} - 2\Sigma_{1,1}\Sigma_{3,0}\Sigma_{3,1}^3 + \Sigma_{5,0}\Sigma_{2,0}^2\Sigma_{2,2}^2 - 2\Sigma_{2,0}^2\Sigma_{2,2}\Sigma_{3,1}\Sigma_{4,1} \\ + \Sigma_{3,2}\Sigma_{2,0}^2\Sigma_{3,1}^2 + \Sigma_{1,2}\Sigma_{2,0}^2\Sigma_{4,1}^2 - \Sigma_{1,2}\Sigma_{3,2}\Sigma_{5,0}\Sigma_{2,0}^2 - 2\Sigma_{5,0}\Sigma_{2,0}\Sigma_{2,1}^2\Sigma_{2,2} + 2\Sigma_{2,0}\Sigma_{2,1}^2\Sigma_{3,1}\Sigma_{4,1} \\ + 2\Sigma_{2,0}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,0}\Sigma_{4,1} + 2\Sigma_{2,0}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1}\Sigma_{4,0} - 2\Sigma_{3,2}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1} - 2\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1}^3 \\ + 2\Sigma_{1,2}\Sigma_{5,0}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1} - 2\Sigma_{1,2}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{4,0}\Sigma_{4,1} - 2\Sigma_{2,0}\Sigma_{2,2}^2\Sigma_{3,0}\Sigma_{4,0} + 2\Sigma_{2,0}\Sigma_{2,2}\Sigma_{3,0}\Sigma_{3,1}^2 \\ - 2\Sigma_{1,2}\Sigma_{2,0}\Sigma_{3,0}\Sigma_{3,1}\Sigma_{4,1} + 2\Sigma_{1,2}\Sigma_{3,2}\Sigma_{2,0}\Sigma_{3,0}\Sigma_{4,0} + \Sigma_{5,0}\Sigma_{2,1}^4 - 2\Sigma_{2,1}^3\Sigma_{3,0}\Sigma_{4,1} - 2\Sigma_{2,1}^3\Sigma_{3,1}\Sigma_{4,0} \\ + 2\Sigma_{2,1}^2\Sigma_{2,2}\Sigma_{3,0}\Sigma_{4,0} + \Sigma_{3,2}\Sigma_{2,1}^2\Sigma_{3,0}^2 + 3\Sigma_{2,1}^2\Sigma_{3,0}\Sigma_{3,1}^2 - \Sigma_{1,2}\Sigma_{5,0}\Sigma_{2,1}^2\Sigma_{3,0} + \Sigma_{1,2}\Sigma_{2,1}^2\Sigma_{4,0}^2 + \Sigma_{2,2}^2\Sigma_{3,0}^3 \\ - \Sigma_{1,0}\Sigma_{3,2}\Sigma_{5,0}\Sigma_{2,1}^2 - 4\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,0}^2\Sigma_{3,1} + 2\Sigma_{1,0}\Sigma_{5,0}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,1} - 2\Sigma_{1,0}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{4,0}\Sigma_{4,1} \\ + 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,0}^2\Sigma_{4,1} - 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1}\Sigma_{4,0} - 2\Sigma_{1,0}\Sigma_{2,1}\Sigma_{3,1}^2\Sigma_{4,1} + 2\Sigma_{1,0}\Sigma_{3,2}\Sigma_{2,1}\Sigma_{3,1}\Sigma_{4,0} \\ - \Sigma_{1,0}\Sigma_{5,0}\Sigma_{2,2}^2\Sigma_{3,0} + \Sigma_{1,0}\Sigma_{2,2}^2\Sigma_{4,0}^2 + 2\Sigma_{1,0}\Sigma_{2,2}\Sigma_{3,0}\Sigma_{3,1}\Sigma_{4,1} - 2\Sigma_{1,0}\Sigma_{2,2}\Sigma_{3,1}^2\Sigma_{4,0} - \Sigma_{1,2}\Sigma_{3,2}\Sigma_{3,0}^3 \\ + \Sigma_{1,2}\Sigma_{3,0}^2\Sigma_{3,1}^2 - \Sigma_{1,0}\Sigma_{3,2}\Sigma_{3,0}\Sigma_{3,1}^2 - \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,0}\Sigma_{4,1}^2 + \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,2}\Sigma_{5,0}\Sigma_{3,0} + \Sigma_{3,2}\Sigma_{1,1}^2\Sigma_{4,0}^2 \\ - \Sigma_{1,0}\Sigma_{1,2}\Sigma_{5,0}\Sigma_{3,1}^2 + 2\Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,1}\Sigma_{4,0}\Sigma_{4,1} - \Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,2}\Sigma_{4,0}^2 + \Sigma_{1,0}\Sigma_{2,1}^2\Sigma_{4,1}^2$$

$$v_4(\infty, \infty) = -\Sigma_{0,2} - \Sigma_{2,0} - \Sigma_{2,2} - \Sigma_{4,0} - 5$$

$$v_3(\infty, \infty) = 5\Sigma_{0,2} + 5\Sigma_{2,0} + 5\Sigma_{2,2} + 5\Sigma_{4,0} + \Sigma_{0,2}\Sigma_{2,0} + \Sigma_{0,2}\Sigma_{2,2} + \Sigma_{0,2}\Sigma_{4,0} + \Sigma_{2,0}\Sigma_{2,2} + \Sigma_{2,0}\Sigma_{4,0} + \Sigma_{2,2}\Sigma_{4,0} \\ - \Sigma_{0,1}^2 - \Sigma_{1,0}^2 - 2\Sigma_{1,1}^2 - \Sigma_{1,2}^2 - \Sigma_{2,0}^2 - 2\Sigma_{2,1}^2 - \Sigma_{3,0}^2 - \Sigma_{3,1}^2$$

$$v_2(\infty, \infty) = \Sigma_{0,2}\Sigma_{1,0}^2 - 5\Sigma_{0,2}\Sigma_{2,2} - 5\Sigma_{0,2}\Sigma_{4,0} - 5\Sigma_{2,0}\Sigma_{2,2} - 5\Sigma_{2,0}\Sigma_{4,0} - 5\Sigma_{2,2}\Sigma_{4,0} - 5\Sigma_{0,2}\Sigma_{2,0} - 2\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1} \\ + \Sigma_{0,1}^2\Sigma_{2,0} + \Sigma_{0,2}\Sigma_{2,0}^2 + \Sigma_{0,2}\Sigma_{2,1}^2 + \Sigma_{0,1}^2\Sigma_{2,2} + \Sigma_{1,1}^2\Sigma_{2,0} + \Sigma_{0,2}\Sigma_{3,0}^2 + \Sigma_{1,0}^2\Sigma_{2,2} + \Sigma_{1,2}^2\Sigma_{2,0} + \Sigma_{0,2}\Sigma_{3,1}^2 \\ + \Sigma_{1,1}^2\Sigma_{2,2} + \Sigma_{2,0}\Sigma_{2,1}^2 + \Sigma_{0,1}^2\Sigma_{4,0} + \Sigma_{2,0}^2\Sigma_{2,2} + \Sigma_{2,1}^2\Sigma_{2,2} + \Sigma_{1,0}^2\Sigma_{4,0} + \Sigma_{2,0}\Sigma_{3,1}^2 + 2\Sigma_{1,1}^2\Sigma_{4,0} + \Sigma_{2,2}\Sigma_{3,0}^2 \\ + \Sigma_{1,2}^2\Sigma_{4,0} + \Sigma_{2,1}^2\Sigma_{4,0} + 5\Sigma_{1,1}^2 + 5\Sigma_{1,2}^2 + 10\Sigma_{2,1}^2 + 5\Sigma_{3,0}^2 + 5\Sigma_{3,1}^2 - 2\Sigma_{0,1}\Sigma_{1,0}\Sigma_{1,1} - 2\Sigma_{0,1}\Sigma_{1,1}\Sigma_{1,2} \\ - 2\Sigma_{0,1}\Sigma_{2,0}\Sigma_{2,1} - 2\Sigma_{1,0}\Sigma_{1,1}\Sigma_{2,1} - \Sigma_{0,2}\Sigma_{2,0}\Sigma_{2,2} - 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,1} - 2\Sigma_{1,0}\Sigma_{2,0}\Sigma_{3,0} - \Sigma_{0,2}\Sigma_{2,0}\Sigma_{4,0} \\ - 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{3,1} - 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,0} - \Sigma_{0,2}\Sigma_{2,2}\Sigma_{4,0} - 2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,1} - \Sigma_{2,0}\Sigma_{2,2}\Sigma_{4,0} + \Sigma_{0,2}\Sigma_{1,1}^2 + \Sigma_{2,0}^3$$

$$v_1(\infty, \infty) = -5\Sigma_{0,2}\Sigma_{2,1}^2 - 5\Sigma_{0,2}\Sigma_{3,0}^2 - 5\Sigma_{1,2}^2\Sigma_{2,0} - 5\Sigma_{0,2}\Sigma_{3,1}^2 - 5\Sigma_{1,1}^2\Sigma_{2,2} - 5\Sigma_{2,0}\Sigma_{2,1}^2 - \Sigma_{2,0}^3\Sigma_{2,2} - 5\Sigma_{2,1}^2\Sigma_{2,2} \\ - 5\Sigma_{2,0}\Sigma_{3,1}^2 - 5\Sigma_{1,1}^2\Sigma_{4,0} - 5\Sigma_{2,2}\Sigma_{3,0}^2 - 5\Sigma_{1,2}^2\Sigma_{4,0} - 5\Sigma_{2,1}^2\Sigma_{4,0} - \Sigma_{0,2}\Sigma_{2,0}^3 + \Sigma_{2,1}^4 + \Sigma_{0,1}^2\Sigma_{2,1}^2 + \Sigma_{1,0}^2\Sigma_{1,2}^2 \\ + \Sigma_{0,1}^2\Sigma_{3,0}^2 + \Sigma_{1,0}^2\Sigma_{2,1}^2 + \Sigma_{1,1}^2\Sigma_{2,0}^2 + \Sigma_{0,1}^2\Sigma_{3,1}^2 + \Sigma_{1,1}^2\Sigma_{2,1}^2 + \Sigma_{1,2}^2\Sigma_{2,0}^2 + \Sigma_{1,0}^2\Sigma_{3,1}^2 + \Sigma_{1,1}^2\Sigma_{3,0}^2 + \Sigma_{2,0}^2\Sigma_{2,1}^2 \\ + 2\Sigma_{0,1}\Sigma_{2,0}^2\Sigma_{2,1} + 5\Sigma_{0,2}\Sigma_{2,0}\Sigma_{2,2} + 10\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,1} + 5\Sigma_{0,2}\Sigma_{2,0}\Sigma_{4,0} + 10\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,0} + 5\Sigma_{0,2}\Sigma_{2,2}\Sigma_{4,0} \\ + 10\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,1} + 5\Sigma_{2,0}\Sigma_{2,2}\Sigma_{4,0} + 10\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1} - 2\Sigma_{0,1}\Sigma_{1,1}^2\Sigma_{2,1} - \Sigma_{0,2}\Sigma_{1,1}^2\Sigma_{2,0} - 2\Sigma_{1,0}\Sigma_{1,1}^2\Sigma_{1,2} \\ - \Sigma_{0,2}\Sigma_{1,0}^2\Sigma_{2,2} + 2\Sigma_{1,1}\Sigma_{2,1}\Sigma_{2,2}\Sigma_{3,0} - \Sigma_{0,1}^2\Sigma_{2,0}\Sigma_{2,2} - \Sigma_{0,2}\Sigma_{2,0}^2\Sigma_{2,2} - \Sigma_{0,2}\Sigma_{1,0}^2\Sigma_{4,0} - \Sigma_{0,2}\Sigma_{2,0}\Sigma_{3,1}^2 \\ - \Sigma_{0,2}\Sigma_{1,1}^2\Sigma_{4,0} + \Sigma_{1,1}^4 - \Sigma_{0,2}\Sigma_{2,2}\Sigma_{3,0}^2 - \Sigma_{0,1}^2\Sigma_{2,0}\Sigma_{4,0} + 2\Sigma_{1,1}\Sigma_{2,0}^2\Sigma_{3,1} - \Sigma_{0,2}\Sigma_{2,1}^2\Sigma_{4,0} - 2\Sigma_{1,1}\Sigma_{2,1}^2\Sigma_{3,1} \\ - 2\Sigma_{1,2}\Sigma_{2,1}^2\Sigma_{3,0} - \Sigma_{2,0}\Sigma_{2,1}^2\Sigma_{2,2} + 2\Sigma_{1,2}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1} - \Sigma_{1,1}^2\Sigma_{2,0}\Sigma_{4,0} - \Sigma_{1,0}^2\Sigma_{2,2}\Sigma_{4,0} - \Sigma_{1,2}^2\Sigma_{2,0}\Sigma_{4,0} \\ - \Sigma_{1,1}^2\Sigma_{2,2}\Sigma_{4,0} + \Sigma_{1,1}^2\Sigma_{3,1}^2 + \Sigma_{1,2}^2\Sigma_{3,0}^2 - 2\Sigma_{0,1}\Sigma_{1,0}\Sigma_{1,2}\Sigma_{2,1} + 2\Sigma_{0,1}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,0} + 2\Sigma_{0,2}\Sigma_{1,0}\Sigma_{1,1}\Sigma_{2,1} \\ + 2\Sigma_{0,1}\Sigma_{1,0}\Sigma_{1,1}\Sigma_{4,0} - 2\Sigma_{0,1}\Sigma_{1,0}\Sigma_{2,1}\Sigma_{3,0} - 2\Sigma_{0,1}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{3,0} + 2\Sigma_{0,2}\Sigma_{1,0}\Sigma_{2,0}\Sigma_{3,0} - 2\Sigma_{1,0}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1} \\ + 2\Sigma_{0,1}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{4,0} - 2\Sigma_{0,1}\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,1} - 2\Sigma_{0,1}\Sigma_{1,2}\Sigma_{2,0}\Sigma_{3,1} + 2\Sigma_{0,1}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{2,2} + 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{3,1} \\ - 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,0}\Sigma_{2,1} + 2\Sigma_{1,0}\Sigma_{1,1}\Sigma_{2,1}\Sigma_{4,0} - 2\Sigma_{1,0}\Sigma_{1,1}\Sigma_{3,0}\Sigma_{3,1} - 2\Sigma_{1,0}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1} + 2\Sigma_{1,0}\Sigma_{2,0}\Sigma_{2,2}\Sigma_{3,0} \\ - 2\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,0} + \Sigma_{0,2}\Sigma_{2,0}\Sigma_{2,2}\Sigma_{4,0} + 2\Sigma_{0,2}\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1} + 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{4,0} - 2\Sigma_{1,1}\Sigma_{1,2}\Sigma_{3,0}\Sigma_{3,1} \\ - \Sigma_{0,1}^2\Sigma_{2,2}\Sigma_{4,0} + 2\Sigma_{0,1}\Sigma_{1,0}\Sigma_{1,1}\Sigma_{2,2}$$

$$v_0(\infty, \infty) = -\Sigma_{0,1}^2\Sigma_{2,0}\Sigma_{3,1}^2 + \Sigma_{2,2}\Sigma_{4,0}\Sigma_{0,1}^2\Sigma_{2,0} - \Sigma_{4,0}\Sigma_{0,1}^2\Sigma_{2,1}^2 + 2\Sigma_{0,1}^2\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1} - \Sigma_{2,2}\Sigma_{0,1}^2\Sigma_{3,0}^2 - 5\Sigma_{2,1}^4 \\ - 2\Sigma_{2,2}\Sigma_{4,0}\Sigma_{0,1}\Sigma_{1,0}\Sigma_{1,1} + 2\Sigma_{4,0}\Sigma_{0,1}\Sigma_{1,0}\Sigma_{1,2}\Sigma_{2,1} - 2\Sigma_{0,1}\Sigma_{1,0}\Sigma_{1,2}\Sigma_{3,0}\Sigma_{3,1} - 2\Sigma_{0,1}\Sigma_{1,0}\Sigma_{2,1}^2\Sigma_{3,1} \\ + 2\Sigma_{2,2}\Sigma_{0,1}\Sigma_{1,0}\Sigma_{2,1}\Sigma_{3,0} - 10\Sigma_{0,2}\Sigma_{2,1}\Sigma_{3,0}\Sigma_{3,1} - 2\Sigma_{0,1}\Sigma_{1,1}^2\Sigma_{3,0}\Sigma_{3,1} - 2\Sigma_{4,0}\Sigma_{0,1}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,0} \\ + 2\Sigma_{0,1}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{3,0}^2 - 5\Sigma_{1,2}^2\Sigma_{3,0}^2 + 2\Sigma_{2,2}\Sigma_{0,1}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{3,0} - 2\Sigma_{0,1}\Sigma_{1,1}\Sigma_{2,1}^2\Sigma_{3,0} + 2\Sigma_{0,1}\Sigma_{1,2}\Sigma_{2,0}^2\Sigma_{3,1} \\ - 2\Sigma_{0,1}\Sigma_{1,2}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,0} - 2\Sigma_{2,2}\Sigma_{0,1}\Sigma_{2,0}^2\Sigma_{2,1} + 2\Sigma_{0,1}\Sigma_{2,0}\Sigma_{2,1}^3 - \Sigma_{4,0}\Sigma_{1,0}^2\Sigma_{1,2}^2 + 2\Sigma_{1,0}^2\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,1} \\ - \Sigma_{2,2}\Sigma_{1,0}^2\Sigma_{2,1}^2 - \Sigma_{0,2}\Sigma_{1,0}^2\Sigma_{3,1}^2 + \Sigma_{0,2}\Sigma_{2,2}\Sigma_{4,0}\Sigma_{1,0}^2 + 2\Sigma_{4,0}\Sigma_{1,0}\Sigma_{1,1}^2\Sigma_{1,2} - 2\Sigma_{1,0}\Sigma_{1,1}^2\Sigma_{2,1}\Sigma_{3,1} \\ - 2\Sigma_{1,0}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,0}\Sigma_{3,1} - 2\Sigma_{1,0}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,1}\Sigma_{3,0} + 2\Sigma_{2,2}\Sigma_{1,0}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1} + 2\Sigma_{1,0}\Sigma_{1,1}\Sigma_{2,1}^3 \\ - 2\Sigma_{0,2}\Sigma_{4,0}\Sigma_{1,0}\Sigma_{1,1}\Sigma_{2,1} + 2\Sigma_{0,2}\Sigma_{1,0}\Sigma_{1,1}\Sigma_{3,0}\Sigma_{3,1} + 2\Sigma_{1,0}\Sigma_{1,2}^2\Sigma_{2,0}\Sigma_{3,0} - 2\Sigma_{1,0}\Sigma_{1,2}\Sigma_{2,0}\Sigma_{2,1}^2 \\ + 2\Sigma_{0,2}\Sigma_{1,0}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1} - 2\Sigma_{0,2}\Sigma_{2,2}\Sigma_{1,0}\Sigma_{2,0}\Sigma_{3,0} - \Sigma_{4,0}\Sigma_{1,1}^4 + 2\Sigma_{1,1}^3\Sigma_{2,0}\Sigma_{3,1} + 2\Sigma_{1,1}^3\Sigma_{2,1}\Sigma_{3,0} \\ - 2\Sigma_{1,1}^2\Sigma_{1,2}\Sigma_{2,0}\Sigma_{3,0} - \Sigma_{2,2}\Sigma_{1,1}^2\Sigma_{2,0}^2 - 3\Sigma_{1,1}^2\Sigma_{2,0}\Sigma_{2,1}^2 + \Sigma_{0,2}\Sigma_{4,0}\Sigma_{1,1}^2\Sigma_{2,0} - \Sigma_{0,2}\Sigma_{1,1}^2\Sigma_{3,0}^2 - 5\Sigma_{1,1}^2\Sigma_{3,1}^2 \\ + 5\Sigma_{2,2}\Sigma_{4,0}\Sigma_{1,1}^2 + 4\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,0}^2\Sigma_{2,1} - 10\Sigma_{4,0}\Sigma_{1,1}\Sigma_{1,2}\Sigma_{2,1} + 10\Sigma_{1,1}\Sigma_{1,2}\Sigma_{3,0}\Sigma_{3,1} - 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{2,0}^2\Sigma_{3,1} \\ + 2\Sigma_{0,2}\Sigma_{1,1}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,0} + 10\Sigma_{1,1}\Sigma_{2,1}^2\Sigma_{3,1} - 10\Sigma_{2,2}\Sigma_{1,1}\Sigma_{2,1}\Sigma_{3,0} - \Sigma_{1,2}^2\Sigma_{2,0}^3 + 5\Sigma_{4,0}\Sigma_{1,2}^2\Sigma_{2,0} \\ + 10\Sigma_{1,2}\Sigma_{2,1}^2\Sigma_{3,0} + 5\Sigma_{0,2}\Sigma_{2,2}\Sigma_{3,0}^2 + \Sigma_{0,2}\Sigma_{2,2}\Sigma_{2,0}^3 - \Sigma_{0,2}\Sigma_{2,0}^2\Sigma_{2,1}^2 + 5\Sigma_{2,2}\Sigma_{2,0}\Sigma_{2,1}^2 + 5\Sigma_{0,2}\Sigma_{2,0}\Sigma_{3,1}^2 \\ - 5\Sigma_{0,2}\Sigma_{2,2}\Sigma_{4,0}\Sigma_{2,0} + 2\Sigma_{0,1}\Sigma_{1,0}\Sigma_{1,1}\Sigma_{3,1}^2 + 2\Sigma_{4,0}\Sigma_{0,1}\Sigma_{1,1}^2\Sigma_{2,1} + 5\Sigma_{0,2}\Sigma_{4,0}\Sigma_{2,1}^2 - 10\Sigma_{1,2}\Sigma_{2,0}\Sigma_{2,1}\Sigma_{3,1}$$

Let  $V(a, b)$  be the number of consecutive sign changes in  $[1, v_4(a, b), v_3(a, b), v_2(a, b), v_1(a, b), v_0(a, b)]$  where  $a$  and  $b$  are either 0 or  $\infty$ . The formula of  $V(a, b)$  is shown below

$$V(a, b) = \frac{1 - \text{sign}(v_4(a, b))}{2} + \frac{1 - \text{sign}(v_4(a, b))\text{sign}(v_3(a, b))}{2} + \frac{1 - \text{sign}(v_3(a, b))\text{sign}(v_2(a, b))}{2} \\ + \frac{1 - \text{sign}(v_2(a, b))\text{sign}(v_1(a, b))}{2} + \frac{1 - \text{sign}(v_1(a, b))\text{sign}(v_0(a, b))}{2} \quad \text{where } a, b \in \{0, \infty\}$$

From the  $V$ 's, we can find the formula of the number of feasible roots of  $f_1(N_1, N_2)$  and  $f_2(N_1, N_2)$  which is given by  $F(\Psi) = (V(0, 0) - V(\infty, 0) - V(0, \infty) + V(\infty, \infty))/2$ . The feasibility table for this example is huge and instead of finding the link between all parameters while maintaining feasibility, we will perform a demo on how to find the link between the parameters  $h$  and  $a_{21}$  while they are in a restricted domain. Let us consider the parameter vector  $\Psi = (r_1, r_2, a_{11}, a_{12}, a_{21}, a_{22}, h) = (0.5, -1.5, 1, -1.5, a_{21}, 1, h)$  where the parameters  $a_{21} \in [-6, -1]$  and  $h \in [0.5, 4]$  are restricted, we find that feasibility (i.e,  $F(\Psi) \geq 1$ ) can only be satisfied under the single condition that is shown below:

$$\begin{aligned} v_4(0, 0) : +, & \quad v_3(0, 0) : -, & \quad v_2(0, 0) : +, & \quad v_1(0, 0) : +, & \quad v_0(0, 0) : - \\ v_4(\infty, 0) : +, & \quad v_3(\infty, 0) : +, & \quad v_2(\infty, 0) : +, & \quad v_1(\infty, 0) : X, & \quad v_0(\infty, 0) : - \\ v_4(0, \infty) : -, & \quad v_3(0, \infty) : -, & \quad v_2(0, \infty) : X, & \quad v_1(0, \infty) : +, & \quad v_0(0, \infty) : + \\ v_4(\infty, \infty) : -, & \quad v_3(\infty, \infty) : +, & \quad v_2(\infty, \infty) : -, & \quad v_1(\infty, \infty) : -, & \quad v_0(\infty, \infty) : + \end{aligned}$$

Without the need to compute conditional probabilities, upon plotting the signs of the  $v$ 's in the single condition above, we find that feasibility is maintained if and only if  $v_0(0, 0) < 0$ . To check that our finding is correct, we plot both  $F(\Psi)$  and  $\text{sign}(v_0(0, 0))$  in the grid  $a_{21} \in [-6, -1]$  and  $h \in [0.5, 4]$ . From the two plots, we can see that  $F(\Psi) > 0$  if and only if  $v_0(0, 0) < 0$  and that  $a_{21}$  and  $h$  are related. Nevertheless, in other domains,  $a_{21}$  and  $h$  may not be linked. For example, with the same parameter values that were chosen earlier, if we change  $r_1$  from 0.5 to  $-0.5$ , the number of feasible roots in the domain  $a_{21} \in [-6, -1]$  and  $h \in [0.5, 4]$  will be exactly 1 no matter what values  $a_{21}$  and  $h$  take. Of course, the demo that we have illustrated here can be applied to any parameter ranges and combination. It is true that the expression of  $v_0(0, 0)$  is huge and messy, however it can be compacted by factoring it after plugging the fixed values into it, which is not needed for this example.

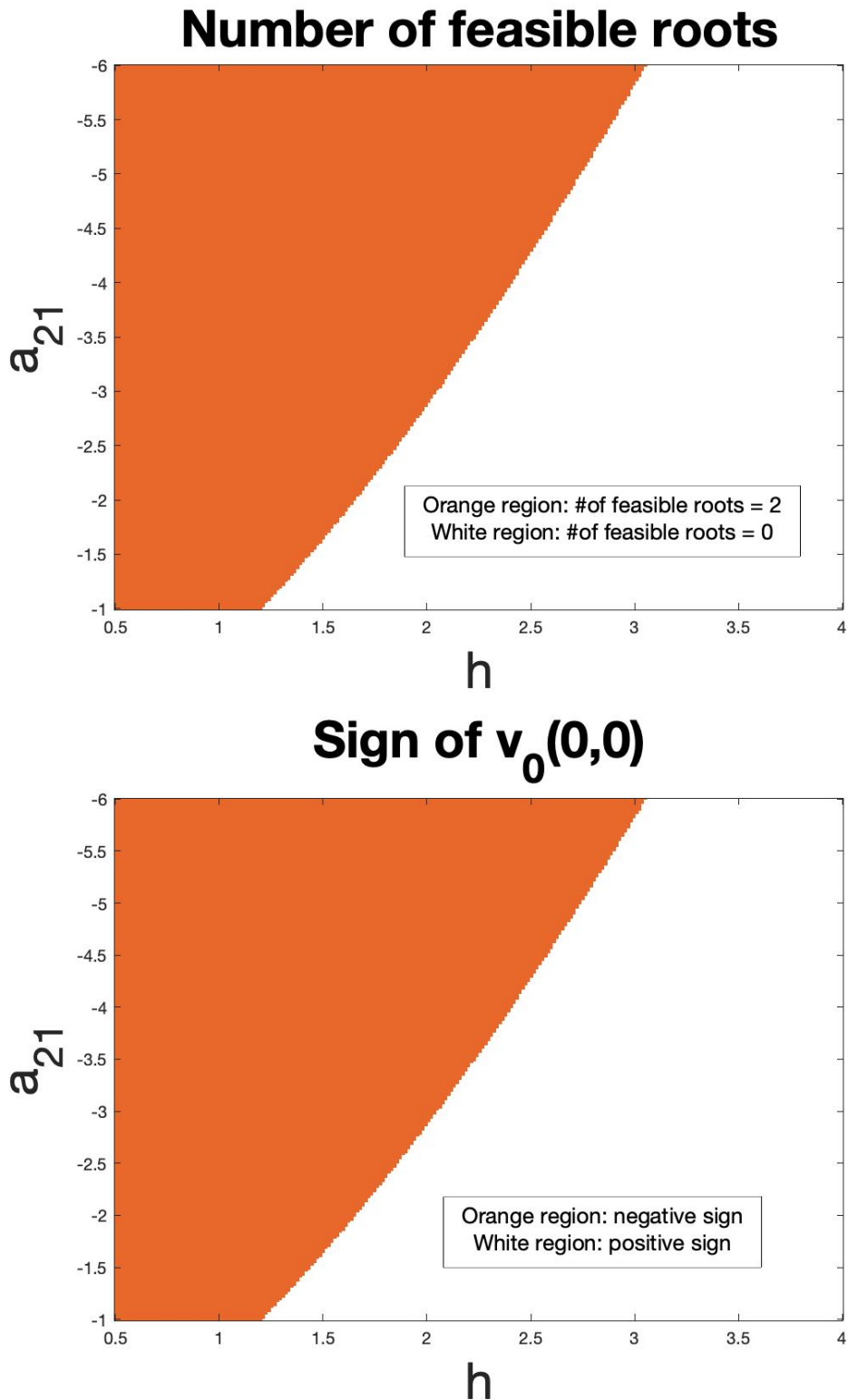


Figure 4-1: The top figure shows the number of feasible roots  $F$  in Lotka-Volterra model with type III functional responses where  $(r_1, r_2, a_{11}, a_{12}, a_{22}) = (0.5, -1.5, 1, -1.5, 1)$ ,  $a_{21} \in [-6, -1]$  and  $h \in [0.5, 4]$ . The bottom figure shows the sign of  $v_0(0,0)$  with the same model and parameter values and ranges. Both figures confirm that  $F > 0$  if and only if  $v_0(0,0) < 0$ . Simulations done via solving the isocline equations numerically and checking for the feasibility of roots match the two figures displayed here.

## 4.4 Higher-Dimensional Systems (3 or more species)

Consider the dynamical system that is shown below:

$$\begin{aligned} \frac{dN_1}{dt} &= \frac{N_1 f_1(N_1, \dots, N_n)}{q_1(N_1, \dots, N_n)} \\ &\vdots \\ \frac{dN_n}{dt} &= \frac{N_n f_n(N_1, \dots, N_n)}{q_n(N_1, \dots, N_n)} \end{aligned} \tag{4.3}$$

Here, the  $f$ 's and  $q$ 's are multivariate polynomials in species abundances. Let  $\Psi$  be the vector of model parameters that include, for example, species growth rates and species interaction coefficients. Feasibility conditions are conditions on model parameters  $\Psi$  that guarantee at least one feasible equilibrium point in the system. That is, the number roots of the system of polynomial equations  $f_i(N_1, \dots, N_n) = 0$  for  $i = 1, \dots, n$  whose components are all real and positive is at least 1. To find such conditions, we construct an analytical formula of the number of positive roots of that system of equations  $f_i(N_1, \dots, N_n) = 0$  for  $i = 1, \dots, n$  and we call that function  $F(\Psi)$ . We use theoretical work done by Pedersen which deals with counting real roots of polynomial systems in arbitrary algebraic domains to derive the formula of  $F(\Psi)$  [117]. To derive  $F(\Psi)$ , we apply Pedersen's work to count the number of real roots in an orthotope that lies in the 1<sup>st</sup> quadrant (i.e, feasible region) which rests on all the positive axes then we provide a methodology that expands the orthotope allowing all its vertices (except the origin) to go to infinity to cover the entire feasible domain. In multi-dimensional systems, given polynomial systems  $f_i(N_1, \dots, N_n)$  for  $i = 1, \dots, n$ , the process of finding feasibility conditions goes as follows:

### Finding symmetric sums of the roots

1. Fix  $i$ , assume that variable  $N_i$  is constant, and find the total degree of each polynomial equation  $f_j(N_1, \dots, N_n) = 0$  for  $j = 1, \dots, n$ . The total degree of  $f_j$  is the maximum sum of the variables' exponents in each term of  $f_j$  while treating  $N_i$  as constant. Denote the total degree of polynomial  $f_j$  by  $d_{i,j}$  for  $j = 1, \dots, n$ . Next, homogenize each term in each of the  $f$ 's with an artificial variable  $W$  so that the total degree of each term in  $f_j$  is  $d_{i,j}$ . Denote to the homogenized equation by  $F_{N_i,j}$ . For example, if  $f_2(N_1, N_2, N_3) = 1 + N_1^3 + N_1 N_2 N_3$  and  $N_1$  is assumed to be constant, then  $d_{1,2} = 2$

and the homogenized equation is  $F_{N_1,2} = W^2 + N_1^3 W^2 + N_1 N_2 N_3$ .

2. Let  $L_i = 1 + \sum_{j=1}^n (d_{i,j} - 1)$  and form the set  $H_i$  as a union of  $n$  monomial sets, where  $H_i = (W^{d_{i,1}} \cdot H_{i,1}^{L_i - d_{i,1}}) \cup (\cup_{1 \leq j \leq i-1} N_j^{d_{i,j+1}} \cdot H_{i,j+1}^{L_i - d_{i,j+1}}) \cup (\cup_{i+1 \leq j \leq n} N_j^{d_{i,j}} \cdot H_{i,j}^{L_i - d_{i,j}})$ . Define the outer-term of  $H_{i,k}^{L_i - d_{i,k}}$  to be the one that is dotted or multiplied by it. For example  $W^{d_{i,1}}$  is the outer-term of  $H_{i,1}^{L_i - d_{i,1}}$ . Here,  $H_{i,k}^{L_i - d_{i,k}}$  is the set of all monomials in  $W, N_1, \dots, N_n$  not including  $N_i$  that are of total degree  $L_i - d_{i,k}$  and does not contain the outer-terms of any of  $H_{i,1}^{L_i - d_{i,1}}, \dots, H_{i,k-1}^{L_i - d_{i,k-1}}$ . For example, if  $d_{2,1} = 2, d_{2,2} = 2$  and  $d_{2,3} = 1$ , then using variables  $W, N_1, N_3$  where  $N_2$  is constant, we have  $L_2 = 3$  and  $H_2 = W^2 \cdot \{W, N_1, N_3\} \cup N_1^2 \cdot \{W, N_1, N_3\} \cup N_3 \cdot \{N_3^2, W N_1, W N_1, N_1 N_3\}$ . Note that the second curly bracket does not contain  $W^2$  (i.e., outer term of the first curly bracket) and the third curly bracket does not contain  $W^2$  nor  $N_1^2$  (i.e., the outer-terms of the first and second curly brackets).
3. Form the set  $H_{i,\text{row}} = \cup_{1 \leq j \leq n} f_j \cdot H_{i,j}^{L_i - d_{i,j}}$  evaluated at  $W = 1$ . Note that  $H_{i,\text{row}}$  is simply  $H_i$  with outer-term of every  $H_{i,j}^{L_i - d_{i,j}}$  being replaced by  $f_j$ . Next, form the monomial set  $H_{i,\text{col}}$  which is simply  $H_i$  evaluated at  $W = 1$ . After that, form the Macaulay matrix  $M_{N_i}$ , which is a square matrix whose size is  $\binom{n-1+L_i}{n-1}$  and whose  $(i, j)$  entry is the coefficient of  $H_{i,\text{col}}(j)$  in the expression of  $H_{i,\text{row}}(i)$  assuming that  $N_i$  is a constant. Then, find the resultant  $\text{Res}_{N_1, \dots, N_{i-1}, N_{i+1}, \dots, N_n}(f_1, \dots, f_n)$  which equals to the determinant of  $M_{N_i}$ . This resultant is a univariate polynomial in  $N_i$  that contains no other  $N$ 's.
4. Next, form the matrix  $M'_{N_i}$ , whose first column is  $H_{i,\text{row}}$  and its remaining columns are the remaining columns of the matrix  $M_{N_i}$ . Then, compute its determinant (i.e.,  $\det(M'_{N_i})$ ), which has the form  $T_{i1}f_1 + T_{i2}f_2 + \dots + T_{in}f_n$  to obtain the  $i^{\text{th}}$  row of the eliminant matrix. Repeat all previous steps for  $i = 1, \dots, n$  to obtain all entries of the eliminant matrix as well as all resultants. Then, obtain the Jacobian of the original polynomial system whose  $(i, j)$  entry is  $\partial f_i / \partial N_j$ . Next, find the determinant of both the eliminant matrix  $T$  and the determinant of the Jacobian  $J$ .
5. If the determinant of  $M_{N_i}$  is 0, use the generalized characteristic polynomial formalism [118] to obtain the resultant. In this case, the resultant is the non-vanishing coefficient of the smallest power of  $\epsilon$  in  $\det(M_{N_i} - \epsilon I)$ , where  $I$  is the identity matrix of same size as matrix  $M_{N_i}$ . To find  $T_{ij}$  for  $j = 1, \dots, n$ , form the matrix  $M''_{N_i}$ , whose

first column is  $H_{i,\text{row}}$  and its remaining columns are the remaining columns of the matrix  $M_{N_i} - \epsilon I$ . Then, compute its determinant and find the first non-zero coefficient of powers of  $\epsilon$  in ascending order, which has the form  $T_{i1}f_1 + T_{i2}f_2 + \dots + T_{in}f_n$  (see the illustrative example in the next section for an example of this scenario).

6. Expand the generating function  $G(f_1(N_1, \dots, N_n), \dots, f_n(N_1, \dots, N_n))$  that is shown below, around  $N_1 = \infty, \dots, N_n = \infty$  to obtain the  $\Sigma$ 's (symmetric sums of the roots).

$$\begin{aligned} G(f_1, \dots, f_n) &= \frac{T(f_1, \dots, f_n)J(f_1, \dots, f_n)}{\prod_{i=1}^n \text{Res}_{N_1, \dots, N_{i-1}, N_{i+1}, \dots, N_n}(f_1, \dots, f_n)} \\ &= \sum_{m_1=0}^{\infty} \sum_{m_2=0}^{\infty} \dots \sum_{m_n=0}^{\infty} \frac{\Sigma_{m_1, m_2, \dots, m_n}}{N_1^{m_1+1} N_2^{m_2+1} \dots N_n^{m_n+1}} \end{aligned}$$

The expansion of  $G$  is done via performing series expansion of the reciprocal of each resultant separately then multiplying them along with  $T$  and  $J$ . For example, the reciprocal of each resultant can be expanded via MATLAB's "taylor" command after performing change of variables  $N_i = 1/x_i$  and expanding around  $x_i = 0$ . Alternatively, if the resultant is expressed as  $\text{Res}_{N_1, \dots, N_{i-1}, N_{i+1}, \dots, N_n}(f_1, \dots, f_n) = \sum_{l_i=0}^{K_i} h_{(i,l_i)} N_i^{l_i}$ , then

$$\frac{1}{\text{Res}_{N_1, \dots, N_{i-1}, N_{i+1}, \dots, N_n}} = \frac{1}{N_i^{K_i-1}} \sum_{m_i=1}^{\infty} \frac{p_{(i,m_i)}}{N_i^{m_i}}, \quad p_{(i,m_i)} = \frac{(-1)^{m_i+1}}{h_{(i,K_i)}^{m_i}} \det(A_i[1:m_i, 1:m_i]),$$

$$\text{where } A_i = \begin{bmatrix} 1 & 0 & 0 & 0 & \dots \\ h_{(i,K_i)} & h_{(i,K_i-1)} & h_{(i,K_i-2)} & h_{(i,K_i-3)} & \dots \\ 0 & h_{(i,K_i)} & h_{(i,K_i-1)} & h_{(i,K_i-2)} & \dots \\ 0 & 0 & h_{(i,K_i)} & h_{(i,K_i-1)} & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{bmatrix}, \quad i = 1, \dots, n.$$

Finally, denote the roots of  $f_i(N_1, \dots, N_n)$  for  $i = 1, \dots, n$  by  $\boldsymbol{\eta}_{\mathbf{k}} = [\eta_{\mathbf{k},1}, \eta_{\mathbf{k},2}, \dots, \eta_{\mathbf{k},n}]^T$  for  $\mathbf{k} = 1, \dots, \Theta$ . The symmetric sum  $\Sigma_{m_1, m_2, \dots, m_n}$  is given by  $\sum_{\mathbf{k}=1}^{\Theta} \eta_{\mathbf{k},1}^{m_1} \eta_{\mathbf{k},2}^{m_2} \dots \eta_{\mathbf{k},n}^{m_n}$ . In particular, note that  $\Theta = \Sigma_{0,0,\dots,0}$  is the number of complex roots of  $f_i(N_1, \dots, N_n)$  for  $i = 1, \dots, n$  with general coefficients. It is important to record that number.

**1-dimensional system:** In the univariate systems where the roots of  $f(N)$  are considered, the jacobian determinant is simply  $J = f'(N)$ , the resultant is  $f(N)$  itself as it is the



only univariate polynomial in the system, and the eliminant determinant is  $T = 1$  as the resultant when written in the form  $T_{11}f(N)$  implies  $T_{11} = 1$ . Thus the generating function  $G = f'(N)/f(N)$  is consistent with the one mentioned in the univariate section.

**2-dimensional systems:** In 2-dimensional systems, the two resultants simplify significantly and are determinants of Sylvester matrices involving the coefficients of two polynomial inputs. To find the eliminant matrix, a single column in each of the two Sylvester matrices are modified without changing their determinant to enable us writing the resultants in the form  $T_{i1}f_1 + T_{i2}f_2$  (see the 2-dimensional section).

### Assembling $F(\Psi)$ the function that counts the number of feasible roots

1. Choose a map  $m(N_1, N_2, \dots, N_n)$  of length  $\Theta$  and with independent monomial entries. Typically, the first entry of  $m$  is the constant 1 such monomials are chosen so that the coefficients of the characteristic equation shown in the following step do not vanish. Next, let  $Q(N_1, N_2, \dots, N_n) = N_1 N_2 \dots N_n$  and compute the symmetric matrix  $S(s_1, s_2, \dots, s_n) = W\Delta W^t$  where  $W_{ij} = m_i(\eta_{j,1}, \eta_{j,2}, \dots, \eta_{j,n})$  and  $\Delta_{ii} = Q(\eta_{i,1} - s_1, \eta_{i,2} - s_2, \dots, \eta_{i,n} - s_n)$  is a diagonal matrix.
2. The next task is to evaluate the determinant of  $S(s_1, s_2, \dots, s_n)$  and write it in the form  $\det(S(s_1, s_2, \dots, s_n) - \lambda I) = (-1)^\Theta \lambda^\Theta + v_{\Theta-1}(s_1, s_2, \dots, s_n) \lambda^{\Theta-1} + \dots + v_0(s_1, s_2, \dots, s_n)$ . After that consider the sequence  $\mathbf{v} = [v_\Theta(s_1, s_2, \dots, s_n) = (-1)^\Theta, v_{\Theta-1}(s_1, s_2, \dots, s_n), \dots, v_0(s_1, s_2, \dots, s_n)]$  and let  $V(s_1, s_2, \dots, s_n)$  be the number of consecutive sign changes in  $\mathbf{v}$ . The formula of  $V(s_1, s_2, \dots, s_n)$  is

$$V(s_1, s_2, \dots, s_n) = \sum_{i=0}^{\Theta-1} \frac{1 - \text{sign}(v_i(s_1, s_2, \dots, s_n)v_{i+1}(s_1, s_2, \dots, s_n))}{2}.$$

Consider the feasibility domain and think of it as a box whose  $2^n$  vertices compose of zeros and infinities. Note that  $v_i(m_1, m_2, \dots, m_n)$  where  $m_1, m_2, \dots, m_n \in \{0, \infty\}$  is the coefficient of the highest power of  $s_1^{k_1} s_2^{k_2} \dots s_n^{k_n}$  in  $v_i(s_1, s_2, \dots, s_n)$  where  $k_i = 0$  when  $m_i = 0$  and  $k_i = 1$  when  $m_i = \infty$ . Finally, let  $\#(s_1, s_2, \dots, s_n)$  be the number of infinities that appear in the string  $s_1, s_2, \dots, s_n$ . The the expression of  $F(\Psi)$  is

$$F(\Psi) = \frac{1}{2^{n-1}} \sum_{s_1, s_2, \dots, s_n \in \{0, \infty\}} (-1)^{\#(s_1, s_2, \dots, s_n)} V(s_1, s_2, \dots, s_n)$$

## Obtaining minimized feasibility conditions

1. Call  $v_i(m_1, m_2, \dots, m_n)$  where  $m_1, m_2, \dots, m_n \in \{0, \infty\}$  and  $i = 0, 1, \dots, \Theta - 1$  the feasibility basis which involves  $\Theta^{2^n}$  quantities as feasibility conditions are only dependent on those quantities. Since there are  $\Theta^{2^n}$  quantities and each can take a positive or a negative sign (we neglect the zero case as the values of ecological parameters are never exact), then there are  $2^{\Theta^{2^n}}$  sign combinations. Many of those combinations are impossible to occur (empty) for any choice of real  $\Psi$ . To detect the non-empty sign combinations, we compute the signs of all the  $v$ 's (the feasibility basis) as well as  $F(\Psi)$  for a range of parameters  $\Psi$ , where each component of  $\Psi$  varies independently in a large domain (say uniformly between  $-100$  and  $100$  or in any suitable domain) when parameters are unrestricted. If one or more parameters are restricted, they are varied in the domains they are defined at. This operation is cheaply computed as it is evaluation a few functions and not solving systems of equations. After that, we extract unique sign combinations of the  $v$ 's which yield  $F(\Psi) \geq 1$  and put them in a feasibility table (i.e, matrix) whose rows are the signs of the  $v$ 's and columns are the individual feasibility conditions.
2. After we obtain the feasibility table, we perform minimization to it. Here we illustrate a simple minimization technique. If two columns differ by a single sign (in one row), the two columns are combined into one and an X (or 0) is placed in the row where there is a single sign difference. We repeat the same process until no two columns differ by a single sign. After that we go through a single column at a time and iterate through each quantity in the basis then compute the conditional probabilities that the quantity takes its correspondent sign given that all remaining quantities have their correspondent signs. If one or more conditional probabilities are 1, the sign of one of those quantities may be replaced by **X** in the table. We then repeat computing the same conditional probabilities which were 1 but without the **X**'ed quantity being part of the calculation. If any conditional probability we repeat the process until no conditional probability is 1. We then go through all columns and repeat the same process until it terminates. These are not the only minimization approaches. For instance, comparing signs of  $v$ 's with  $F(\Psi)$  may reveal to us redundant quantities in the system (see examples).

#### 4.4.1 Illustrative Example

Consider the dynamical system that is shown below

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(r_1 + a_{11}N_1 + a_{12}N_2 + a_{13}N_3 + b_1N_1N_2), \\ \frac{dN_2}{dt} &= N_2(r_2 + a_{21}N_1 + a_{22}N_2 + a_{23}N_3 + b_2N_1N_2), \\ \frac{dN_3}{dt} &= N_3(r_3 + a_{31}N_1 + a_{32}N_2 + a_{33}N_3 + b_3N_1N_2).\end{aligned}$$

To study feasibility, the polynomials that are needed to be considered are  $f_1(N_1, N_2, N_3) = r_1 + a_{11}N_1 + a_{12}N_2 + a_{13}N_3 + b_1N_1N_2$ ,  $f_2(N_1, N_2, N_3) = r_2 + a_{21}N_1 + a_{22}N_2 + a_{23}N_3 + b_2N_1N_2$  and  $f_3(N_1, N_2, N_3) = r_3 + a_{31}N_1 + a_{32}N_2 + a_{33}N_3 + b_3N_1N_2$ . Next, assume that  $N_1$  is constant and homogenize  $f_1$ ,  $f_2$  and  $f_3$  with a fourth variable  $W$  as follows:

$$\begin{aligned}F_{N_1,1} &= r_1W + a_{11}N_1W + a_{12}N_2 + a_{13}N_3 + b_1N_1N_2, \\ F_{N_1,2} &= r_2W + a_{21}N_1W + a_{22}N_2 + a_{23}N_3 + b_2N_1N_2, \\ F_{N_1,3} &= r_3W + a_{31}N_1W + a_{32}N_2 + a_{33}N_3 + b_3N_1N_2,\end{aligned}$$

Note that the total degree of each of  $F_{N_1,1}$ ,  $F_{N_1,2}$  and  $F_{N_1,3}$  (or the total degree of  $f_1$ ,  $f_2$  and  $f_3$  assuming  $N_1$  is a constant) is  $d_{1,1} = 1$ ,  $d_{1,2} = 1$  and  $d_{1,3} = 1$  respectively. From the  $d$ 's, we compute  $L_1 = 1 + \sum_{i=1}^3 (d_{1,i} - 1) = 1$ . Now, we form the monomial set  $H_1$ , which is a union of three disjoint monomials  $H_1 = W^{d_{1,1}} \cdot H_{1,1}^{L_1 - d_{1,1}} \cup N_2^{d_{1,2}} \cdot H_{1,2}^{L_1 - d_{1,2}} \cup N_3^{d_{1,3}} \cdot H_{1,3}^{L_1 - d_{1,3}}$  where none of these  $H$ 's involve  $N_1$  and each is indicated below in curly brackets:

$$\begin{aligned}W^{d_{1,1}} \cdot H_{1,1}^{L_1 - d_{1,1}} &= W \cdot \{1\}, \\ N_2^{d_{1,2}} \cdot H_{1,2}^{L_1 - d_{1,2}} &= N_2 \cdot \{1\}, \\ N_3^{d_{1,3}} \cdot H_{1,3}^{L_1 - d_{1,3}} &= N_3 \cdot \{1\}\end{aligned}$$

Next, form the monomial set  $H_{1,\text{row}} = f_1 \cdot H_{1,1}^{L_1 - d_{1,1}} \cup f_2 \cdot H_{1,2}^{L_1 - d_{1,2}} \cup f_3 \cdot H_{1,3}^{L_1 - d_{1,3}}$  evaluated at  $W = 1$  that is shown below. In addition, form the monomial set  $H_{1,\text{col}}$  which is simply  $H_1$  evaluated at  $W = 1$  to get

$$\begin{aligned}H_{1,\text{row}} &= \{f_1, f_2, f_3\} \\ H_{1,\text{col}} &= \{1, N_2, N_3\}\end{aligned}$$

After that, form the Macaulay matrix  $M_{N_1}$  which is a square matrix whose size is  $\binom{n-1+L_1}{n-1} = 3$ . The  $(i, j)$  entry of the Macaulay matrix is the coefficient of  $H_{1,\text{col}}(j)$  in the expression of  $H_{1,\text{row}}(i)$  assuming that  $N_1$  is a constant. For example, the  $(1, 2)$  entry in the matrix is the coefficient of  $N_2$  in  $f_1$  which is  $a_{12} + b_1 N_1$ . The matrix  $M_{N_1}$  is shown below:

$$\begin{array}{c|ccc} & 1 & N_2 & N_3 \\ \hline f_1 & r_1 + N_1 a_{11} & a_{12} + N_1 b_1 & a_{13} \\ f_2 & r_2 + N_1 a_{21} & a_{22} + N_1 b_2 & a_{23} \\ f_3 & r_3 + N_1 a_{31} & a_{32} + N_1 b_3 & a_{33} \end{array}$$

Next, form the matrix  $M'_{N_1}$  whose first column is  $H_{1,\text{row}}$  and its remaining columns are the remaining columns (i.e, columns 2 to 3) of the matrix  $M_{N_1}$  (i.e, replace the first column of  $M_{N_1}$  whose top header is 1 with the leftmost column which contains the  $f$ 's). From the formula of  $H_{1,\text{row}} = \text{col}_1(M_{N_1}) + \sum_{j=2}^3 \text{col}_j(M_{N_1})H_{1,\text{col}}(j)$ , we can see that  $H_{1,\text{row}}$  is the first column of  $M_{N_1}$  added to it a multiple of every other column of  $M_{N_1}$ , implying that  $\det(M_{N_1}) = \det(M'_{N_1})$ . This determinant (i.e,  $\det(M'_{N_1})$ ) can be written as  $T_{11}f_1 + T_{12}f_2 + T_{13}f_3$  where the formulas of  $T_{11}$ ,  $T_{12}$  and  $T_{13}$  are shown below.

$$T_{11} = a_{22}a_{33} - a_{23}a_{32} - N_1 a_{23}b_3 + N_1 a_{33}b_2$$

$$T_{12} = a_{13}a_{32} - a_{12}a_{33} + N_1 a_{13}b_3 - N_1 a_{33}b_1$$

$$T_{13} = a_{12}a_{23} - a_{13}a_{22} - N_1 a_{13}b_2 + N_1 a_{23}b_1$$

Upon substituting  $f_1, f_2$  and  $f_3$  into  $T_{11}f_1 + T_{12}f_2 + T_{13}f_3$  and simplifying the expression (or evaluating the determinant of the matrix  $M_{N_1}$  directly), we have the formula of the resultant  $\text{Res}_{N_2, N_3}(f_1, f_2, f_3) = \sum_{l_1=0}^2 h_{(1, l_1)} N_1^{l_1}$  which is a polynomial of degree 2 in  $N_1$  and contains no  $N_2$ 's nor  $N_3$ 's. The three coefficients of the resultant  $h_{(1,2)}, h_{(1,1)}$  and  $h_{(1,0)}$  are shown below. Notice that none of the coefficients contain any of the  $N$ 's.

$$h_{(1,2)} = a_{13}a_{21}b_3 - a_{11}a_{23}b_3 + a_{11}a_{33}b_2 - a_{13}a_{31}b_2 - a_{21}a_{33}b_1 + a_{23}a_{31}b_1$$

$$\begin{aligned} h_{(1,1)} &= a_{11}a_{22}a_{33} - a_{11}a_{23}a_{32} - a_{12}a_{21}a_{33} + a_{12}a_{23}a_{31} + a_{13}a_{21}a_{32} - a_{13}a_{22}a_{31} - a_{13}b_2r_3 \\ &\quad + a_{13}b_3r_2 + a_{23}b_1r_3 - a_{23}b_3r_1 - a_{33}b_1r_2 + a_{33}b_2r_1 \end{aligned}$$

$$h_{(1,0)} = a_{12}a_{23}r_3 - a_{13}a_{22}r_3 - a_{12}a_{33}r_2 + a_{13}a_{32}r_2 + a_{22}a_{33}r_1 - a_{23}a_{32}r_1$$

Next, assume that  $N_2$  is constant and homogenize  $f_1$ ,  $f_2$  and  $f_3$  with a fourth variable  $W$  as follows:

$$F_{N_2,1} = r_1W + a_{11}N_1 + a_{12}N_2W + a_{13}N_3 + b_1N_1N_2,$$

$$F_{N_2,2} = r_2W + a_{21}N_1 + a_{22}N_2W + a_{23}N_3 + b_2N_1N_2,$$

$$F_{N_2,3} = r_3W + a_{31}N_1 + a_{32}N_2W + a_{33}N_3 + b_3N_1N_2,$$

Note that the total degree of each of  $F_{N_2,1}$ ,  $F_{N_2,2}$  and  $F_{N_2,3}$  (or the total degree of  $f_1$ ,  $f_2$  and  $f_3$  assuming  $N_2$  is a constant) is  $d_{2,1} = 1$ ,  $d_{2,2} = 1$  and  $d_{2,3} = 1$  respectively. From the  $d$ 's, we compute  $L_2 = 1 + \sum_{i=1}^3 (d_{2,i} - 1) = 1$ . Now, we form the monomial set  $H_2$ , which is a union of three disjoint monomials  $H_2 = W^{d_{2,1}} \cdot H_{2,1}^{L_2-d_{2,1}} \cup N_1^{d_{2,2}} \cdot H_{2,2}^{L_2-d_{2,2}} \cup N_3^{d_{2,3}} \cdot H_{2,3}^{L_2-d_{2,3}}$  where none of these  $H$ 's involve  $N_2$  and each is indicated below:

$$W^{d_{2,1}} \cdot H_{2,1}^{L_2-d_{2,1}} = W \cdot \{1\},$$

$$N_1^{d_{2,2}} \cdot H_{2,2}^{L_2-d_{2,2}} = N_1 \cdot \{1\},$$

$$N_3^{d_{2,3}} \cdot H_{2,3}^{L_2-d_{2,3}} = N_3 \cdot \{1\}$$

Next, form the monomial set  $H_{2,\text{row}} = f_1 \cdot H_{2,1}^{L_2-d_{2,1}} \cup f_2 \cdot H_{2,2}^{L_2-d_{2,2}} \cup f_3 \cdot H_{2,3}^{L_2-d_{2,3}}$  evaluated at  $W = 1$  that is shown below. In addition, form the monomial set  $H_{2,\text{col}}$  which is simply  $H_2$  evaluated at  $W = 1$  to get

$$H_{2,\text{row}} = \{f_1, f_2, f_3\}$$

$$H_{2,\text{col}} = \{1, N_1, N_3\}$$

After that, form the Macaulay matrix  $M_{N_2}$  which is a square matrix whose size is  $\binom{n-1+L_2}{n-1} = 3$ . The  $(i, j)$  entry of the Macaulay matrix is the coefficient of  $H_{2,\text{col}}(j)$  in the expression of  $H_{2,\text{row}}(i)$  assuming that  $N_2$  is a constant. For example, the  $(1, 2)$  entry in the matrix is the coefficient of  $N_1$  in  $f_1$  which is  $a_{11} + N_2b_1$ . The matrix  $M_{N_2}$  is shown below:

	1	$N_1$	$N_3$
$f_1$	$r_1 + N_2a_{12}$	$a_{11} + N_2b_1$	$a_{13}$
$f_2$	$r_2 + N_2a_{22}$	$a_{21} + N_2b_2$	$a_{23}$
$f_3$	$r_3 + N_2a_{32}$	$a_{31} + N_2b_3$	$a_{33}$

Next, form the matrix  $M'_{N_2}$  whose first column is  $H_{2,\text{row}}$  and its remaining columns are the remaining columns (i.e, columns 2 to 3) of the matrix  $M_{N_2}$  (i.e, replace the first column of  $M_{N_2}$  whose top header is 1 with the leftmost column which contains the  $f$ 's). Again, from the formula of  $H_{2,\text{row}} = \text{col}_1(M_{N_2}) + \sum_{j=2}^3 \text{col}_j(M_{N_2})H_{2,\text{col}(j)}$ , we can see that  $H_{2,\text{row}}$  is the first column of  $M_{N_2}$  added to it a multiple of every other column of  $M_{N_2}$ , implying that  $\det(M_{N_2}) = \det(M'_{N_2})$ . This determinant (i.e,  $\det(M'_{N_2})$ ) can be written as  $T_{21}f_1 + T_{22}f_2 + T_{23}f_3$  where the formulas of  $T_{21}$ ,  $T_{22}$  and  $T_{23}$  are shown below.

$$T_{21} = a_{21}a_{33} - a_{23}a_{31} - N_2a_{23}b_3 + N_2a_{33}b_2$$

$$T_{22} = a_{13}a_{31} - a_{11}a_{33} + N_2a_{13}b_3 - N_2a_{33}b_1$$

$$T_{23} = a_{11}a_{23} - a_{13}a_{21} - N_2a_{13}b_2 + N_2a_{23}b_1$$

Upon substituting  $f_1$ ,  $f_2$  and  $f_3$  into  $T_{21}f_1 + T_{22}f_2 + T_{23}f_3$  and simplifying the expression (or evaluating the determinant of the matrix  $M_{N_2}$  directly), we have the formula of the resultant  $\text{Res}_{N_1, N_3}(f_1, f_2, f_3) = \sum_{l_2=0}^2 h_{(2, l_2)} N_2^{l_2}$  which is a polynomial of degree 2 in  $N_2$  and contains no  $N_1$ 's nor  $N_3$ 's. The three coefficients of the resultant  $h_{(2,2)}$ ,  $h_{(2,1)}$  and  $h_{(2,0)}$  are shown below. Notice that none of the coefficients contain any of the  $N$ 's.

$$h_{(2,2)} = a_{13}a_{22}b_3 - a_{12}a_{23}b_3 + a_{12}a_{33}b_2 - a_{13}a_{32}b_2 - a_{22}a_{33}b_1 + a_{23}a_{32}b_1$$

$$h_{(2,1)} = a_{11}a_{23}a_{32} - a_{11}a_{22}a_{33} + a_{12}a_{21}a_{33} - a_{12}a_{23}a_{31} - a_{13}a_{21}a_{32} + a_{13}a_{22}a_{31} - a_{13}b_2r_3 \\ + a_{13}b_3r_2 + a_{23}b_1r_3 - a_{23}b_3r_1 - a_{33}b_1r_2 + a_{33}b_2r_1$$

$$h_{(2,0)} = a_{11}a_{23}r_3 - a_{13}a_{21}r_3 - a_{11}a_{33}r_2 + a_{13}a_{31}r_2 + a_{21}a_{33}r_1 - a_{23}a_{31}r_1$$

Next, assume that  $N_3$  is constant and homogenize  $f_1$ ,  $f_2$  and  $f_3$  with a fourth variable  $W$  as follows:

$$F_{N_3,1} = r_1W + a_{11}N_1W + a_{12}N_2W + a_{13}N_3W^2 + b_1N_1N_2,$$

$$F_{N_3,2} = r_2W + a_{21}N_1W + a_{22}N_2W + a_{23}N_3W^2 + b_2N_1N_2,$$

$$F_{N_3,3} = r_3W + a_{31}N_1W + a_{32}N_2W + a_{33}N_3W^2 + b_3N_1N_2,$$

Note that the total degree of each of  $F_{N_3,1}$ ,  $F_{N_3,2}$  and  $F_{N_3,3}$  (or the total degree of  $f_1$ ,  $f_2$  and  $f_3$  assuming  $N_3$  is a constant) is  $d_{3,1} = 2$ ,  $d_{3,2} = 2$  and  $d_{3,3} = 2$  respectively. From the  $d$ 's, we compute  $L_3 = 1 + \sum_{i=1}^3 (d_{3,i} - 1) = 4$ . Now, we form the monomial set  $H_3$ , which is

a union of three disjoint monomials  $H_3 = W^{d_{3,1}} \cdot H_{3,1}^{L_3-d_{3,1}} \cup N_1^{d_{3,2}} \cdot H_{3,2}^{L_3-d_{3,2}} \cup N_2^{d_{3,3}} \cdot H_{3,3}^{L_3-d_{3,3}}$

where none of these  $H$ 's involve  $N_3$  and each is indicated below in curly brackets:

$$W^{d_{3,1}} \cdot H_{3,1}^{L_3-d_{3,1}} = W^2 \cdot \{W^2, WN_1, WN_2, N_1N_2, N_1^2, N_2^2\},$$

$$N_1^{d_{3,2}} \cdot H_{3,2}^{L_3-d_{3,2}} = N_1^2 \cdot \{WN_1, WN_2, N_1N_2, N_1^2, N_2^2\},$$

$$N_2^{d_{3,3}} \cdot H_{3,3}^{L_3-d_{3,3}} = N_2^2 \cdot \{WN_1, WN_2, N_1N_2, N_2^2\}$$

Next, form the monomial set  $H_{3,\text{row}} = f_1 \cdot H_{3,1}^{L_3-d_{3,1}} \cup f_2 \cdot H_{3,2}^{L_3-d_{3,2}} \cup f_3 \cdot H_{3,3}^{L_3-d_{3,3}}$  evaluated at  $W = 1$  that is shown below. In addition, form the monomial set  $H_{3,\text{col}}$  which is simply  $H_3$  evaluated at  $W = 1$  to get

$$H_{3,\text{row}} = \{f_1, N_1f_1, N_2f_1, N_1N_2f_1, N_1^2f_1, N_2^2f_1, N_1f_2, N_2f_2, N_1N_2f_2, N_1^2f_2, N_2^2f_2, N_1f_3, \\ N_2f_3, N_1N_2f_3, N_2^2f_3\}$$

$$H_{3,\text{col}} = \{1, N_1, N_2, N_1N_2, N_1^2, N_2^2, N_1^3, N_1^2N_2, N_1^3N_2, N_1^4, N_1^2N_2^2, N_1N_2^2, N_2^3, N_1N_2^3, N_2^4\}$$

After that, form the Macaulay matrix  $M_{N_3}$  which is a square matrix whose size is  $\binom{n-1+L_3}{n-1} = 15$ . The  $(i, j)$  entry of the Macaulay matrix is the coefficient of  $H_{3,\text{col}}(j)$  in the expression of  $H_{3,\text{row}}(i)$  assuming that  $N_3$  is a constant. For example, the  $(1, 2)$  entry in the matrix is the coefficient of  $N_1$  in  $f_1$  which is  $a_{11}$ . The matrix  $M_{N_3}$  is shown below:

	1	$N_1$	$N_2$	$N_1N_2$	$N_1^2$	$N_2^2$	$N_1^3$	$N_1^2N_2$	$N_1^3N_2$	$N_1^4$	$N_1^2N_2^2$	$N_1N_2^2$	$N_2^3$	$N_1N_2^3$	$N_2^4$
$f_1$	$r_1 + N_3a_{13}$	$a_{11}$	$a_{12}$	$b_1$	0	0	0	0	0	0	0	0	0	0	0
$N_1f_1$	0	$r_1 + N_3a_{13}$	0	$a_{12}$	$a_{11}$	0	0	$b_1$	0	0	0	0	0	0	0
$N_2f_1$	0	0	$r_1 + N_3a_{13}$	$a_{11}$	0	$a_{12}$	0	0	0	0	0	$b_1$	0	0	0
$N_1N_2f_1$	0	0	0	$r_1 + N_3a_{13}$	0	0	0	$a_{11}$	0	0	$b_1$	$a_{12}$	0	0	0
$N_1^2f_1$	0	0	0	0	$r_1 + N_3a_{13}$	0	$a_{11}$	$a_{12}$	$b_1$	0	0	0	0	0	0
$N_2^2f_1$	0	0	0	0	0	$r_1 + N_3a_{13}$	0	0	0	0	0	$a_{11}$	$a_{12}$	$b_1$	0
$N_1f_2$	0	$r_2 + N_3a_{23}$	0	$a_{22}$	$a_{21}$	0	0	$b_2$	0	0	0	0	0	0	0
$N_2f_2$	0	0	$r_2 + N_3a_{23}$	$a_{21}$	0	$a_{22}$	0	0	0	0	0	$b_2$	0	0	0
$N_1N_2f_2$	0	0	0	$r_2 + N_3a_{23}$	0	0	0	$a_{21}$	0	0	$b_2$	$a_{22}$	0	0	0
$N_1^2f_2$	0	0	0	0	$r_2 + N_3a_{23}$	0	$a_{21}$	$a_{22}$	$b_2$	0	0	0	0	0	0
$N_2^2f_2$	0	0	0	0	0	$r_2 + N_3a_{23}$	0	0	0	0	0	$a_{21}$	$a_{22}$	$b_2$	0
$N_1f_3$	0	$r_3 + N_3a_{33}$	0	$a_{32}$	$a_{31}$	0	0	$b_3$	0	0	0	0	0	0	0
$N_2f_3$	0	0	$r_3 + N_3a_{33}$	$a_{31}$	0	$a_{32}$	0	0	0	0	0	$b_3$	0	0	0
$N_1N_2f_3$	0	0	0	$r_3 + N_3a_{33}$	0	0	0	$a_{31}$	0	0	$b_3$	$a_{32}$	0	0	0
$N_2^2f_3$	0	0	0	0	0	$r_3 + N_3a_{33}$	0	0	0	0	0	$a_{31}$	$a_{32}$	$b_3$	0

From columns 10 and 15 which are all zeros, we can see that the determinant of the matrix  $M_{N_3}$  is zero. Therefore, the resultant substitution is the non-vanishing coefficient of the

smallest power of  $\epsilon$  in  $\det(M_{N_3} - \epsilon I_{15})$  where  $I_{15}$  is the identity matrix of size 15. Next, form the matrix  $M'_{N_3}$  whose first column is given by  $\sum_{j=1}^{15} \text{col}_j(M_{N_3} - \epsilon I_{15})H_{L_3, \text{col}}(j) = H_{3, \text{row}} - \epsilon H_{3, \text{col}}$  and its remaining columns are the remaining columns (i.e, columns 2 to 15) of the matrix  $M_{N_3} - \epsilon I_{15}$ . From properties of determinants,  $\det(M'_{N_3}) = \det(M_{N_3} - \epsilon I_{15})$  as the first column of  $M'_{N_3}$  is the first column of  $M_{N_3} - \epsilon I_{15}$  added to it a multiple of every other column of  $M_{N_3} - \epsilon I_{15}$  which does not alter the value of the determinant.

	1	$N_1$	$N_2$	$N_1 N_2$	$N_1^2$	$N_2^2$	$N_1^3$	$N_1^2 N_2$	$N_1^3 N_2$	$N_1^4$	$N_1^2 N_2^2$	$N_1 N_2^2$	$N_2^3$	$N_1 N_2^3$	$N_2^4$
$f_1$	$f_1 - \epsilon$	$a_{11}$	$a_{12}$	$b_1$	0	0	0	0	0	0	0	0	0	0	0
$N_1 f_1$	$N_1 f_1 - N_1 \epsilon$	$r_1 + N_3 a_{13} - \epsilon$	0	$a_{12}$	$a_{11}$	0	0	$b_1$	0	0	0	0	0	0	0
$N_2 f_1$	$N_2 f_1 - N_2 \epsilon$	0	$r_1 + N_3 a_{13} - \epsilon$	$a_{11}$	0	$a_{12}$	0	0	0	0	0	$b_1$	0	0	0
$N_1 N_2 f_1$	$N_1 N_2 f_1 - N_1 N_2 \epsilon$	0	0	$r_1 + N_3 a_{13} - \epsilon$	0	0	0	$a_{11}$	0	0	$b_1$	$a_{12}$	0	0	0
$N_1^2 f_1$	$N_1^2 f_1 - N_1^2 \epsilon$	0	0	0	$r_1 + N_3 a_{13} - \epsilon$	0	$a_{11}$	$a_{12}$	$b_1$	0	0	0	0	0	0
$N_2^2 f_1$	$N_2^2 f_1 - N_2^2 \epsilon$	0	0	0	0	$r_1 + N_3 a_{13} - \epsilon$	0	0	0	0	0	$a_{11}$	$a_{12}$	$b_1$	0
$N_1 f_2$	$N_1 f_2 - N_1^3 \epsilon$	$r_2 + N_3 a_{23}$	0	$a_{22}$	$a_{21}$	0	$-\epsilon$	$b_2$	0	0	0	0	0	0	0
$N_2 f_2$	$N_2 f_2 - N_1^2 N_2 \epsilon$	0	$r_2 + N_3 a_{23}$	$a_{21}$	0	$a_{22}$	0	$-\epsilon$	0	0	0	$b_2$	0	0	0
$N_1 N_2 f_2$	$N_1 N_2 f_2 - N_1^3 N_2 \epsilon$	0	0	$r_2 + N_3 a_{23}$	0	0	0	$a_{21}$	$-\epsilon$	0	$b_2$	$a_{22}$	0	0	0
$N_1^2 f_2$	$N_1^2 f_2 - N_1^4 \epsilon$	0	0	0	$r_2 + N_3 a_{23}$	0	$a_{21}$	$a_{22}$	$b_2$	$-\epsilon$	0	0	0	0	0
$N_2^2 f_2$	$N_2^2 f_2 - N_1^2 N_2^2 \epsilon$	0	0	0	0	$r_2 + N_3 a_{23}$	0	0	0	0	$-\epsilon$	$a_{21}$	$a_{22}$	$b_2$	0
$N_1 f_3$	$N_1 f_3 - N_1 N_2^2 \epsilon$	$r_3 + N_3 a_{33}$	0	$a_{32}$	$a_{31}$	0	0	$b_3$	0	0	0	$-\epsilon$	0	0	0
$N_2 f_3$	$N_2 f_3 - N_2^3 \epsilon$	0	$r_3 + N_3 a_{33}$	$a_{31}$	0	$a_{32}$	0	0	0	0	0	$b_3$	$-\epsilon$	0	0
$N_1 N_2 f_3$	$N_1 N_2 f_3 - N_1 N_2^3 \epsilon$	0	0	$r_3 + N_3 a_{33}$	0	0	0	$a_{31}$	0	0	$b_3$	$a_{32}$	0	$-\epsilon$	0
$N_2^2 f_3$	$N_2^2 f_3 - N_2^4 \epsilon$	0	0	0	0	$r_3 + N_3 a_{33}$	0	0	0	0	0	$a_{31}$	$a_{32}$	$b_3$	$-\epsilon$

The determinant of the matrix above can be computed and the coefficient of the lowest power of  $\epsilon$  can be extracted. Alternatively and for easier computation, let  $M''_{N_3}$  be the matrix  $M'_{N_3}$  but whose first column is  $H_{3, \text{row}}$  instead of  $H_{3, \text{row}} - \epsilon H_{3, \text{col}}$ . Note that  $\det(M'_{N_3}) \neq \det(M''_{N_3})$ , however the first non-zero coefficient of powers of  $\epsilon$  in ascending order  $\epsilon$  in  $\det(M'_{N_3})$  is exactly the first non-zero coefficient of powers of  $\epsilon$  in ascending order in  $\det(M''_{N_3})$ . This can be proven by expanding  $\det(M'_{N_3})$  along the first column. After evaluating  $\det(M''_{N_3})$ , we find that the first non-zero coefficient of powers of  $\epsilon$  in ascending order is the coefficient of  $\epsilon^3$  (i.e, coefficients of  $\epsilon^2$ ,  $\epsilon^1$  and  $\epsilon^0$  are all zero). This coefficient, which acts as a substitution to the resultant, can be written as  $T_{31}f_1 + T_{32}f_2 + T_{33}f_3$  where  $T_{31}$ ,  $T_{32}$  and  $T_{33}$  have the following form.

$$\begin{aligned}
T_{31} &= (a_{12}b_2 - a_{22}b_1)(a_{11}b_3 - a_{31}b_1)(r_1 + N_3 a_{13})(t_{31,1} + t_{31,N_1}N_1 + t_{31,N_2}N_2 + t_{31,N_3}N_3 \\
&\quad + t_{31,N_1 N_2}N_1 N_2 + t_{31,N_1 N_3}N_1 N_3 + t_{31,N_2 N_3}N_2 N_3 + t_{31,N_3^2}N_3^2 + t_{31,N_1 N_2 N_3}N_1 N_2 N_3) \\
T_{32} &= (a_{12}b_2 - a_{22}b_1)(a_{11}b_3 - a_{31}b_1)(r_1 + N_3 a_{13})(t_{32,N_1}N_1 + t_{32,N_2}N_2 + t_{32,N_1 N_2}N_1 N_2 \\
&\quad + t_{32,N_1 N_3}N_1 N_3 + t_{32,N_2 N_3}N_2 N_3 + t_{32,N_1 N_2 N_3}N_1 N_2 N_3)
\end{aligned}$$



$$T_{33} = (a_{12}b_2 - a_{22}b_1)(a_{11}b_3 - a_{31}b_1)(r_1 + N_3a_{13})(t_{33,N_1}N_1 + t_{33,N_2}N_2 + t_{33,N_1N_2}N_1N_2 \\ + t_{33,N_1N_3}N_1N_3 + t_{33,N_2N_3}N_2N_3 + t_{33,N_1N_2N_3}N_1N_2N_3)$$

The  $t$ 's are polynomials in model parameters (i.e, the  $r$ 's,  $a$ 's and  $b$ 's) and their expressions are too large to display here. However, for illustration purposes, closed form expressions for  $t_{31,N_1N_2N_3}$ ,  $t_{32,N_1N_2N_3}$  and  $t_{33,N_1N_2N_3}$  are shown below

$$t_{31,N_1N_2N_3} = a_{12}a_{21}a_{23}b_1b_3^2 - a_{13}a_{21}a_{22}b_1b_3^2 + a_{12}a_{31}a_{33}b_1b_2^2 - a_{13}a_{31}a_{32}b_1b_2^2 + a_{21}a_{22}a_{33}b_1^2b_3 \\ - a_{21}a_{23}a_{32}b_1^2b_3 - a_{22}a_{31}a_{33}b_1^2b_2 + a_{23}a_{31}a_{32}b_1^2b_2 - a_{12}a_{21}a_{33}b_1b_2b_3 - a_{12}a_{23}a_{31}b_1b_2b_3 \\ + a_{13}a_{21}a_{32}b_1b_2b_3 + a_{13}a_{22}a_{31}b_1b_2b_3$$

$$t_{32,N_1N_2N_3} = a_{22}a_{31}a_{33}b_1^3 - a_{23}a_{31}a_{32}b_1^3 - a_{11}a_{12}a_{23}b_1b_3^2 + a_{11}a_{13}a_{22}b_1b_3^2 - a_{11}a_{22}a_{33}b_1^2b_3 \\ + a_{11}a_{23}a_{32}b_1^2b_3 + a_{12}a_{23}a_{31}b_1^2b_3 - a_{13}a_{22}a_{31}b_1^2b_3 - a_{12}a_{31}a_{33}b_1^2b_2 + a_{13}a_{31}a_{32}b_1^2b_2 \\ + a_{11}a_{12}a_{33}b_1b_2b_3 - a_{11}a_{13}a_{32}b_1b_2b_3$$

$$t_{33,N_1N_2N_3} = a_{21}a_{23}a_{32}b_1^3 - a_{21}a_{22}a_{33}b_1^3 - a_{11}a_{12}a_{33}b_1b_2^2 + a_{11}a_{13}a_{32}b_1b_2^2 - a_{12}a_{21}a_{23}b_1^2b_3 \\ + a_{13}a_{21}a_{22}b_1^2b_3 + a_{11}a_{22}a_{33}b_1^2b_2 - a_{11}a_{23}a_{32}b_1^2b_2 + a_{12}a_{21}a_{33}b_1^2b_2 - a_{13}a_{21}a_{32}b_1^2b_2 \\ + a_{11}a_{12}a_{23}b_1b_2b_3 - a_{11}a_{13}a_{22}b_1b_2b_3$$

Upon substituting  $f_1, f_2$  and  $f_3$  into  $T_{21}f_1 + T_{22}f_2 + T_{23}f_3$  and simplifying the expression (or finding the coefficient of  $\epsilon^3$  in the determinant of the matrix  $M_{N_3}$  directly), we have the formula of the resultant  $\text{Res}_{N_1, N_2}(f_1, f_2, f_3) = \sum_{l_3=0}^4 h_{(3,l_3)}N_3^{l_3}$  which is a polynomial of degree 4 in  $N_3$  and contains no  $N_1$ 's nor  $N_2$ 's. The coefficients of the resultant  $h_{(3,4)}, h_{(3,3)}, h_{(3,2)}, h_{(3,1)}$  and  $h_{(3,0)}$  are too large to display here and can found via any symbolic toolbox. After finding the resultants, we evaluate  $T(f_1, f_2, f_3)$  (i.e, the determinant of the eliminating matrix) as well as  $J(f_1, f_2, f_3)$  (i.e, the determinant of the Jacobian of  $f_1, f_2$  and  $f_3$ ) which are shown below:

$$T(f_1, f_2, f_3) = \begin{vmatrix} T_{11} & T_{12} & T_{13} \\ T_{21} & T_{22} & T_{23} \\ T_{31} & T_{32} & T_{33} \end{vmatrix}, \quad J(f_1, f_2, f_3) = \begin{vmatrix} a_{11} + N_2b_1 & a_{12} + N_1b_1 & a_{13} \\ a_{21} + N_2b_2 & a_{22} + N_1b_2 & a_{23} \\ a_{31} + N_2b_3 & a_{32} + N_1b_3 & a_{33} \end{vmatrix}$$

Let  $\text{Res}_{(N_1, N_2, N_3)/N_1} \equiv \text{Res}_{N_2, N_3}$ ,  $\text{Res}_{(N_1, N_2, N_3)/N_2} \equiv \text{Res}_{N_1, N_3}$  and  $\text{Res}_{(N_1, N_2, N_3)/N_3} \equiv \text{Res}_{N_1, N_2}$ .

Next, expand the generating function  $G(f_1, f_2, f_3)$  around  $N_1 = \infty, N_2 = \infty$  and  $N_3 = \infty$ . Since the three resultants are univariate polynomials in a single variable, we can expand their reciprocal individually using MATLAB's taylor command upon substituting  $N_1 = 1/x, N_2 = 1/y, N_3 = 1/z$  or via the following expression

$$\frac{1}{\text{Res}_{(N_1, N_2, N_3)/N_i}} = \frac{1}{N_i^{K_i-1}} \sum_{m_i=1}^{\infty} \frac{p_{(i, m_i)}}{N_i^{m_i}}, \quad p_{(i, m_i)} = \frac{(-1)^{m_i+1}}{h_{(i, K_i)}^{m_i}} \det(A_i[1 : m_i, 1 : m_i]), \quad i = 1, 2, 3$$

$$\text{where } A_i = \begin{bmatrix} 1 & 0 & 0 & 0 & \dots \\ h_{(i, K_i)} & h_{(i, K_i-1)} & h_{(i, K_i-2)} & h_{(i, K_i-3)} & \dots \\ 0 & h_{(i, K_i)} & h_{(i, K_i-1)} & h_{(i, K_i-2)} & \dots \\ 0 & 0 & h_{(i, K_i)} & h_{(i, K_i-1)} & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{bmatrix}, \quad i = 1, 2, 3$$

Here,  $A_i[1 : m_i, 1 : m_i]$  is the sub-matrix of  $A_i$  that contains its first  $m_i$  rows and columns. After obtaining both series expansion of the resultant reciprocal, multiply the result by  $T(f_1, f_2, f_3)J(f_1, f_2, f_3)$  to obtain

$$G(f_1, f_2, f_3) = \frac{T(f_1, f_2, f_3)J(f_1, f_2, f_3)}{\text{Res}_{N_1, N_2}(f_1, f_2, f_3)\text{Res}_{N_1, N_3}(f_1, f_2, f_3)\text{Res}_{N_2, N_3}(f_1, f_2, f_3)} = \frac{\Sigma_{0,0,0}}{N_1 N_2 N_3} + \frac{\Sigma_{1,0,0}}{N_1^2 N_2 N_3} + \frac{\Sigma_{0,1,0}}{N_1 N_2^2 N_3} + \frac{\Sigma_{0,0,1}}{N_1 N_2 N_3^2} + \frac{\Sigma_{1,1,0}}{N_1^2 N_2^2 N_3} + \frac{\Sigma_{1,0,1}}{N_1^2 N_2 N_3^2} + \frac{\Sigma_{0,1,1}}{N_1 N_2^2 N_3^2} + \frac{\Sigma_{2,0,0}}{N_1^3 N_2 N_3} + \frac{\Sigma_{0,2,0}}{N_1 N_2^3 N_3} + \dots$$

Without factorization, expressions of some of the  $\Sigma$ 's can extend to multiple pages. The expression for some of the lower  $\Sigma$ 's are shown below where  $\Sigma_{i,j,k} = \Sigma_{i,j,k}^U / \Sigma_{i,j,k}^D$  is written as a fraction of two polynomials.

$$\Sigma_{0,0,0}^U = 2$$

$$\Sigma_{0,0,0}^D = 1$$

$$\Sigma_{1,0,0}^U = a_{11}a_{23}a_{32} - a_{11}a_{22}a_{33} + a_{12}a_{21}a_{33} - a_{12}a_{23}a_{31} - a_{13}a_{21}a_{32} + a_{13}a_{22}a_{31} + a_{13}b_2r_3 - a_{13}b_3r_2 - a_{23}b_1r_3 + a_{23}b_3r_1 + a_{33}b_1r_2 - a_{33}b_2r_1$$

$$\Sigma_{1,0,0}^D = a_{13}a_{21}b_3 - a_{11}a_{23}b_3 + a_{11}a_{33}b_2 - a_{13}a_{31}b_2 - a_{21}a_{33}b_1 + a_{23}a_{31}b_1$$

$$\Sigma_{0,1,0}^U = a_{11}a_{23}a_{32} - a_{11}a_{22}a_{33} + a_{12}a_{21}a_{33} - a_{12}a_{23}a_{31} - a_{13}a_{21}a_{32} + a_{13}a_{22}a_{31} - a_{13}b_2r_3 + a_{13}b_3r_2 + a_{23}b_1r_3 - a_{23}b_3r_1 - a_{33}b_1r_2 + a_{33}b_2r_1$$

$$\Sigma_{0,1,0}^D = a_{12}a_{23}b_3 - a_{13}a_{22}b_3 - a_{12}a_{33}b_2 + a_{13}a_{32}b_2 + a_{22}a_{33}b_1 - a_{23}a_{32}b_1$$

Since  $\Sigma_{0,0,0} = 2$ , then the system  $f_i(N_1, N_2, N_3) = 0$  for  $i = 1, 2, 3$  has exactly 2 complex roots. Denote to these roots by  $\boldsymbol{\eta}_1 = [\eta_{1,1}, \eta_{1,2}]^T$ ,  $\boldsymbol{\eta}_2 = [\eta_{2,1}, \eta_{2,2}]^T$  and  $\boldsymbol{\eta}_3 = [\eta_{3,1}, \eta_{3,2}]^T$ . Choose a map  $m(N_1, N_2, N_3) = [1, N_1]^T$  then, let  $q(N_1, N_2, N_3) = N_1 N_2 N_3$  and compute  $S(s_1, s_2, s_3) = W\Delta W^t$  where  $W_{ij} = m_i(\eta_{1,j}, \eta_{2,j}, \eta_{3,j})$  and  $\Delta_{ii} = q(\eta_{1,i-s_1}, \eta_{2,i-s_2}, \eta_{3,i-s_3})$  is a diagonal matrix as follows.

$$W = \begin{bmatrix} 1 & 1 \\ \eta_{1,1} & \eta_{1,2} \end{bmatrix}$$

$$\Delta = \text{diag}[(\eta_{1,1} - s_1)(\eta_{2,1} - s_2)(\eta_{3,1} - s_3), (\eta_{1,2} - s_1)(\eta_{2,2} - s_2)(\eta_{3,2} - s_3)]$$

$$S(s_1, s_2, s_3) = W\Delta W^t$$

Note that  $\Sigma_{k,m,n} = \eta_{1,1}^k \eta_{2,1}^m \eta_{3,1}^n + \eta_{1,2}^k \eta_{2,2}^m \eta_{3,2}^n$  for  $k, m, n = 0, 1, 2, \dots$ . The components of the symmetric 2x2 matrix  $S$  are shown below:

$$S_{1,1}(s_1, s_2, s_3) = \Sigma_{111} - \Sigma_{011}s_1 - \Sigma_{101}s_2 - \Sigma_{110}s_3 + \Sigma_{001}s_1s_2 + \Sigma_{010}s_1s_3 + \Sigma_{100}s_2s_3 - 2s_1s_2s_3$$

$$\begin{aligned} S_{1,2}(s_1, s_2, s_3) &= \Sigma_{211} - \Sigma_{111}s_1 - \Sigma_{201}s_2 - \Sigma_{210}s_3 + \Sigma_{101}s_1s_2 + \Sigma_{110}s_1s_3 + \Sigma_{200}s_2s_3 - \Sigma_{100}s_1s_2s_3 \\ &= S_{2,1}(s_1, s_2, s_3) \end{aligned}$$

$$S_{2,2}(s_1, s_2, s_3) = \Sigma_{311} - \Sigma_{211}s_1 - \Sigma_{301}s_2 - \Sigma_{310}s_3 + \Sigma_{201}s_1s_2 + \Sigma_{210}s_1s_3 + \Sigma_{300}s_2s_3 - \Sigma_{200}s_1s_2s_3$$

The characteristic equation of the matrix  $S$  is  $\det(S(s_1, s_2, s_3)) = \lambda^2 + v_1(s_1, s_2, s_3)\lambda + v_0(s_1, s_2, s_3)$ . The coefficients of the characteristic equation evaluated at  $(s_1, s_2, s_3) = \{(0, 0, 0), (\infty, 0, 0), (0, \infty, 0), (\infty, \infty, 0), (0, 0, \infty), (\infty, 0, \infty), (0, \infty, \infty), (\infty, \infty, \infty)\}$  are displayed below. Note that  $v_i(m_1, m_2, m_3)$  where  $m_1, m_2, m_3 \in \{0, \infty\}$  is the coefficient of  $s_1^{k_1} s_2^{k_2} s_3^{k_3}$  in  $v_i(s_1, s_2, s_3)$  where  $k_j = 0$  if  $m_j = 0$  and  $k_j = 2 - i$  if  $m_j = \infty$  for  $j = 1, 2, 3$ .

$$\begin{array}{ll} v_1(0, 0, 0) = -\Sigma_{1,1,1} - \Sigma_{3,1,1}, & v_0(0, 0, 0) = -\Sigma_{2,1,1}^2 + \Sigma_{1,1,1}\Sigma_{3,1,1} \\ v_1(\infty, 0, 0) = \Sigma_{0,1,1} + \Sigma_{2,1,1}, & v_0(\infty, 0, 0) = -\Sigma_{1,1,1}^2 + \Sigma_{0,1,1}\Sigma_{2,1,1} \\ v_1(0, \infty, 0) = \Sigma_{1,0,1} + \Sigma_{3,0,1}, & v_0(0, \infty, 0) = -\Sigma_{2,0,1}^2 + \Sigma_{1,0,1}\Sigma_{3,0,1} \\ v_1(\infty, \infty, 0) = -\Sigma_{0,0,1} - \Sigma_{2,0,1}, & v_0(\infty, \infty, 0) = -\Sigma_{1,0,1}^2 + \Sigma_{0,0,1}\Sigma_{2,0,1} \\ v_1(0, 0, \infty) = \Sigma_{1,1,0} + \Sigma_{3,1,0}, & v_0(0, 0, \infty) = -\Sigma_{2,1,0}^2 + \Sigma_{1,1,0}\Sigma_{3,1,0} \\ v_1(\infty, 0, \infty) = -\Sigma_{0,1,0} - \Sigma_{2,1,0}, & v_0(\infty, 0, \infty) = -\Sigma_{1,1,0}^2 + \Sigma_{0,1,0}\Sigma_{2,1,0} \\ v_1(0, \infty, \infty) = -\Sigma_{1,0,0} - \Sigma_{3,0,0}, & v_0(0, \infty, \infty) = -\Sigma_{2,0,0}^2 + \Sigma_{1,0,0}\Sigma_{3,0,0} \\ v_1(\infty, \infty, \infty) = \Sigma_{2,0,0} + 2, & v_0(\infty, \infty, \infty) = -\Sigma_{1,0,0}^2 + 2\Sigma_{2,0,0} \end{array}$$

Let  $V(a, b, c)$  be the number of consecutive sign changes in  $[1, v_1(a, b, c), v_0(a, b, c)]$  where  $a, b$  and  $c$  are either 0 or  $\infty$ . The formula of  $V(a, b, c)$  is shown below

$$V(a, b, c) = \frac{1 - \text{sign}(v_1(a, b, c))}{2} + \frac{1 - \text{sign}(v_1(a, b, c))\text{sign}(v_0(a, b, c))}{2} \quad \text{where } a, b, c \in \{0, \infty\}$$

From the  $V$ 's, we can find the formula of the number of feasible roots of  $f_1(N_1, N_2, N_3)$ ,  $f_2(N_1, N_2, N_3)$  and  $f_3(N_1, N_2, N_3)$  which is given by  $F(\Psi) = (V(0, 0, 0) - V(\infty, 0, 0) - V(0, \infty, 0) - V(0, 0, \infty) + V(\infty, \infty, 0) + V(\infty, 0, \infty) + V(0, \infty, \infty) - V(\infty, \infty, \infty))/4$ . Let us consider the parameter  $\Psi = (r_1, r_2, r_3, a_{11}, a_{12}, a_{13}, a_{21}, a_{22}, a_{23}, a_{31}, a_{32}, a_{33}, b_1, b_2, b_3) = (0.5, -1.5, -0.5, 0.5, -1.5, -0.5, a_{21}, 2.6, -5, -0.5, -10, 1, 0.2, -0.1, b_3)$  where the parameters  $a_{21} \in [-7, -1]$  and  $b_3 \in [1.5, 5]$  are restricted, we find that feasibility (i.e,  $F(\Psi) \geq 1$ ) can only be satisfied under the two condition that are shown below:

$$\begin{aligned} v_1(0, 0, 0) : -, & \quad v_0(0, 0, 0) : -, & \quad v_1(\infty, 0, 0) : +, & \quad v_0(\infty, 0, 0) : +, \\ v_1(0, \infty, 0) : X, & \quad v_0(0, \infty, 0) : -, & \quad v_1(\infty, \infty, 0) : -, & \quad v_0(\infty, \infty, 0) : +, \\ v_1(0, 0, \infty) : +, & \quad v_0(0, 0, \infty) : -, & \quad v_1(\infty, 0, \infty) : -, & \quad v_0(\infty, 0, \infty) : +, \\ v_1(0, \infty, \infty) : -, & \quad v_0(0, \infty, \infty) : -, & \quad v_1(\infty, \infty, \infty) : +, & \quad v_0(\infty, \infty, \infty) : +, \end{aligned}$$

$$\begin{aligned} v_1(0, 0, 0) : -, & \quad v_0(0, 0, 0) : -, & \quad v_1(\infty, 0, 0) : +, & \quad v_0(\infty, 0, 0) : +, \\ v_1(0, \infty, 0) : +, & \quad v_0(0, \infty, 0) : +, & \quad v_1(\infty, \infty, 0) : X, & \quad v_0(\infty, \infty, 0) : -, \\ v_1(0, 0, \infty) : +, & \quad v_0(0, 0, \infty) : +, & \quad v_1(\infty, 0, \infty) : -, & \quad v_0(\infty, 0, \infty) : -, \\ v_1(0, \infty, \infty) : -, & \quad v_0(0, \infty, \infty) : -, & \quad v_1(\infty, \infty, \infty) : +, & \quad v_0(\infty, \infty, \infty) : +, \end{aligned}$$

When we plot the sign of each of the quantities (i.e, the  $v_i$ 's) in the two conditions above, we find that feasibility is satisfied if any of the following four conditions hold:  $v_1(0, 0, 0) < 0, v_0(0, 0, 0) < 0, v_1(\infty, 0, 0) > 0$  or  $v_0(\infty, 0, 0) > 0$  which are equivalent to each other in the domain prescribed by  $\Psi$ . Note that these four inequalities are shared among the two conditions described above. In addition, note that the simplest inequality among those (i.e, with lowest symmetric sums) is  $v_1(\infty, 0, 0) > 0$ . In the next plots, we plot the sign of  $v_1(\infty, 0, 0)$  and verify that it matches the feasibility region given by  $F(\Psi)$  which verifies the correctness of our methodology.

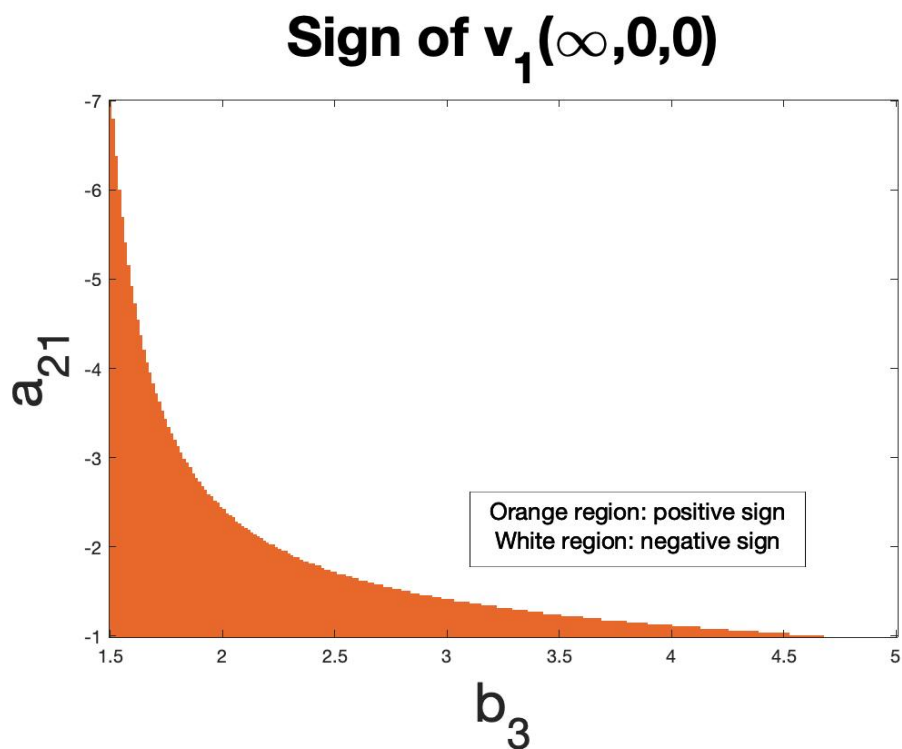
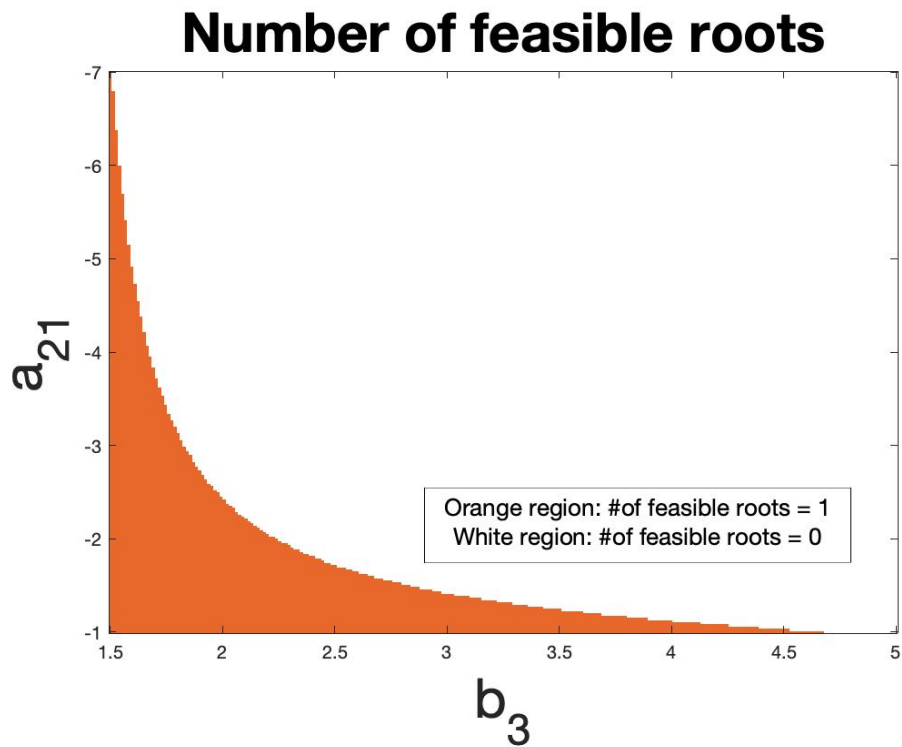


Figure 4-2: The top figure shows the number of feasible roots  $F$  in Lotka-Volterra model with simple higher-order terms where  $(r_1, r_2, r_3, a_{11}, a_{12}, a_{13}, a_{22}, a_{23}, a_{31}, a_{32}, a_{33}, b_1, b_2) = (0.5, -1.5, -0.5, 0.5, -1.5, -0.5, 2.6, -5, -0.5, -10, 1, 0.2, -0.1, )$ ,  $a_{21} \in [-7, -1]$  and  $b_3 \in [1.5, 5]$ . The bottom figure shows the sign of  $v_1(\infty, 0, 0)$  with the same model and parameter values and ranges. Both figures confirm that  $F > 0$  when  $v_1(\infty, 0, 0) > 0$ . Simulations done via solving the isocline equations numerically and checking for the feasibility of roots match the two figures displayed here.

#### 4.4.2 Application: 3-Species with Higher-Order Interactions

Consider Lotka-Volterra model with higher-order interactions that is shown below:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(r_1 + a_{11}N_1 + a_{12}N_2 + a_{13}N_3 + b_1N_2N_3), \\ \frac{dN_2}{dt} &= N_2(r_2 + a_{21}N_1 + a_{22}N_2 + a_{23}N_3 + b_2N_1N_3), \\ \frac{dN_3}{dt} &= N_3(r_3 + a_{31}N_1 + a_{32}N_2 + a_{33}N_3 + b_3N_1N_2).\end{aligned}$$

To study feasibility, the polynomials that are needed to be considered are  $f_1(N_1, N_2, N_3) = r_1 + a_{11}N_1 + a_{12}N_2 + a_{13}N_3 + b_1N_2N_3$ ,  $f_2(N_1, N_2, N_3) = r_2 + a_{21}N_1 + a_{22}N_2 + a_{23}N_3 + b_2N_1N_3$  and  $f_3(N_1, N_2, N_3) = r_3 + a_{31}N_1 + a_{32}N_2 + a_{33}N_3 + b_3N_1N_2$ . Next, assume that  $N_1$  is constant and homogenize  $f_1$ ,  $f_2$  and  $f_3$  with a fourth variable  $W$  as follows:

$$\begin{aligned}F_{N_1,1} &= r_1W^2 + a_{11}N_1W^2 + a_{12}N_2W + a_{13}N_3W + b_1N_2N_3, \\ F_{N_1,2} &= r_2W + a_{21}N_1W + a_{22}N_2 + a_{23}N_3 + b_2N_1N_3, \\ F_{N_1,3} &= r_3W + a_{31}N_1W + a_{32}N_2 + a_{33}N_3 + b_3N_1N_2,\end{aligned}$$

Note that the total degree of each of  $F_{N_1,1}$ ,  $F_{N_1,2}$  and  $F_{N_1,3}$  (or the total degree of  $f_1$ ,  $f_2$  and  $f_3$  assuming  $N_1$  is a constant) is  $d_{1,1} = 2$ ,  $d_{1,2} = 1$  and  $d_{1,3} = 1$  respectively. From the  $d$ 's, we compute  $L_1 = 1 + \sum_{i=1}^3 (d_{1,i} - 1) = 2$ . Now, we form the monomial set  $H_1$ , which is a union of three disjoint monomials  $H_1 = W^{d_{1,1}} \cdot H_{1,1}^{L_1 - d_{1,1}} \cup N_2^{d_{1,2}} \cdot H_{1,2}^{L_1 - d_{1,2}} \cup N_3^{d_{1,3}} \cdot H_{1,3}^{L_1 - d_{1,3}}$  where none of these  $H$ 's involve  $N_1$  and each is indicated below in curly brackets:

$$\begin{aligned}W^{d_{1,1}} \cdot H_{1,1}^{L_1 - d_{1,1}} &= W^2 \cdot \{1\}, \\ N_2^{d_{1,2}} \cdot H_{1,2}^{L_1 - d_{1,2}} &= N_2 \cdot \{W, N_2, N_3\}, \\ N_3^{d_{1,3}} \cdot H_{1,3}^{L_1 - d_{1,3}} &= N_3 \cdot \{W, N_3\}\end{aligned}$$

Form the monomial set  $H_{1,\text{row}} = f_1 \cdot H_{1,1}^{L_1 - d_{1,1}} \cup f_2 \cdot H_{1,2}^{L_1 - d_{1,2}} \cup f_3 \cdot H_{1,3}^{L_1 - d_{1,3}}$  evaluated at  $W = 1$  that is shown below. In addition, form the monomial set  $H_{1,\text{col}}$  which is simply  $H_1$  evaluated at  $W = 1$  to get

$$\begin{aligned}H_{1,\text{row}} &= \{f_1, f_2, f_2N_2, f_2N_3, f_3, f_3N_3\} \\ H_{1,\text{col}} &= \{1, N_2, N_2^2, N_2N_3, N_3, N_3^2\}\end{aligned}$$

After that, form the Macaulay matrix  $M_{N_1}$  which is a square matrix whose size is  $\binom{n-1+L_1}{n-1} = 6$ . The  $(i, j)$  entry of the Macaulay matrix is the coefficient of  $H_{1, \text{col}}(j)$  in the expression of  $H_{1, \text{row}}(i)$  assuming that  $N_1$  is a constant. For example, the  $(3, 2)$  entry in the matrix is the coefficient of  $N_2$  in  $N_2 f_2$  which is  $r_2 + N_1 a_{21}$ . The matrix  $M_{N_1}$  is shown below:

	1	$N_2$	$N_2^2$	$N_2 N_3$	$N_3$	$N_3^2$
$f_1$	$r_1 + N_1 a_{11}$	$a_{12}$	0	$b_1$	$a_{13}$	0
$f_2$	$r_2 + N_1 a_{21}$	$a_{22}$	0	0	$a_{23} + N_1 b_2$	0
$f_2 N_2$	0	$r_2 + N_1 a_{21}$	$a_{22}$	$a_{23} + N_1 b_2$	0	0
$f_2 N_3$	0	0	0	$a_{22}$	$r_2 + N_1 a_{21}$	$a_{23} + N_1 b_2$
$f_3$	$r_3 + N_1 a_{31}$	$a_{32} + N_1 b_3$	0	0	$a_{33}$	0
$f_3 N_3$	0	0	0	$a_{32} + N_1 b_3$	$r_3 + N_1 a_{31}$	$a_{33}$

Next, form the matrix  $M'_{N_1}$  whose first column is  $H_{1, \text{row}}$  and its remaining columns are the remaining columns (i.e, columns 2 to 6) of the matrix  $M_{N_1}$  (i.e, replace the first column of  $M_{N_1}$  whose top header is 1 with the leftmost column which contains the  $f$ 's). From the formula of  $H_{1, \text{row}} = \text{col}_1(M_{N_1}) + \sum_{j=2}^{r_1} \text{col}_j(M_{N_1}) H_{1, \text{col}}(j)$ , we can see that  $H_{1, \text{row}}$  is the first column of  $M_{N_1}$  added to it a multiple of every other column of  $M_{N_1}$ , implying that  $\det(M_{N_1}) = \det(M'_{N_1})$ . This determinant (i.e,  $\det(M'_{N_1})$ ) can be written as  $T_{11} f_1 + T_{12} f_2 + T_{13} f_3$  which is shown below

$$T_{11} = a_{22}(a_{23} a_{32} - a_{22} a_{33} + N_1 a_{23} b_3 + N_1 a_{32} b_2 + N_1^2 b_2 b_3)^2$$

$$\begin{aligned} T_{12} = & a_{22}(a_{12} a_{23} a_{32} a_{33} - a_{13} a_{23} a_{32}^2 - N_1 a_{13} a_{32}^2 b_2 - N_3 a_{22} a_{33}^2 b_1 - N_1^2 a_{13} a_{23} b_3^2 - N_1^3 a_{13} b_2 b_3^2 - a_{12} a_{22} a_{33}^2 \\ & + a_{13} a_{22} a_{32} a_{33} + a_{23} a_{32} b_1 r_3 - a_{32} a_{33} b_1 r_2 + N_1 a_{12} a_{23} a_{33} b_3 + N_1 a_{13} a_{22} a_{33} b_3 - 2N_1 a_{13} a_{23} a_{32} b_3 \\ & + N_1 a_{12} a_{32} a_{33} b_2 - N_1 a_{21} a_{32} a_{33} b_1 + N_1 a_{23} a_{31} a_{32} b_1 + N_3 a_{23} a_{32} a_{33} b_1 + N_1 a_{23} b_1 b_3 r_3 + N_1 a_{32} b_1 b_2 r_3 \\ & - N_1 a_{33} b_1 b_3 r_2 + N_1^2 a_{12} a_{33} b_2 b_3 - 2N_1^2 a_{13} a_{32} b_2 b_3 - N_1^2 a_{21} a_{33} b_1 b_3 + N_1^2 a_{23} a_{31} b_1 b_3 + N_1^2 a_{31} a_{32} b_1 b_2 \\ & + N_1^3 a_{31} b_1 b_2 b_3 + N_1^2 b_1 b_2 b_3 r_3 + N_1 N_3 a_{23} a_{33} b_1 b_3 + N_1 N_3 a_{32} a_{33} b_1 b_2 + N_1^2 N_3 a_{33} b_1 b_2 b_3) \end{aligned}$$

$$\begin{aligned} T_{13} = & a_{22}(a_{12} a_{22} a_{23} a_{33} - a_{13} a_{22}^2 a_{33} - N_1 a_{12} a_{23}^2 b_3 - N_3 a_{23}^2 a_{32} b_1 - N_1^2 a_{12} a_{32} b_2^2 - N_1^3 a_{12} b_2^2 b_3 - a_{12} a_{23}^2 a_{32} \\ & + a_{13} a_{22} a_{23} a_{32} - a_{22} a_{23} b_1 r_3 + a_{22} a_{33} b_1 r_2 + N_1 a_{13} a_{22} a_{23} b_3 + N_1 a_{12} a_{22} a_{33} b_2 - 2N_1 a_{12} a_{23} a_{32} b_2 \\ & + N_1 a_{13} a_{22} a_{32} b_2 + N_1 a_{21} a_{22} a_{33} b_1 - N_1 a_{22} a_{23} a_{31} b_1 + N_3 a_{22} a_{23} a_{33} b_1 - N_1 a_{22} b_1 b_2 r_3 - N_1 N_3 a_{23}^2 b_1 b_3 \\ & - 2N_1^2 a_{12} a_{23} b_2 b_3 + N_1^2 a_{13} a_{22} b_2 b_3 - N_1^2 a_{22} a_{31} b_1 b_2 - N_1^2 N_3 a_{32} b_1 b_2^2 - N_1^3 N_3 b_1 b_2^2 b_3 + N_1 N_3 a_{22} a_{33} b_1 b_2 \\ & - 2N_1 N_3 a_{23} a_{32} b_1 b_2 - 2N_1^2 N_3 a_{23} b_1 b_2 b_3) \end{aligned}$$

Upon substituting  $f_1, f_2$  and  $f_3$  into  $T_{11}f_1 + T_{12}f_2 + T_{13}f_3$  and simplify the expression, we have the formula of the resultant  $\text{Res}_{N_2, N_3}(N_1) = \sum_{l_1=0}^5 h_{(1, l_1)} N_1^{l_1}$  which is a polynomial of degree 5 in  $N_1$  and contains no  $N_2$ 's nor  $N_3$ 's. The six coefficients of the resultant  $h_{(1,5)}, h_{(1,4)}, \dots, h_{(1,0)}$  are shown below and none of them contain any of the  $N$ 's.

$$h_{(1,5)} = a_{22}a_{11}b_2^2b_3^2$$

$$h_{(1,4)} = a_{22}b_2b_3(2a_{11}a_{23}b_3 - a_{13}a_{21}b_3 + 2a_{11}a_{32}b_2 - a_{12}a_{31}b_2 + a_{21}a_{31}b_1 + b_2b_3r_1)$$

$$\begin{aligned} h_{(1,3)} = & a_{22}(a_{11}a_{23}^2b_3^2 + a_{11}a_{32}^2b_2^2 - a_{13}a_{21}a_{23}b_3^2 - a_{12}a_{31}a_{32}b_2^2 - a_{22}a_{31}^2b_1b_2 - a_{21}^2a_{33}b_1b_3 - a_{12}b_2^2b_3r_3 \\ & - a_{13}b_2b_3^2r_2 + 2a_{23}b_2b_3^2r_1 + 2a_{32}b_2^2b_3r_1 - 2a_{11}a_{22}a_{33}b_2b_3 + 4a_{11}a_{23}a_{32}b_2b_3 + a_{12}a_{21}a_{33}b_2b_3 \\ & - 2a_{12}a_{23}a_{31}b_2b_3 - 2a_{13}a_{21}a_{32}b_2b_3 + a_{13}a_{22}a_{31}b_2b_3 + a_{21}a_{23}a_{31}b_1b_3 + a_{21}a_{31}a_{32}b_1b_2 + a_{21}b_1b_2b_3r_3 \\ & + a_{31}b_1b_2b_3r_2) \end{aligned}$$

$$\begin{aligned} h_{(1,2)} = & a_{22}(a_{23}^2b_3^2r_1 + a_{32}^2b_2^2r_1 + 2a_{11}a_{23}a_{32}^2b_2 - a_{13}a_{21}a_{32}^2b_2 + 2a_{11}a_{23}^2a_{32}b_3 - a_{12}a_{23}^2a_{31}b_3 - a_{22}a_{23}a_{31}^2b_1 \\ & - a_{21}^2a_{32}a_{33}b_1 - a_{13}a_{23}b_3^2r_2 - a_{12}a_{32}b_2^2r_3 - 2a_{11}a_{22}a_{23}a_{33}b_3 + a_{12}a_{21}a_{23}a_{33}b_3 + a_{13}a_{21}a_{22}a_{33}b_3 \\ & - 2a_{13}a_{21}a_{23}a_{32}b_3 + a_{13}a_{22}a_{23}a_{31}b_3 - 2a_{11}a_{22}a_{32}a_{33}b_2 + a_{12}a_{21}a_{32}a_{33}b_2 + a_{12}a_{22}a_{31}a_{33}b_2 \\ & - 2a_{12}a_{23}a_{31}a_{32}b_2 + a_{13}a_{22}a_{31}a_{32}b_2 + a_{21}a_{22}a_{31}a_{33}b_1 + a_{21}a_{23}a_{31}a_{32}b_1 - 2a_{12}a_{23}b_2b_3r_3 \\ & + a_{13}a_{22}b_2b_3r_3 + a_{21}a_{23}b_1b_3r_3 + a_{12}a_{33}b_2b_3r_2 - 2a_{13}a_{32}b_2b_3r_2 + a_{21}a_{32}b_1b_2r_3 - 2a_{22}a_{31}b_1b_2r_3 \\ & - 2a_{21}a_{33}b_1b_3r_2 + a_{23}a_{31}b_1b_3r_2 - 2a_{22}a_{33}b_2b_3r_1 + 4a_{23}a_{32}b_2b_3r_1 + a_{31}a_{32}b_1b_2r_2 + b_1b_2b_3r_2r_3) \end{aligned}$$

$$\begin{aligned} h_{(1,1)} = & a_{22}(a_{11}a_{22}^2a_{33}^2 + a_{11}a_{23}^2a_{32}^2 - a_{12}a_{21}a_{22}a_{33}^2 - a_{13}a_{21}a_{23}a_{32}^2 - a_{12}a_{23}^2a_{31}a_{32} - a_{13}a_{22}^2a_{31}a_{33} \\ & - a_{12}a_{23}^2b_3r_3 - a_{13}a_{32}^2b_2r_2 + 2a_{23}a_{32}^2b_2r_1 + 2a_{23}^2a_{32}b_3r_1 - a_{22}b_1b_2r_3^2 - a_{33}b_1b_3r_2^2 + a_{32}b_1b_2r_2r_3 \\ & - 2a_{11}a_{22}a_{23}a_{32}a_{33} + a_{12}a_{21}a_{23}a_{32}a_{33} + a_{12}a_{22}a_{23}a_{31}a_{33} + a_{13}a_{21}a_{22}a_{32}a_{33} + a_{13}a_{22}a_{23}a_{31}a_{32} \\ & + a_{13}a_{22}a_{23}b_3r_3 + a_{12}a_{22}a_{33}b_2r_3 - 2a_{12}a_{23}a_{32}b_2r_3 + a_{13}a_{22}a_{32}b_2r_3 + a_{12}a_{23}a_{33}b_3r_2 + a_{13}a_{22}a_{33}b_3r_2 \\ & - 2a_{13}a_{23}a_{32}b_3r_2 + a_{21}a_{22}a_{33}b_1r_3 + a_{21}a_{23}a_{32}b_1r_3 - 2a_{22}a_{23}a_{31}b_1r_3 + a_{12}a_{32}a_{33}b_2r_2 - 2a_{22}a_{23}a_{33}b_3r_1 \\ & - 2a_{21}a_{32}a_{33}b_1r_2 + a_{22}a_{31}a_{33}b_1r_2 + a_{23}a_{31}a_{32}b_1r_2 - 2a_{22}a_{32}a_{33}b_2r_1 + a_{23}b_1b_3r_2r_3) \end{aligned}$$

$$\begin{aligned} h_{(1,0)} = & a_{22}(r_1a_{22}^2a_{33}^2 - a_{13}a_{22}^2a_{33}r_3 - 2r_1a_{22}a_{23}a_{32}a_{33} + a_{13}a_{22}a_{23}a_{32}r_3 + a_{12}a_{22}a_{23}a_{33}r_3 - b_1a_{22}a_{23}r_3^2 \\ & + a_{13}a_{22}a_{32}a_{33}r_2 - a_{12}a_{22}a_{33}^2r_2 + b_1a_{22}a_{33}r_2r_3 + r_1a_{23}^2a_{32}^2 - a_{12}a_{23}^2a_{32}r_3 - a_{13}a_{23}a_{32}^2r_2 \\ & + a_{12}a_{23}a_{32}a_{33}r_2 + b_1a_{23}a_{32}r_2r_3 - b_1a_{32}a_{33}r_2^2) \end{aligned}$$

Next, assume that  $N_2$  is constant and homogenize  $f_1, f_2$  and  $f_3$  with a fourth variable  $W$  as follows:



$$\begin{aligned}
F_{N_2,1} &= r_1W + a_{11}N_1 + a_{12}N_2W + a_{13}N_3 + b_1N_2N_3, \\
F_{N_2,2} &= r_2W^2 + a_{21}N_1W + a_{22}N_2W^2 + a_{23}N_3W + b_2N_1N_3, \\
F_{N_2,3} &= r_3W + a_{31}N_1 + a_{32}N_2W + a_{33}N_3 + b_3N_1N_2,
\end{aligned}$$

Note that the total degree of each of  $F_{N_2,1}$ ,  $F_{N_2,2}$  and  $F_{N_2,3}$  (or the total degree of  $f_1$ ,  $f_2$  and  $f_3$  assuming  $N_2$  is a constant) is  $d_{2,1} = 1$ ,  $d_{2,2} = 2$  and  $d_{2,3} = 1$  respectively. From the  $d$ 's, we compute  $L_2 = 1 + \sum_{i=1}^3 (d_{2,i} - 1) = 2$ . Now, we form the monomial set  $H_2$ , which is a union of three disjoint monomials  $H_2 = W^{d_{2,1}} \cdot H_{2,1}^{L_2-d_{2,1}} \cup N_1^{d_{2,2}} \cdot H_{2,2}^{L_2-d_{2,2}} \cup N_3^{d_{2,3}} \cdot H_{2,3}^{L_2-d_{2,3}}$  where none of these  $H$ 's involve  $N_2$  and each is indicated below:

$$\begin{aligned}
W^{d_{2,1}} \cdot H_{2,1}^{L_2-d_{2,1}} &= W \cdot \{W, N_1, N_3\}, \\
N_1^{d_{2,2}} \cdot H_{2,2}^{L_2-d_{2,2}} &= N_1^2 \cdot \{1\}, \\
N_3^{d_{2,3}} \cdot H_{2,3}^{L_2-d_{2,3}} &= N_3 \cdot \{N_1, N_3\}
\end{aligned}$$

Next, form the monomial set  $H_{2,\text{row}} = f_1 \cdot H_{2,1}^{L_2-d_{2,1}} \cup f_2 \cdot H_{2,2}^{L_2-d_{2,2}} \cup f_3 \cdot H_{2,3}^{L_2-d_{2,3}}$  evaluated at  $W = 1$  that is shown below. In addition, form the monomial set  $H_{2,\text{col}}$  which is simply  $H_2$  evaluated at  $W = 1$  to get

$$\begin{aligned}
H_{2,\text{row}} &= \{f_1, f_1N_1, f_1N_3, f_2, f_3N_1, f_3N_3\} \\
H_{2,\text{col}} &= \{1, N_1, N_3, N_1^2, N_1N_3, N_3^2\}
\end{aligned}$$

After that, form the Macaulay matrix  $M_{N_2}$  which is a square matrix whose size is  $\binom{n-1+L_2}{n-1} = 6$ . The  $(i, j)$  entry of the Macaulay matrix is the coefficient of  $H_{2,\text{col}}(j)$  in the expression of  $H_{2,\text{row}}(i)$  assuming that  $N_2$  is a constant. The matrix  $M_{N_2}$  is shown below:

	1	$N_1$	$N_3$	$N_1^2$	$N_1N_3$	$N_3^2$
$f_1$	$r_1 + N_2a_{12}$	$a_{11}$	$a_{13} + N_2b_1$	0	0	0
$f_1N_1$	0	$r_1 + N_2a_{12}$	0	$a_{11}$	$a_{13} + N_2b_1$	0
$f_1N_3$	0	0	$r_1 + N_2a_{12}$	0	$a_{11}$	$a_{13} + N_2b_1$
$f_2$	$r_2 + N_2a_{22}$	$a_{21}$	$a_{23}$	0	$b_2$	0
$f_3N_1$	0	$r_3 + N_2a_{32}$	0	$a_{31} + N_2b_3$	$a_{33}$	0
$f_3N_3$	0	0	$r_3 + N_2a_{32}$	0	$a_{31} + N_2b_3$	$a_{33}$

Next, form the matrix  $M'_{N_2}$  whose first column is  $H_{2,\text{row}}$  and its remaining columns are the remaining columns (i.e, columns 2 to 6) of the matrix  $M_{N_2}$  (i.e, replace the first column of  $M_{N_2}$  whose top header is 1 with the leftmost column which contains the  $f$ 's). Again, from the formula of  $H_{2,\text{row}} = \text{col}_1(M_{N_2}) + \sum_{j=2}^6 \text{col}_j(M_{N_2})H_{2,\text{col}}(j)$ , we can see that  $H_{2,\text{row}}$  is the first column of  $M_{N_2}$  added to it a multiple of every other column of  $M_{N_2}$ , implying that  $\det(M_{N_2}) = \det(M'_{N_2})$ . This determinant (i.e,  $\det(M'_{N_2})$ ) can be written as  $T_{21}f_1 + T_{22}f_2 + T_{23}f_3$ . The expressions of  $T_{21}$  and  $T_{23}$  are too large to be displayed here, however, their forms are shown below:

$$\begin{aligned}
T_{21} &= t_{21,1} + t_{21,N_1}N_1 + t_{21,N_2}N_2 + t_{21,N_3}N_3 + t_{21,N_1N_2}N_1N_2 + t_{21,N_2^2}N_2^2 + t_{21,N_2N_3}N_2N_3 + t_{21,N_2^4}N_2^4 \\
&\quad + t_{21,N_2^3N_3}N_2^3N_3 + t_{21,N_2^3}N_2^3 + t_{21,N_2^2N_3}N_2^2N_3 + t_{21,N_1N_2^4}N_1N_2^4 + t_{21,N_1N_2^3}N_1N_2^3 + t_{21,N_1N_2^2}N_1N_2^2 \\
T_{22} &= (r_1 + N_2a_{12})(a_{13}a_{31} - a_{11}a_{33} + N_2a_{13}b_3 + N_2a_{31}b_1 + N_2^2b_1b_3)(a_{13}a_{31} - a_{11}a_{33} + N_2a_{13}b_3 \\
&\quad + N_2a_{31}b_1 + N_2^2b_1b_3) \\
T_{23} &= t_{23,N_1}N_1 + t_{23,N_3}N_3 + t_{23,N_1N_2}N_1N_2 + t_{23,N_2N_3}N_2N_3 + t_{23,N_1N_2^3}N_1N_2^3 + t_{23,N_1N_2^2}N_1N_2^2 \\
&\quad + t_{23,N_2^4N_3}N_2^4N_3 + t_{23,N_2^3N_3}N_2^3N_3 + t_{23,N_2^2N_3}N_2^2N_3
\end{aligned}$$

Again, the  $t$ 's are polynomials in model parameters (i.e, the  $r$ 's,  $a$ 's and  $b$ 's). For illustration purposes, closed form expressions for  $t_{21,N_1}$  and  $t_{23,N_1}$  are shown below:

$$\begin{aligned}
t_{21,N_1} &= a_{11}a_{13}a_{23}a_{31}^2 - a_{13}^2a_{21}a_{31}^2 - a_{11}^2a_{23}a_{31}a_{33} + a_{11}a_{13}a_{21}a_{31}a_{33} - a_{11}a_{13}a_{31}b_2r_3 + a_{11}a_{31}a_{33}b_2r_1 \\
t_{23,N_1} &= a_{11}^3a_{23}a_{33} + a_{11}a_{13}^2a_{21}a_{31} - a_{11}^2a_{13}a_{21}a_{33} - a_{11}^2a_{13}a_{23}a_{31} + a_{11}^2a_{13}b_2r_3 - a_{11}^2a_{33}b_2r_1
\end{aligned}$$

Upon substituting  $f_1$ ,  $f_2$  and  $f_3$  into  $T_{21}f_1 + T_{22}f_2 + T_{23}f_3$  and simplify the expression, we have the formula of the resultant  $\text{Res}_{N_1,N_3}(N_2) = \sum_{l_2=0}^6 h_{(2,l_2)}N_2^{l_2}$  which is a polynomial of degree 6 in  $N_2$  and contains no  $N_1$ 's nor  $N_3$ 's. The seven coefficients of the resultant  $h_{(2,6)}, h_{(2,5)}, \dots, h_{(2,0)}$  are shown below and none of them contain any of the  $N$ 's.

$$\begin{aligned}
h_{(2,6)} &= a_{12}a_{22}b_1^2b_3^2 \\
h_{(2,5)} &= a_{12}b_1^2b_3^2r_2 - a_{12}^2a_{23}b_1b_3^2 + a_{22}b_1^2b_3^2r_1 + 2a_{12}a_{13}a_{22}b_1b_3^2 - a_{12}a_{21}a_{32}b_1^2b_3 + 2a_{12}a_{22}a_{31}b_1^2b_3 + a_{12}^2a_{32}b_1b_2b_3 \\
h_{(2,4)} &= a_{12}a_{13}^2a_{22}b_3^2 - a_{12}^3a_{33}b_2b_3 - a_{12}^2a_{13}a_{23}b_3^2 + a_{12}a_{22}a_{31}^2b_1^2 + b_1^2b_3^2r_1r_2 - a_{12}a_{21}a_{31}a_{32}b_1^2 - a_{11}a_{12}a_{32}^2b_1b_2 \\
&\quad + a_{12}^2a_{13}a_{32}b_2b_3 + a_{12}^2a_{21}a_{33}b_1b_3 - 2a_{12}^2a_{23}a_{31}b_1b_3 + a_{12}^2a_{31}a_{32}b_1b_2 + 2a_{12}a_{13}b_1b_3^2r_2 - a_{12}a_{21}b_1^2b_3r_3 \\
&\quad - 2a_{12}a_{23}b_1b_3^2r_1 + 2a_{13}a_{22}b_1b_3^2r_1 + 2a_{12}a_{31}b_1^2b_3r_2 - a_{21}a_{32}b_1^2b_3r_1 + 2a_{22}a_{31}b_1^2b_3r_1 + a_{12}^2b_1b_2b_3r_3 \\
&\quad - 2a_{11}a_{12}a_{22}a_{33}b_1b_3 + a_{11}a_{12}a_{23}a_{32}b_1b_3 - 2a_{12}a_{13}a_{21}a_{32}b_1b_3 + 4a_{12}a_{13}a_{22}a_{31}b_1b_3 + 2a_{12}a_{32}b_1b_2b_3r_1
\end{aligned}$$

$$\begin{aligned}
h_{(2,3)} = & 2a_{12}b_1b_2b_3r_1r_3 - a_{12}^2a_{23}a_{31}^2b_1 - a_{12}^3a_{31}a_{33}b_2 + a_{13}^2a_{22}b_3^2r_1 + a_{12}a_{31}^2b_1^2r_2 + a_{22}a_{31}^2b_1^2r_1 - a_{23}b_1b_3^2r_1^2 \\
& - a_{11}a_{12}a_{13}a_{32}^2b_2 + 2a_{12}a_{13}a_{22}a_{31}^2b_1 - a_{12}a_{13}^2a_{21}a_{32}b_3 + 2a_{12}a_{13}^2a_{22}a_{31}b_3 + a_{11}a_{12}^2a_{23}a_{33}b_3 \\
& + a_{12}^2a_{13}a_{21}a_{33}b_3 - 2a_{12}^2a_{13}a_{23}a_{31}b_3 + a_{11}a_{12}^2a_{32}a_{33}b_2 + a_{12}^2a_{13}a_{31}a_{32}b_2 + a_{12}^2a_{21}a_{31}a_{33}b_1 \\
& - 2a_{12}a_{13}a_{23}b_3^2r_1 - a_{12}a_{21}a_{31}b_1^2r_3 - a_{21}a_{31}a_{32}b_1^2r_1 + a_{12}^2a_{13}b_2b_3r_3 - a_{11}a_{32}^2b_1b_2r_1 + a_{12}^2a_{31}b_1b_2r_3 \\
& - 3a_{12}^2a_{33}b_2b_3r_1 + a_{32}b_1b_2b_3r_1^2 + 2a_{13}b_1b_3^2r_1r_2 - a_{21}b_1^2b_3r_1r_3 + 2a_{31}b_1^2b_3r_1r_2 - 2a_{11}a_{12}a_{13}a_{22}a_{33}b_3 \\
& + a_{11}a_{12}a_{13}a_{23}a_{32}b_3 + a_{11}a_{12}a_{21}a_{32}a_{33}b_1 - 2a_{11}a_{12}a_{22}a_{31}a_{33}b_1 + a_{11}a_{12}a_{23}a_{31}a_{32}b_1 + a_{12}a_{13}^2b_3^2r_2 \\
& - 2a_{12}a_{13}a_{21}a_{31}a_{32}b_1 + a_{11}a_{12}a_{23}b_1b_3r_3 - 2a_{12}a_{13}a_{21}b_1b_3r_3 - 2a_{11}a_{12}a_{32}b_1b_2r_3 - 2a_{11}a_{12}a_{33}b_1b_3r_2 \\
& + 4a_{12}a_{13}a_{31}b_1b_3r_2 + 2a_{12}a_{13}a_{32}b_2b_3r_1 - 2a_{11}a_{22}a_{33}b_1b_3r_1 + a_{11}a_{23}a_{32}b_1b_3r_1 + 2a_{12}a_{21}a_{33}b_1b_3r_1 \\
& - 4a_{12}a_{23}a_{31}b_1b_3r_1 - 2a_{13}a_{21}a_{32}b_1b_3r_1 + 4a_{13}a_{22}a_{31}b_1b_3r_1 + 2a_{12}a_{31}a_{32}b_1b_2r_1 \\
h_{(2,2)} = & - a_{23}a_{11}^2a_{12}a_{32}a_{33} + a_{22}a_{11}^2a_{12}a_{33}^2 + a_{23}a_{11}a_{12}^2a_{31}a_{33} - a_{21}a_{11}a_{12}^2a_{33}^2 + b_2a_{11}a_{12}^2a_{33}r_3 + a_{21}a_{33}b_1b_3r_1^2 \\
& + a_{23}a_{11}a_{12}a_{13}a_{31}a_{32} - 2a_{22}a_{11}a_{12}a_{13}a_{31}a_{33} + a_{21}a_{11}a_{12}a_{13}a_{32}a_{33} - 2b_2a_{11}a_{12}a_{13}a_{32}r_3 + b_2b_1b_3r_1^2r_3 \\
& - 2r_2a_{11}a_{12}a_{13}a_{33}b_3 + a_{23}a_{11}a_{12}a_{13}b_3r_3 - 2r_2a_{11}a_{12}a_{31}a_{33}b_1 + a_{23}a_{11}a_{12}a_{31}b_1r_3 + 2b_2a_{11}a_{12}a_{32}a_{33}r_1 \\
& + a_{21}a_{11}a_{12}a_{33}b_1r_3 + 2a_{23}a_{11}a_{12}a_{33}b_3r_1 - b_2a_{11}a_{12}b_1r_3^2 - b_2a_{11}a_{13}a_{32}^2r_1 + a_{23}a_{11}a_{13}a_{32}b_3r_1 \\
& - 2a_{22}a_{11}a_{13}a_{33}b_3r_1 + a_{23}a_{11}a_{31}a_{32}b_1r_1 - 2a_{22}a_{11}a_{31}a_{33}b_1r_1 + a_{21}a_{11}a_{32}a_{33}b_1r_1 - 2b_2a_{11}a_{32}b_1r_1r_3 \\
& - 2r_2a_{11}a_{33}b_1b_3r_1 + a_{23}a_{11}b_1b_3r_1r_3 - a_{23}a_{12}^2a_{13}a_{31}^2 + a_{21}a_{12}^2a_{13}a_{31}a_{33} + b_2a_{12}^2a_{13}a_{31}r_3 - 3b_2a_{12}^2a_{31}a_{33}r_1 \\
& + a_{22}a_{12}a_{13}^2a_{31}^2 - a_{21}a_{12}a_{13}^2a_{31}a_{32} + 2r_2a_{12}a_{13}^2a_{31}b_3 - a_{21}a_{12}a_{13}^2b_3r_3 + 2r_2a_{12}a_{13}a_{31}^2b_1 + 2b_2a_{12}a_{13}a_{31}a_{32}r_1 \\
& - 2a_{21}a_{12}a_{13}a_{31}b_1r_3 - 4a_{23}a_{12}a_{13}a_{31}b_3r_1 + 2a_{21}a_{12}a_{13}a_{33}b_3r_1 + 2b_2a_{12}a_{13}b_3r_1r_3 - 2a_{23}a_{12}a_{31}^2b_1r_1 \\
& + 2a_{21}a_{12}a_{31}a_{33}b_1r_1 + 2b_2a_{12}a_{31}b_1r_1r_3 - 3b_2a_{12}a_{33}b_3r_1^2 + 2a_{22}a_{13}^2a_{31}b_3r_1 - a_{21}a_{13}^2a_{32}b_3r_1 + r_2a_{13}^2b_3^2r_1 \\
& + 2a_{22}a_{13}a_{31}^2b_1r_1 - 2a_{21}a_{13}a_{31}a_{32}b_1r_1 + 4r_2a_{13}a_{31}b_1b_3r_1 + b_2a_{13}a_{32}b_3r_1^2 - 2a_{21}a_{13}b_1b_3r_1r_3 - a_{23}a_{13}b_3^2r_1^2 \\
& + r_2a_{31}^2b_1^2r_1 + b_2a_{31}a_{32}b_1r_1^2 - a_{21}a_{31}b_1^2r_1r_3 - 2a_{23}a_{31}b_1b_3r_1^2 \\
h_{(2,1)} = & a_{12}a_{13}^2a_{31}^2r_2 - a_{33}b_2b_3r_1^3 + a_{11}^2a_{12}a_{33}^2r_2 + a_{11}^2a_{22}a_{33}^2r_1 + a_{13}^2a_{22}a_{31}^2r_1 - a_{23}a_{31}^2b_1r_1^2 - 2a_{11}a_{12}a_{21}a_{33}^2r_1 \\
& - 2a_{12}a_{13}a_{23}a_{31}^2r_1 - a_{12}a_{13}^2a_{21}a_{31}r_3 - a_{11}^2a_{12}a_{23}a_{33}r_3 - a_{13}^2a_{21}a_{31}a_{32}r_1 - a_{11}^2a_{23}a_{32}a_{33}r_1 - a_{11}a_{12}a_{13}b_2r_1^2 \\
& + a_{11}a_{23}a_{33}b_3r_1^2 + a_{13}a_{21}a_{33}b_3r_1^2 - 2a_{13}a_{23}a_{31}b_3r_1^2 + a_{11}a_{32}a_{33}b_2r_1^2 - 3a_{12}a_{31}a_{33}b_2r_1^2 + a_{13}a_{31}a_{32}b_2r_1^2 \\
& + a_{21}a_{31}a_{33}b_1r_1^2 - a_{13}^2a_{21}b_3r_1r_3 + 2a_{13}a_{31}^2b_1r_1r_2 + 2a_{13}^2a_{31}b_3r_1r_2 - a_{11}b_1b_2r_1r_3^2 + a_{13}b_2b_3r_1^2r_3 \\
& + a_{31}b_1b_2r_1^2r_3 + a_{11}a_{12}a_{13}a_{21}a_{33}r_3 + a_{11}a_{12}a_{13}a_{23}a_{31}r_3 - 2a_{11}a_{12}a_{13}a_{31}a_{33}r_2 + 2a_{11}a_{12}a_{23}a_{31}a_{33}r_1 \\
& + a_{11}a_{13}a_{21}a_{32}a_{33}r_1 - 2a_{11}a_{13}a_{22}a_{31}a_{33}r_1 + a_{11}a_{13}a_{23}a_{31}a_{32}r_1 + 2a_{12}a_{13}a_{21}a_{31}a_{33}r_1 + a_{11}a_{13}a_{23}b_3r_1r_3 \\
& + 2a_{11}a_{12}a_{33}b_2r_1r_3 - 2a_{11}a_{13}a_{32}b_2r_1r_3 + 2a_{12}a_{13}a_{31}b_2r_1r_3 - 2a_{11}a_{13}a_{33}b_3r_1r_2 + a_{11}a_{21}a_{33}b_1r_1r_3 \\
& + a_{11}a_{23}a_{31}b_1r_1r_3 - 2a_{13}a_{21}a_{31}b_1r_1r_3 - 2a_{11}a_{31}a_{33}b_1r_1r_2 \\
h_{(2,0)} = & r_2a_{11}^2a_{33}^2r_1 - a_{23}a_{11}^2a_{33}r_1r_3 - 2r_2a_{11}a_{13}a_{31}a_{33}r_1 + a_{23}a_{11}a_{13}a_{31}r_1r_3 + a_{21}a_{11}a_{13}a_{33}r_1r_3 \\
& - b_2a_{11}a_{13}r_1r_3^2 + a_{23}a_{11}a_{31}a_{33}r_1^2 - a_{21}a_{11}a_{33}^2r_1^2 + b_2a_{11}a_{33}^2r_1^2r_3 + r_2a_{13}^2a_{31}^2r_1 - a_{21}a_{13}^2a_{31}r_1r_3 \\
& - a_{23}a_{13}a_{31}^2r_1^2 + a_{21}a_{13}a_{31}a_{33}r_1^2 + b_2a_{13}a_{31}r_1^2r_3 - b_2a_{31}a_{33}r_1^3
\end{aligned}$$

Next, assume that  $N_3$  is constant and homogenize  $f_1$ ,  $f_2$  and  $f_3$  with a fourth variable  $W$ :

$$\begin{aligned}
F_{N_3,1} &= r_1W + a_{11}N_1 + a_{12}N_2 + a_{13}N_3W + b_1N_2N_3, \\
F_{N_3,2} &= r_2W + a_{21}N_1 + a_{22}N_2 + a_{23}N_3W + b_2N_1N_3, \\
F_{N_3,3} &= r_3W^2 + a_{31}N_1W + a_{32}N_2W + a_{33}N_3W^2 + b_3N_1N_2,
\end{aligned}$$

Note that the total degree of each of  $F_{N_3,1}$ ,  $F_{N_3,2}$  and  $F_{N_3,3}$  (or the total degree of  $f_1$ ,  $f_2$  and  $f_3$  assuming  $N_3$  is a constant) is  $d_{3,1} = 1$ ,  $d_{3,2} = 1$  and  $d_{3,3} = 2$  respectively. From the  $d$ 's, we compute  $L_3 = 1 + \sum_{i=1}^3 (d_{3,i} - 1) = 2$ . Now, we form the monomial set  $H_3$ , which is a union of three disjoint monomials  $H_3 = W^{d_{3,1}} \cdot H_{3,1}^{L_3-d_{3,1}} \cup N_1^{d_{3,2}} \cdot H_{3,2}^{L_3-d_{3,2}} \cup N_2^{d_{3,3}} \cdot H_{3,3}^{L_3-d_{3,3}}$  where none of these  $H$ 's involve  $N_3$  and each is indicated below:

$$\begin{aligned}
W^{d_{3,1}} \cdot H_{3,1}^{L_3-d_{3,1}} &= W \cdot \{W, N_1, N_2\}, \\
N_1^{d_{3,2}} \cdot H_{3,2}^{L_3-d_{3,2}} &= N_1 \cdot \{N_1, N_2\}, \\
N_2^{d_{3,3}} \cdot H_{3,3}^{L_3-d_{3,3}} &= N_2^2 \cdot \{1\}
\end{aligned}$$

Next, form the monomial set  $H_{3,\text{row}} = f_1 \cdot H_{3,1}^{L_3-d_{3,1}} \cup f_2 \cdot H_{3,2}^{L_3-d_{3,2}} \cup f_3 \cdot H_{3,3}^{L_3-d_{3,3}}$  evaluated at  $W = 1$  that is shown below. In addition, form the monomial set  $H_{3,\text{col}}$  which is simply  $H_3$  evaluated at  $W = 1$  to get

$$\begin{aligned}
H_{3,\text{row}} &= \{f_1, f_1N_1, f_1N_2, f_2N_1, f_2N_2, f_3\} \\
H_{3,\text{col}} &= \{1, N_1, N_2, N_1^2, N_1N_2, N_2^2\}
\end{aligned}$$

After that, form the Macaulay matrix  $M_{N_3}$  which is a square matrix whose size is  $\binom{n-1+L_3}{n-1} = 6$ . The  $(i, j)$  entry of the Macaulay matrix is the coefficient of  $H_{3,\text{col}}(j)$  in the expression of  $H_{3,\text{row}}(i)$  assuming that  $N_3$  is a constant. The matrix  $M_{N_3}$  is shown below:

	1	$N_1$	$N_2$	$N_1^2$	$N_1N_2$	$N_2^2$
$f_1$	$r_1 + N_3a_{13}$	$a_{11}$	$a_{12} + N_3b_1$	0	0	0
$f_1N_1$	0	$r_1 + N_3a_{13}$	0	$a_{11}$	$a_{12} + N_3b_1$	0
$f_1N_2$	0	0	$r_1 + N_3a_{13}$	0	$a_{11}$	$a_{12} + N_3b_1$
$f_2N_1$	0	$r_2 + N_3a_{23}$	0	$a_{21} + N_3b_2$	$a_{22}$	0
$f_2N_2$	0	0	$r_2 + N_3a_{23}$	0	$a_{21} + N_3b_2$	$a_{22}$
$f_3$	$r_3 + N_3a_{33}$	$a_{31}$	$a_{32}$	0	$b_3$	0

Next, form the matrix  $M'_{N_3}$  whose first column is  $H_{3,\text{row}}$  and its remaining columns are the remaining columns (i.e, columns 2 to 6) of the matrix  $M_{N_3}$  (i.e, replace the first column of  $M_{N_3}$  whose top header is 1 with the leftmost column which contains the  $f$ 's). Again, from the formula of  $H_{3,\text{row}} = \text{col}_1(M_{N_3}) + \sum_{j=2}^6 \text{col}_j(M_{N_3})H_{3,\text{col}}(j)$ , we can see that  $H_{3,\text{row}}$  is the first column of  $M_{N_3}$  added to it a multiple of every other column of  $M_{N_3}$ , implying that  $\det(M_{N_3}) = \det(M'_{N_3})$ . This determinant (i.e,  $\det(M'_{N_3})$ ) can be written as  $T_{31}f_1 + T_{32}f_2 + T_{33}f_3$ . The expressions of  $T_{21}$  and  $T_{23}$  are too large to be displayed here, however, their forms are shown below:

$$\begin{aligned}
T_{31} &= t_{31,1} + t_{31,N_1}N_1 + t_{31,N_2}N_2 + t_{31,N_3}N_3 + t_{31,N_1N_3}N_1N_3 + t_{31,N_2N_3}N_2N_3 + t_{31,N_3^2}N_3^2 + t_{31,N_3^3}N_3^3 \\
&\quad + t_{31,N_1N_3^4}N_1N_3^4 + t_{31,N_1N_3^3}N_1N_3^3 + t_{31,N_1N_3^2}N_1N_3^2 + t_{31,N_2N_3^3}N_2N_3^3 + t_{31,N_2N_3^2}N_2N_3^2 + t_{31,N_3^4}N_3^4 \\
T_{32} &= t_{32,N_1}N_1 + t_{32,N_2}N_2 + t_{32,N_1N_3}N_1N_3 + t_{32,N_2N_3}N_2N_3 + t_{32,N_1N_3^3}N_1N_3^3 + t_{32,N_1N_3^2}N_1N_3^2 \\
&\quad + t_{32,N_2N_3^4}N_2N_3^4 + t_{32,N_2N_3^3}N_2N_3^3 + t_{32,N_2N_3^2}N_2N_3^2 \\
T_{33} &= (r_1 + N_3a_{13})(a_{12}a_{21} - a_{11}a_{22} + N_3a_{12}b_2 + N_3a_{21}b_1 + N_3^2b_1b_2)(a_{12}a_{21} - a_{11}a_{22} + N_3a_{12}b_2 \\
&\quad + N_3a_{21}b_1 + N_3^2b_1b_2)
\end{aligned}$$

Again, the  $t$ 's are polynomials in model parameters (i.e, the  $r$ 's,  $a$ 's and  $b$ 's). For illustration purposes, closed form expressions for  $t_{31,N_1}$  and  $t_{32,N_1}$  are shown below:

$$\begin{aligned}
t_{31,N_1} &= a_{11}a_{12}a_{21}^2a_{32} - a_{12}^2a_{21}^2a_{31} - a_{11}^2a_{21}a_{22}a_{32} + a_{11}a_{12}a_{21}a_{22}a_{31} - a_{11}a_{12}a_{21}b_3r_2 + a_{11}a_{21}a_{22}b_3r_1 \\
t_{32,N_1} &= a_{11}^3a_{22}a_{32} + a_{11}a_{12}^2a_{21}a_{31} - a_{11}^2a_{12}a_{21}a_{32} - a_{11}^2a_{12}a_{22}a_{31} + a_{11}^2a_{12}b_3r_2 - a_{11}^2a_{22}b_3r_1
\end{aligned}$$

Upon substituting  $f_1$ ,  $f_2$  and  $f_3$  into  $T_{31}f_1 + T_{32}f_2 + T_{33}f_3$  and simplifying the expression, we have the formula of the resultant  $\text{Res}_{N_1,N_2}(N_3) = \sum_{l_3=0}^6 h_{(3,l_3)}N_3^{l_3}$  which is a polynomial of degree 6 in  $N_3$  and contains no  $N_1$ 's nor  $N_2$ 's. The seven coefficients are shown below

$$\begin{aligned}
h_{(3,6)} &= a_{13}a_{33}b_1^2b_2^2 \\
h_{(3,5)} &= a_{13}b_1^2b_2^2r_3 - a_{13}^2a_{32}b_1b_2^2 + a_{33}b_1^2b_2^2r_1 + 2a_{12}a_{13}a_{33}b_1b_2^2 + 2a_{13}a_{21}a_{33}b_1^2b_2 - a_{13}a_{23}a_{31}b_1^2b_2 + a_{13}^2a_{23}b_1b_2b_3 \\
h_{(3,4)} &= a_{12}^2a_{13}a_{33}b_2^2 - a_{12}a_{13}^2a_{32}b_2^2 - a_{13}^3a_{22}b_2b_3 + a_{13}a_{21}^2a_{33}b_1^2 + b_1^2b_2^2r_1r_3 - a_{13}a_{21}a_{23}a_{31}b_1^2 - a_{11}a_{13}a_{23}^2b_1b_3 \\
&\quad + a_{12}a_{13}^2a_{23}b_2b_3 + a_{13}^2a_{21}a_{23}b_1b_3 - 2a_{13}^2a_{21}a_{32}b_1b_2 + a_{13}^2a_{22}a_{31}b_1b_2 + 2a_{12}a_{13}b_1b_2^2r_3 + 2a_{13}a_{21}b_1^2b_2r_3 \\
&\quad + 2a_{12}a_{33}b_1b_2^2r_1 - a_{13}a_{31}b_1^2b_2r_2 - 2a_{13}a_{32}b_1b_2^2r_1 + 2a_{21}a_{33}b_1^2b_2r_1 - a_{23}a_{31}b_1^2b_2r_1 + a_{13}^2b_1b_2b_3r_2 \\
&\quad - 2a_{11}a_{13}a_{22}a_{33}b_1b_2 + a_{11}a_{13}a_{23}a_{32}b_1b_2 + 4a_{12}a_{13}a_{21}a_{33}b_1b_2 - 2a_{12}a_{13}a_{23}a_{31}b_1b_2 + 2a_{13}a_{23}b_1b_2b_3r_1
\end{aligned}$$

$$\begin{aligned}
h_{(3,3)} = & a_{12}^2 a_{13} b_2^2 r_3 - a_{13}^2 a_{21}^2 a_{32} b_1 - a_{13}^3 a_{21} a_{22} b_3 + a_{13} a_{21}^2 b_1^2 r_3 + a_{12}^2 a_{33} b_2^2 r_1 + a_{21}^2 a_{33} b_1^2 r_1 - a_{32} b_1 b_2^2 r_1^2 \\
& - a_{11} a_{12} a_{13} a_{23}^2 b_3 + a_{11} a_{13}^2 a_{22} a_{23} b_3 + a_{12} a_{13}^2 a_{21} a_{23} b_3 + a_{11} a_{13}^2 a_{22} a_{32} b_2 + 2 a_{12} a_{13} a_{21}^2 a_{33} b_1 \\
& - 2 a_{12} a_{13}^2 a_{21} a_{32} b_2 + a_{12} a_{13}^2 a_{22} a_{31} b_2 + 2 a_{12}^2 a_{13} a_{21} a_{33} b_2 - a_{12}^2 a_{13} a_{23} a_{31} b_2 + a_{13}^2 a_{21} a_{22} a_{31} b_1 \\
& - 2 a_{12} a_{13} a_{32} b_2^2 r_1 - a_{13} a_{21} a_{31} b_1^2 r_2 - a_{21} a_{23} a_{31} b_1^2 r_1 + a_{12} a_{13}^2 b_2 b_3 r_2 - a_{11} a_{23}^2 b_1 b_3 r_1 + a_{13}^2 a_{21} b_1 b_3 r_2 \\
& - 3 a_{13}^2 a_{22} b_2 b_3 r_1 + a_{23} b_1 b_2 b_3 r_1^2 + 2 a_{12} b_1 b_2^2 r_1 r_3 + 2 a_{21} b_1^2 b_2 r_1 r_3 - a_{31} b_1^2 b_2 r_1 r_2 - 2 a_{11} a_{12} a_{13} a_{22} a_{33} b_2 \\
& + a_{11} a_{12} a_{13} a_{23} a_{32} b_2 - 2 a_{11} a_{13} a_{21} a_{22} a_{33} b_1 + a_{11} a_{13} a_{21} a_{23} a_{32} b_1 + a_{11} a_{13} a_{22} a_{23} a_{31} b_1 - 2 a_{12} a_{13} a_{21} a_{23} a_{31} b_1 \\
& - 2 a_{11} a_{13} a_{22} b_1 b_2 r_3 + 4 a_{12} a_{13} a_{21} b_1 b_2 r_3 - 2 a_{11} a_{13} a_{23} b_1 b_3 r_2 + 2 a_{12} a_{13} a_{23} b_2 b_3 r_1 + a_{11} a_{13} a_{32} b_1 b_2 r_2 \\
& - 2 a_{12} a_{13} a_{31} b_1 b_2 r_2 + 2 a_{13} a_{21} a_{23} b_1 b_3 r_1 - 2 a_{11} a_{22} a_{33} b_1 b_2 r_1 + a_{11} a_{23} a_{32} b_1 b_2 r_1 + 4 a_{12} a_{21} a_{33} b_1 b_2 r_1 \\
& - 2 a_{12} a_{23} a_{31} b_1 b_2 r_1 - 4 a_{13} a_{21} a_{32} b_1 b_2 r_1 + 2 a_{13} a_{22} a_{31} b_1 b_2 r_1 + 2 a_{13} b_1 b_2 b_3 r_1 r_2 \\
h_{(3,2)} = & a_{33} a_{11}^2 a_{13} a_{22}^2 - a_{32} a_{11}^2 a_{13} a_{22} a_{23} - 2 a_{33} a_{11} a_{12} a_{13} a_{21} a_{22} + a_{32} a_{11} a_{12} a_{13} a_{21} a_{23} + a_{31} a_{11} a_{12} a_{13} a_{22} a_{23} \\
& - 2 r_3 a_{11} a_{12} a_{13} a_{22} b_2 - 2 b_3 a_{11} a_{12} a_{13} a_{23} r_2 + a_{32} a_{11} a_{12} a_{13} b_2 r_2 - 2 a_{33} a_{11} a_{12} a_{22} b_2 r_1 - b_3 a_{11} a_{12} a_{23}^2 r_1 \\
& + a_{32} a_{11} a_{12} a_{23} b_2 r_1 + a_{32} a_{11} a_{13}^2 a_{21} a_{22} - a_{31} a_{11} a_{13}^2 a_{22}^2 + b_3 a_{11} a_{13}^2 a_{22} r_2 - 2 r_3 a_{11} a_{13} a_{21} a_{22} b_1 \\
& + a_{32} a_{11} a_{13} a_{21} b_1 r_2 + 2 b_3 a_{11} a_{13} a_{22} a_{23} r_1 + a_{31} a_{11} a_{13} a_{22} b_1 r_2 + 2 a_{32} a_{11} a_{13} a_{22} b_2 r_1 - b_3 a_{11} a_{13} b_1 r_2^2 \\
& - 2 a_{33} a_{11} a_{21} a_{22} b_1 r_1 + a_{32} a_{11} a_{21} a_{23} b_1 r_1 + a_{31} a_{11} a_{22} a_{23} b_1 r_1 - 2 r_3 a_{11} a_{22} b_1 b_2 r_1 - 2 b_3 a_{11} a_{23} b_1 r_1 r_2 \\
& + a_{32} a_{11} b_1 b_2 r_1 r_2 + a_{33} a_{12}^2 a_{13} a_{21}^2 - a_{31} a_{12}^2 a_{13} a_{21} a_{23} + 2 r_3 a_{12}^2 a_{13} a_{21} b_2 - a_{31} a_{12}^2 a_{13} b_2 r_2 + 2 a_{33} a_{12}^2 a_{21} b_2 r_1 \\
& - a_{31} a_{12}^2 a_{23} b_2 r_1 + r_3 a_{12}^2 b_2^2 r_1 - a_{32} a_{12} a_{13}^2 a_{21}^2 + a_{31} a_{12} a_{13}^2 a_{21} a_{22} + b_3 a_{12} a_{13}^2 a_{21} r_2 + 2 r_3 a_{12} a_{13} a_{21}^2 b_1 \\
& + 2 b_3 a_{12} a_{13} a_{21} a_{23} r_1 - 2 a_{31} a_{12} a_{13} a_{21} b_1 r_2 - 4 a_{32} a_{12} a_{13} a_{21} b_2 r_1 + 2 a_{31} a_{12} a_{13} a_{22} b_2 r_1 + 2 b_3 a_{12} a_{13} b_2 r_1 r_2 \\
& + 2 a_{33} a_{12} a_{21}^2 b_1 r_1 - 2 a_{31} a_{12} a_{21} a_{23} b_1 r_1 + 4 r_3 a_{12} a_{21} b_1 b_2 r_1 + b_3 a_{12} a_{23} b_2 r_1^2 - 2 a_{31} a_{12} b_1 b_2 r_1 r_2 - a_{32} a_{12} b_2^2 r_1^2 \\
& - 3 b_3 a_{13}^2 a_{21} a_{22} r_1 - 2 a_{32} a_{13} a_{21}^2 b_1 r_1 + 2 a_{31} a_{13} a_{21} a_{22} b_1 r_1 + 2 b_3 a_{13} a_{21} b_1 r_1 r_2 - 3 b_3 a_{13} a_{22} b_2 r_1^2 + r_3 a_{21}^2 b_1^2 r_1 \\
& + b_3 a_{21} a_{23} b_1 r_1^2 - a_{31} a_{21} b_1^2 r_1 r_2 - 2 a_{32} a_{21} b_1 b_2 r_1^2 + a_{31} a_{22} b_1 b_2 r_1^2 + b_3 b_1 b_2 r_1^2 r_2 \\
h_{(3,1)} = & a_{11}^2 a_{13} a_{22}^2 r_3 - a_{22} b_2 b_3 r_1^3 + a_{12}^2 a_{13} a_{21}^2 r_3 + a_{11}^2 a_{22}^2 a_{33} r_1 + a_{12}^2 a_{21}^2 a_{33} r_1 - a_{21}^2 a_{32} b_1 r_1^2 - 2 a_{11} a_{13} a_{22}^2 a_{31} r_1 \\
& - 2 a_{12} a_{13} a_{21}^2 a_{32} r_1 - a_{12}^2 a_{13} a_{21} a_{31} r_2 - a_{11}^2 a_{13} a_{22} a_{32} r_2 - a_{12}^2 a_{21} a_{23} a_{31} r_1 - a_{11}^2 a_{22} a_{23} a_{32} r_1 - a_{11} a_{12} a_{13} b_3 r_2^2 \\
& + a_{11} a_{22} a_{23} b_3 r_1^2 + a_{12} a_{21} a_{23} b_3 r_1^2 - 3 a_{13} a_{21} a_{22} b_3 r_1^2 + a_{11} a_{22} a_{32} b_2 r_1^2 - 2 a_{12} a_{21} a_{32} b_2 r_1^2 + a_{12} a_{22} a_{31} b_2 r_1^2 \\
& + a_{21} a_{22} a_{31} b_1 r_1^2 + 2 a_{12} a_{21}^2 b_1 r_1 r_3 + 2 a_{12}^2 a_{21} b_2 r_1 r_3 - a_{12}^2 a_{31} b_2 r_1 r_2 - a_{11} b_1 b_3 r_1 r_2^2 + a_{12} b_2 b_3 r_1^2 r_2 \\
& + a_{21} b_1 b_3 r_1^2 r_2 - 2 a_{11} a_{12} a_{13} a_{21} a_{22} r_3 + a_{11} a_{12} a_{13} a_{21} a_{32} r_2 + a_{11} a_{12} a_{13} a_{22} a_{31} r_2 - 2 a_{11} a_{12} a_{21} a_{22} a_{33} r_1 \\
& + a_{11} a_{12} a_{21} a_{23} a_{32} r_1 + a_{11} a_{12} a_{22} a_{23} a_{31} r_1 + 2 a_{11} a_{13} a_{21} a_{22} a_{32} r_1 + 2 a_{12} a_{13} a_{21} a_{22} a_{31} r_1 - 2 a_{11} a_{12} a_{22} b_2 r_1 r_3 \\
& - 2 a_{11} a_{12} a_{23} b_3 r_1 r_2 + 2 a_{11} a_{13} a_{22} b_3 r_1 r_2 + 2 a_{12} a_{13} a_{21} b_3 r_1 r_2 - 2 a_{11} a_{21} a_{22} b_1 r_1 r_3 + a_{11} a_{12} a_{32} b_2 r_1 r_2 \\
& + a_{11} a_{21} a_{32} b_1 r_1 r_2 + a_{11} a_{22} a_{31} b_1 r_1 r_2 - 2 a_{12} a_{21} a_{31} b_1 r_1 r_2 \\
h_{(3,0)} = & r_3 a_{11}^2 a_{22}^2 r_1 - a_{32} a_{11}^2 a_{22} r_1 r_2 - 2 r_3 a_{11} a_{12} a_{21} a_{22} r_1 + a_{32} a_{11} a_{12} a_{21} r_1 r_2 + a_{31} a_{11} a_{12} a_{22} r_1 r_2 - b_3 a_{11} a_{12} r_1 r_2^2 \\
& + a_{32} a_{11} a_{21} a_{22} r_1^2 - a_{31} a_{11} a_{22}^2 r_1^2 + b_3 a_{11} a_{22} r_1^2 r_2 + r_3 a_{12}^2 a_{21}^2 r_1 - a_{31} a_{12}^2 a_{21} r_1 r_2 - a_{32} a_{12} a_{21}^2 r_1^2 \\
& + a_{31} a_{12} a_{21} a_{22} r_1^2 + b_3 a_{12} a_{21} r_1^2 r_2 - b_3 a_{21} a_{22} r_1^3
\end{aligned}$$

After finding the resultants, we evaluate  $T(f_1, f_2, f_3)$  (i.e, the determinant of the eliminating matrix) as well as  $J(f_1, f_2, f_3)$  (i.e, the determinant of the Jacobian of  $f_1, f_2$  and  $f_3$ ) which are shown below:

$$T(f_1, f_2, f_3) = \begin{vmatrix} T_{11} & T_{12} & T_{13} \\ T_{21} & T_{22} & T_{23} \\ T_{31} & T_{32} & T_{33} \end{vmatrix}, \quad J(f_1, f_2, f_3) = \begin{vmatrix} a_{11} & a_{12} + N_3 b_1 & a_{13} + N_2 b_1 \\ a_{21} + N_3 b_2 & a_{22} & a_{23} + N_1 b_2 \\ a_{31} + N_2 b_3 & a_{32} + N_1 b_3 & a_{33} \end{vmatrix}$$

Obtain the series expansion of the reciprocal of each resultant individually then multiply the results by  $T(f_1, f_2, f_3)J(f_1, f_2, f_3)$  to obtain

$$G(f_1, f_2, f_3) = \frac{T(f_1, f_2, f_3)J(f_1, f_2, f_3)}{\text{Res}_{N_1, N_2}(f_1, f_2, f_3)\text{Res}_{N_1, N_3}(f_1, f_2, f_3)\text{Res}_{N_2, N_3}(f_1, f_2, f_3)} = \frac{\Sigma_{0,0,0}}{N_1 N_2 N_3} + \frac{\Sigma_{1,0,0}}{N_1^2 N_2 N_3} + \frac{\Sigma_{0,1,0}}{N_1 N_2^2 N_3} + \frac{\Sigma_{0,0,1}}{N_1 N_2 N_3^2} + \frac{\Sigma_{1,1,0}}{N_1^2 N_2^2 N_3} + \frac{\Sigma_{1,0,1}}{N_1^2 N_2 N_3^2} + \frac{\Sigma_{0,1,1}}{N_1 N_2^2 N_3^2} + \frac{\Sigma_{2,0,0}}{N_1^3 N_2 N_3} + \frac{\Sigma_{0,2,0}}{N_1 N_2^3 N_3} + \dots$$

Without factorization, expressions of some of the  $\Sigma$ 's can extend to multiple pages. The expression for some of the lower  $\Sigma$ 's are shown below where  $\Sigma_{i,j,k} = \Sigma_{i,j,k}^U / \Sigma_{i,j,k}^D$  is written as a fraction of two polynomials.

$$\begin{aligned} \Sigma_{0,0,0}^U &= 5 \\ \Sigma_{0,0,0}^D &= 1 \end{aligned}$$

$$\begin{aligned} \Sigma_{1,0,0}^U &= a_{13}a_{21}b_3 - 2a_{11}a_{23}b_3 - 2a_{11}a_{32}b_2 + a_{12}a_{31}b_2 - a_{21}a_{31}b_1 - b_2b_3r_1 \\ \Sigma_{1,0,0}^D &= a_{11}b_2b_3 \end{aligned}$$

$$\begin{aligned} \Sigma_{0,1,0}^U &= a_{12}a_{23}b_3 - 2a_{13}a_{22}b_3 - a_{12}a_{32}b_2 + a_{21}a_{32}b_1 - 2a_{22}a_{31}b_1 - b_1b_3r_2 \\ \Sigma_{0,1,0}^D &= a_{22}b_1b_3 \end{aligned}$$

$$\begin{aligned} \Sigma_{0,0,1}^U &= a_{13}a_{32}b_2 - 2a_{12}a_{33}b_2 - a_{13}a_{23}b_3 - 2a_{21}a_{33}b_1 + a_{23}a_{31}b_1 - b_1b_2r_3 \\ \Sigma_{0,0,1}^D &= a_{33}b_1b_2 \end{aligned}$$

$$\begin{aligned} \Sigma_{1,1,0}^U &= a_{11}a_{12}a_{32}^2b_2^2 + a_{21}a_{22}a_{31}^2b_1^2 + a_{11}a_{13}a_{22}a_{23}b_3^2 - a_{11}a_{21}a_{32}^2b_1b_2 - a_{12}a_{22}a_{31}^2b_1b_2 \\ &\quad + 2a_{11}a_{12}a_{22}a_{33}b_2b_3 - a_{11}a_{12}a_{23}a_{32}b_2b_3 + a_{11}a_{13}a_{22}a_{32}b_2b_3 + 2a_{11}a_{21}a_{22}a_{33}b_1b_3 \\ &\quad + a_{11}a_{22}a_{23}a_{31}b_1b_3 - a_{13}a_{21}a_{22}a_{31}b_1b_3 + 4a_{11}a_{22}a_{31}a_{32}b_1b_2 - 4a_{11}a_{22}b_1b_2b_3r_3 \\ &\quad + a_{11}a_{32}b_1b_2b_3r_2 + a_{22}a_{31}b_1b_2b_3r_1 \end{aligned}$$

$$\Sigma_{1,1,0}^D = a_{11}a_{22}b_1b_2b_3^2$$

Observe that  $\text{Res}_{N_2, N_3}(f_1, f_2, f_3)$  is a polynomial of degree 5 in  $N_1$  only and thus cannot be solved analytically. Similarly,  $\text{Res}_{N_1, N_3}(f_1, f_2, f_3)$  and  $\text{Res}_{N_1, N_2}(f_1, f_2, f_3)$  are polynomials

of degree 6 in  $N_2$  and  $N_3$ . Note that the roots of the three resultants, upon appropriate pairing of roots of each of them, are the roots of the system  $f_i(N_1, N_2, N_3) = 0$  for  $i = 1, 2, 3$ . From Abel's impossibility theorem, since it is impossible to solve for the roots of a quintic or higher degree polynomials in terms of radicals, then the roots of any of the resultants are unattainable analytically which implies that the system  $f_i(N_1, N_2, N_3) = 0$  cannot be solved analytically. Since  $\Sigma_{0,0,0} = 5$ , then the system  $f_i(N_1, N_2, N_3) = 0$  for  $i = 1, 2, 3$  has exactly 5 complex roots. Denote to them by  $\boldsymbol{\eta}_1 = [\eta_{1,1}, \eta_{1,2}, \dots, \eta_{1,5}]^T$ ,  $\boldsymbol{\eta}_2 = [\eta_{2,1}, \eta_{2,2}, \dots, \eta_{2,5}]^T$  and  $\boldsymbol{\eta}_3 = [\eta_{3,1}, \eta_{3,2}, \dots, \eta_{3,5}]^T$ . Choose a map  $m(N_1, N_2, N_3) = [1, N_1, N_1N_2, N_1N_3, N_1N_2N_3]^T$ . Note that if we choose a lower order map such as  $m(N_1, N_2, N_3) = [1, N_1, N_2, N_3, N_1N_2]^T$ , one or more coefficients of the characteristic equation of  $S$  that will be shown in the following pages will vanish; thus a higher-order map is needed. Next, let  $Q(N_1, N_2, N_3) = N_1N_2N_3$  and compute  $S(s_1, s_2, s_3) = W\Delta W^t$  where  $W_{ij} = m_i(\eta_{1,j}, \eta_{2,j}, \eta_{3,j})$  and  $\Delta_{ii} = Q(\eta_{1,i} - s_1, \eta_{2,i} - s_2, \eta_{3,i} - s_3)$  is a diagonal matrix as follows.

$$W = \begin{bmatrix} 1 & 1 & 1 & 1 & 1 \\ \eta_{1,1} & \eta_{1,2} & \eta_{1,3} & \eta_{1,4} & \eta_{1,5} \\ \eta_{1,1}\eta_{2,1} & \eta_{1,2}\eta_{2,2} & \eta_{1,3}\eta_{2,3} & \eta_{1,4}\eta_{2,4} & \eta_{1,5}\eta_{2,5} \\ \eta_{1,1}\eta_{3,1} & \eta_{1,2}\eta_{3,2} & \eta_{1,3}\eta_{3,3} & \eta_{1,4}\eta_{3,4} & \eta_{1,5}\eta_{3,5} \\ \eta_{1,1}\eta_{2,1}\eta_{3,1} & \eta_{1,2}\eta_{2,2}\eta_{3,2} & \eta_{1,3}\eta_{2,3}\eta_{3,3} & \eta_{1,4}\eta_{2,4}\eta_{3,4} & \eta_{1,5}\eta_{2,5}\eta_{3,5} \end{bmatrix}$$

$$\Delta = \text{diag}[(\eta_{1,1} - s_1)(\eta_{2,1} - s_2)(\eta_{3,1} - s_3), \dots, (\eta_{1,5} - s_1)(\eta_{2,5} - s_2)(\eta_{3,5} - s_3)]$$

$$S(s_1, s_2, s_3) = W\Delta W^t$$

Note that  $\Sigma_{k,m,n} = \eta_{1,1}^k \eta_{2,1}^m \eta_{3,1}^n + \eta_{1,2}^k \eta_{2,2}^m \eta_{3,2}^n + \dots + \eta_{1,5}^k \eta_{2,5}^m \eta_{3,5}^n$  for  $k, m, n = 0, 1, 2, \dots$ . The components of the symmetric 5x5 matrix  $S$  are shown below:

$$\begin{aligned} S_{1,1}(s_1, s_2, s_3) &= (-5)s_1s_2s_3 + \Sigma_{001}s_1s_2 + \Sigma_{010}s_1s_3 + (-\Sigma_{011})s_1 + \Sigma_{100}s_2s_3 + (-\Sigma_{101})s_2 \\ &\quad + (-\Sigma_{110})s_3 + \Sigma_{111} \end{aligned}$$

$$\begin{aligned} S_{1,2}(s_1, s_2, s_3) &= (-\Sigma_{100})s_1s_2s_3 + \Sigma_{101}s_1s_2 + \Sigma_{110}s_1s_3 + (-\Sigma_{111})s_1 + \Sigma_{200}s_2s_3 + (-\Sigma_{201})s_2 \\ &\quad + (-\Sigma_{210})s_3 + \Sigma_{211} = S_{2,1}(s_1, s_2, s_3) \end{aligned}$$

$$\begin{aligned} S_{1,3}(s_1, s_2, s_3) &= (-\Sigma_{110})s_1s_2s_3 + \Sigma_{111}s_1s_2 + \Sigma_{120}s_1s_3 + (-\Sigma_{121})s_1 + \Sigma_{210}s_2s_3 + (-\Sigma_{211})s_2 \\ &\quad + (-\Sigma_{220})s_3 + \Sigma_{221} = S_{3,1}(s_1, s_2, s_3) \end{aligned}$$



$$S_{1,4}(s_1, s_2, s_3) = (-\Sigma_{101})s_1s_2s_3 + \Sigma_{102}s_1s_2 + \Sigma_{111}s_1s_3 + (-\Sigma_{112})s_1 + \Sigma_{201}s_2s_3 + (-\Sigma_{202})s_2 \\ + (-\Sigma_{211})s_3 + \Sigma_{212} = S_{4,1}(s_1, s_2, s_3)$$

$$S_{1,5}(s_1, s_2, s_3) = (-\Sigma_{111})s_1s_2s_3 + \Sigma_{112}s_1s_2 + \Sigma_{121}s_1s_3 + (-\Sigma_{122})s_1 + \Sigma_{211}s_2s_3 + (-\Sigma_{212})s_2 \\ + (-\Sigma_{221})s_3 + \Sigma_{222} = S_{5,1}(s_1, s_2, s_3)$$

$$S_{2,2}(s_1, s_2, s_3) = (-\Sigma_{200})s_1s_2s_3 + \Sigma_{201}s_1s_2 + \Sigma_{210}s_1s_3 + (-\Sigma_{211})s_1 + \Sigma_{300}s_2s_3 + (-\Sigma_{301})s_2 \\ + (-\Sigma_{310})s_3 + \Sigma_{311}$$

$$S_{2,3}(s_1, s_2, s_3) = (-\Sigma_{210})s_1s_2s_3 + \Sigma_{211}s_1s_2 + \Sigma_{220}s_1s_3 + (-\Sigma_{221})s_1 + \Sigma_{310}s_2s_3 + (-\Sigma_{311})s_2 \\ + (-\Sigma_{320})s_3 + \Sigma_{321} = S_{3,2}(s_1, s_2, s_3)$$

$$S_{2,4}(s_1, s_2, s_3) = (-\Sigma_{201})s_1s_2s_3 + \Sigma_{202}s_1s_2 + \Sigma_{211}s_1s_3 + (-\Sigma_{212})s_1 + \Sigma_{301}s_2s_3 + (-\Sigma_{302})s_2 \\ + (-\Sigma_{311})s_3 + \Sigma_{312} = S_{4,2}(s_1, s_2, s_3)$$

$$S_{2,5}(s_1, s_2, s_3) = (-\Sigma_{211})s_1s_2s_3 + \Sigma_{212}s_1s_2 + \Sigma_{221}s_1s_3 + (-\Sigma_{222})s_1 + \Sigma_{311}s_2s_3 + (-\Sigma_{312})s_2 \\ + (-\Sigma_{321})s_3 + \Sigma_{322} = S_{5,2}(s_1, s_2, s_3)$$

$$S_{3,3}(s_1, s_2, s_3) = (-\Sigma_{220})s_1s_2s_3 + \Sigma_{221}s_1s_2 + \Sigma_{230}s_1s_3 + (-\Sigma_{231})s_1 + \Sigma_{320}s_2s_3 + (-\Sigma_{321})s_2 \\ + (-\Sigma_{330})s_3 + \Sigma_{331}$$

$$S_{3,4}(s_1, s_2, s_3) = (-\Sigma_{211})s_1s_2s_3 + \Sigma_{212}s_1s_2 + \Sigma_{221}s_1s_3 + (-\Sigma_{222})s_1 + \Sigma_{311}s_2s_3 + (-\Sigma_{312})s_2 \\ + (-\Sigma_{321})s_3 + \Sigma_{322} = S_{4,3}(s_1, s_2, s_3)$$

$$S_{3,5}(s_1, s_2, s_3) = (-\Sigma_{221})s_1s_2s_3 + \Sigma_{222}s_1s_2 + \Sigma_{231}s_1s_3 + (-\Sigma_{232})s_1 + \Sigma_{321}s_2s_3 + (-\Sigma_{322})s_2 \\ + (-\Sigma_{331})s_3 + \Sigma_{332} = S_{5,3}(s_1, s_2, s_3)$$

$$S_{4,4}(s_1, s_2, s_3) = (-\Sigma_{202})s_1s_2s_3 + \Sigma_{203}s_1s_2 + \Sigma_{212}s_1s_3 + (-\Sigma_{213})s_1 + \Sigma_{302}s_2s_3 + (-\Sigma_{303})s_2 \\ + (-\Sigma_{312})s_3 + \Sigma_{313}$$

$$S_{4,5}(s_1, s_2, s_3) = (-\Sigma_{212})s_1s_2s_3 + \Sigma_{213}s_1s_2 + \Sigma_{222}s_1s_3 + (-\Sigma_{223})s_1 + \Sigma_{312}s_2s_3 + (-\Sigma_{313})s_2 \\ + (-\Sigma_{322})s_3 + \Sigma_{323} = S_{5,4}(s_1, s_2, s_3)$$

$$S_{5,5}(s_1, s_2, s_3) = (-\Sigma_{222})s_1s_2s_3 + \Sigma_{223}s_1s_2 + \Sigma_{232}s_1s_3 + (-\Sigma_{233})s_1 + \Sigma_{322}s_2s_3 + (-\Sigma_{323})s_2 \\ + (-\Sigma_{332})s_3 + \Sigma_{333}$$

The characteristic equation of the matrix  $S$  is simply  $\det(S(s_1, s_2, s_3)) = \lambda^5 + v_4(s_1, s_2, s_3)\lambda^4 + v_3(s_1, s_2, s_3)\lambda^3 + v_2(s_1, s_2, s_3)\lambda^2 + v_1(s_1, s_2, s_3)\lambda + v_0(s_1, s_2, s_3)$ . The coefficients of the characteristic equation need to be evaluated at  $(s_1, s_2, s_3) = \{(0, 0, 0), (\infty, 0, 0), (0, \infty, 0),$

$(\infty, \infty, 0), (0, 0, \infty), (\infty, 0, \infty), (0, \infty, \infty), (\infty, \infty, \infty)\}$ . Note that  $v_i(m_1, m_2, m_3)$  where  $m_1, m_2, m_3 \in \{0, \infty\}$  is the coefficient of  $s_1^{k_1} s_2^{k_2} s_3^{k_3}$  in  $v_i(s_1, s_2, s_3)$  where  $k_j = 0$  if  $m_j = 0$  and  $k_j = 5 - i$  if  $m_j = \infty$  for  $j = 1, 2, 3$ . Since some of these 40 quantities are large, we will omit writing them. Next, let  $V(a, b, c)$  be the number of consecutive sign changes in  $[1, v_1(a, b, c), v_0(a, b, c)]$  where  $a, b$  and  $c$  are either 0 or  $\infty$ . The formula of  $V(a, b, c)$  is shown below

$$V(a, b, c) = \frac{1 - \text{sign}(v_4(a, b, c))}{2} + \frac{1 - \text{sign}(v_4(a, b, c))\text{sign}(v_3(a, b, c))}{2} + \frac{1 - \text{sign}(v_3(a, b, c))\text{sign}(v_2(a, b, c))}{2} \\ + \frac{1 - \text{sign}(v_2(a, b, c))\text{sign}(v_1(a, b, c))}{2} + \frac{1 - \text{sign}(v_1(a, b, c))\text{sign}(v_0(a, b, c))}{2} \quad \text{where } a, b, c \in \{0, \infty\}$$

From the  $V$ 's, we can find the formula of the number of feasible roots of  $f_1(N_1, N_2, N_3)$ ,  $f_2(N_1, N_2, N_3)$  and  $f_3(N_1, N_2, N_3)$  which is given by  $F(\Psi) = (V(0, 0, 0) - V(\infty, 0, 0) - V(0, \infty, 0) - V(0, 0, \infty) + V(\infty, \infty, 0) + V(\infty, 0, \infty) + V(0, \infty, \infty) - V(\infty, \infty, \infty))/4$ . Let us consider the parameter  $\Psi = (r_1, r_2, r_3, a_{11}, a_{12}, a_{13}, a_{21}, a_{22}, a_{23}, a_{31}, a_{32}, a_{33}, b_1, b_2, b_3) = (1.5, -1.5, -1.5, 2, -1.5, -1.5, a_{21}, 2, -1.5, -1.5, -1, 1, 1, -1, b_3)$  where the parameters  $a_{21} \in [1, 6]$  and  $b_3 \in [2, 5]$  are restricted. We find that feasibility (i.e,  $F(\Psi) \geq 1$ ) is described by the signs of the  $v_0$ 's. In particular, if any of the conditions below is satisfied, feasibility is guaranteed, which is evident from plotting any of the quantities below (except  $v_0(0, 0, 0) < 0$  (see below)).

$$v_0(0, 0, 0) < 0 \quad v_0(\infty, 0, 0) < 0, \quad v_0(0, \infty, 0) > 0, \quad v_0(\infty, \infty, 0) > 0 \\ v_0(0, 0, \infty) > 0, \quad v_0(\infty, 0, \infty) > 0, \quad v_0(0, \infty, \infty) < 0, \quad v_0(\infty, \infty, \infty) < 0$$

When we plot  $F(\Psi)$ , we find that in some regions, some non-integer values between 0 and 2 are output due to numerical error or  $m(N_1, N_2, N_3)$  having lower order monomial maps. However, we rectified the error quickly via assigning non-integer values to their closest integers. After the rectification process, we obtained a feasibility domain plot that matches the one obtained from simulations (i.e, counting the number of feasible equilibrium points via solving the isocline equations numerically). There was no need to perform any numerical corrections when we plot the sign of  $v_0(0, \infty, 0)$  or any of the 8 inequalities above (except  $v_0(0, 0, 0) < 0$ ) and we see that it matches the feasibility domain as shown in the plots in the following page. When we plot  $v_0(0, 0, 0) < 0$ , its shape has clearly the shape of the feasibility domain but has errors that are rectifiable.

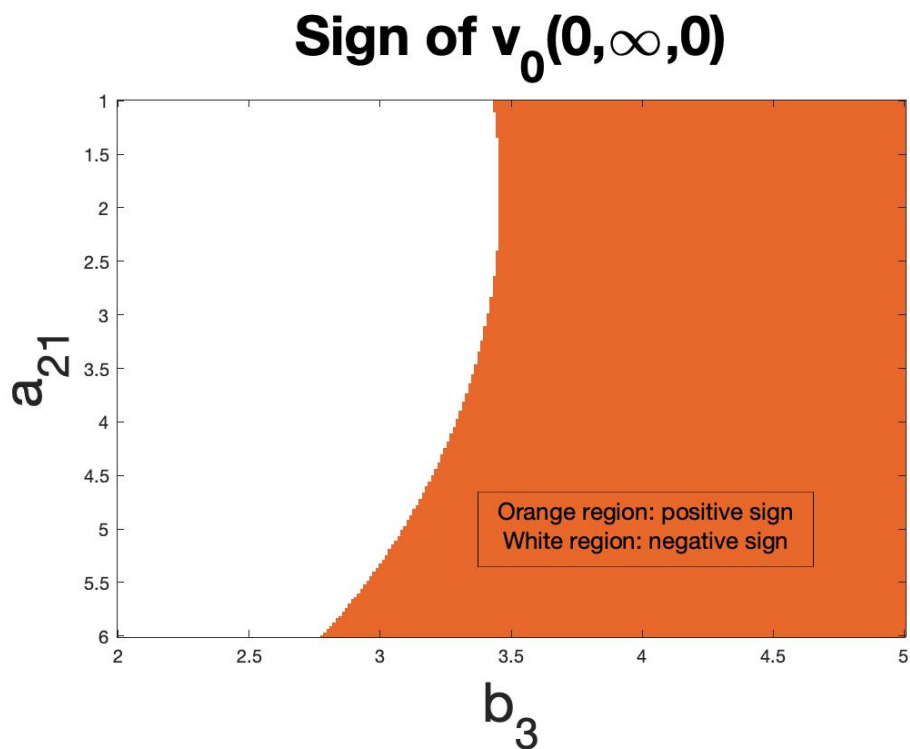
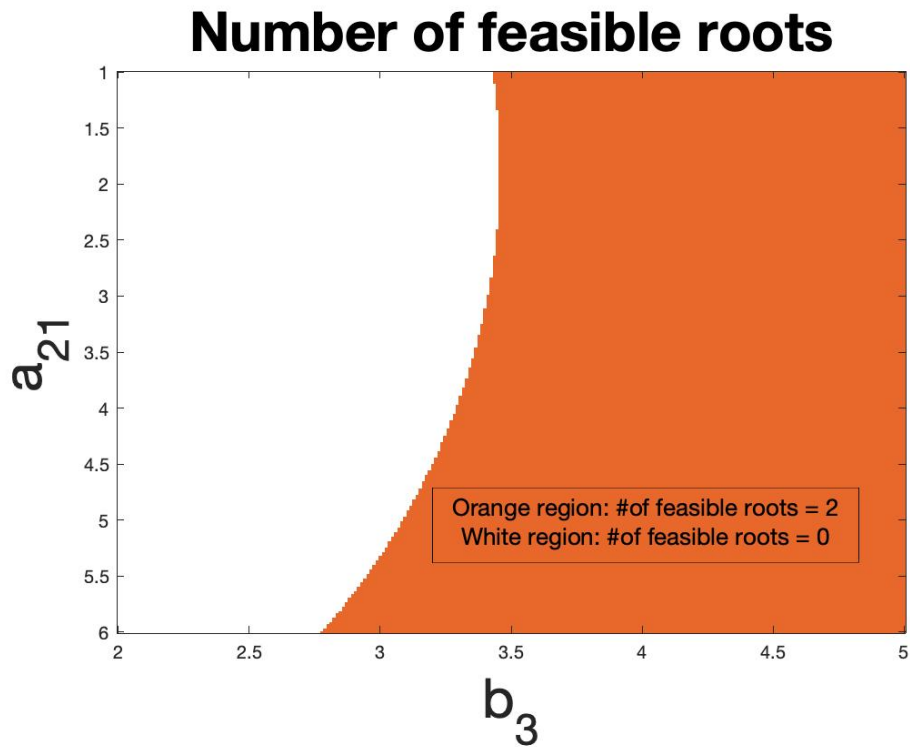


Figure 4-3: The top figure shows the number of feasible roots  $F$  in Lotka-Volterra model with higher-order interactions where  $(r_1, r_2, r_3, a_{11}, a_{12}, a_{13}, a_{22}, a_{23}, a_{31}, a_{32}, a_{33}, b_1, b_2) = (1.5, -1.5, -1.5, 2, -1.5, -1.5, 2, -1.5, -1.5, -1, 1, 1, -1)$ ,  $a_{21} \in [1, 6]$  and  $b_3 \in [2, 5]$ . The bottom figure shows the sign of  $v_0(0, \infty, 0)$  with the same model and parameter values and ranges. Both figures confirm that  $F > 0$  when  $v_0(0, \infty, 0) > 0$ . Simulations done via solving the isocline equations numerically and checking for the feasibility of roots match the two figures displayed here.

## Sign of $v_0(0,0,0)$

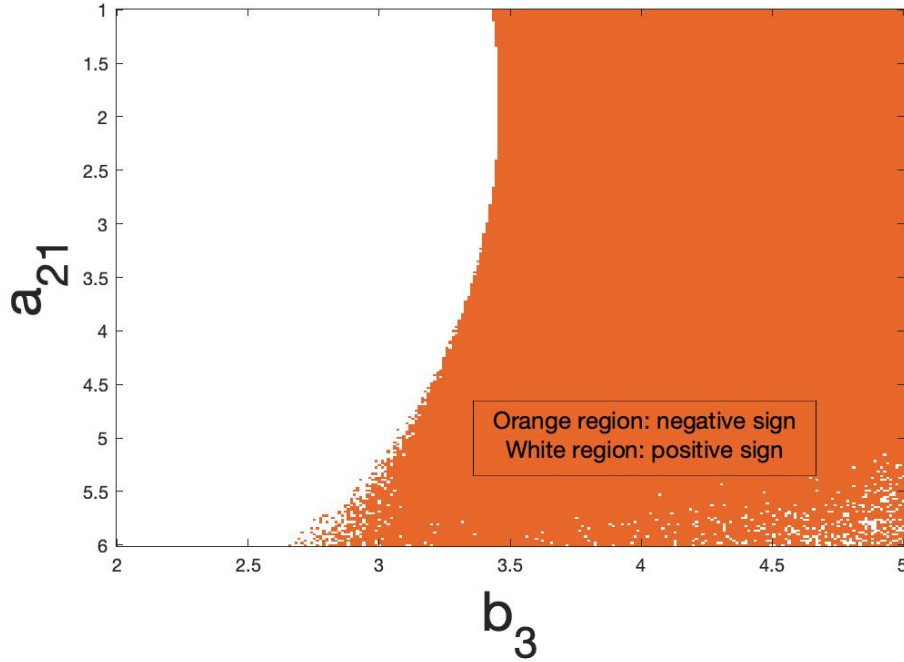


Figure 4-4: The figure plots the sign of  $v_0(0,0,0)$  in Lotka-Volterra model with higher-order interactions when  $(r_1, r_2, r_3, a_{11}, a_{12}, a_{13}, a_{22}, a_{23}, a_{31}, a_{32}, a_{33}, b_1, b_2) = (1.5, -1.5, -1.5, 2, -1.5, -1.5, 2, -1.5, -1.5, -1, 1, 1, -1)$ ,  $a_{21} \in [1, 6]$  and  $b_3 \in [2, 5]$ . The shape of the figure matches the shape of the feasibility domain, yet suffers from errors.

## 4.5 Discussion

Feasibility conditions can be obtained analytically by solving the isocline equations for species abundances  $\mathbf{N}^* = (N_1^*, N_2^*, \dots, N_n^*)^T$  before imposing the positivity condition  $\mathbf{N}^* > \mathbf{0}$ . This approach works well for LV model, whose isocline equations is the linear system  $\mathbf{r} + \mathbf{A}\mathbf{N}^* = \mathbf{0}$  and whose feasibility conditions are given by  $\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{r} > \mathbf{0}$  [18, 106, 119]. However, when the isocline equations have five or more complex roots, the system of polynomial equations cannot be solved analytically. This is a consequence of Grobner elimination theorem combined with Abel's impossibility theorem [112–114]. Specifically, from the elimination theorem, in any system of polynomial equations which has  $\Theta$  complex roots and  $n$  variables, any  $n - 1$  variables can be eliminated from the system to obtain a univariate polynomial with the remaining variable of degree at least  $\Theta$ . The roots of this univariate polynomial are all the correspondent coordinates of the roots of the isocline equations [114]. This is a generalization of Gaussian elimination, which can eliminate any  $n - 1$  variables from the system leaving a single linear univariate polynomial

in the remaining variable to be solved [120]. However, from Abel's impossibility theorem, it is impossible to solve a univariate polynomial in terms of radicals (i.e., analytically) [112, 113] if this polynomial has five or more roots. For instance, this number of roots is quickly reached by adding Type III functional responses to a 2-species LV model or adding higher-order interactions to a 3-species LV model [81].

In this work, we have proposed a general formalism to analytically obtain the feasibility conditions for any multivariate, polynomial, population, dynamics model of any dimensions without the need to solve for the equilibrium locations. We found that feasibility conditions are entirely functions of symmetric sums of the roots of the isocline equations. Unlike the location of the roots, which cannot be obtained analytically, symmetric sums of the roots can be obtained for any polynomial system regardless of order and dimension. We have also created an analytical formula of the number of feasible roots in the system, which are functions of signs of  $\Theta 2^n$  quantities (i.e., the  $v$ 's evaluated at the feasibility box whose coordinates compose of zeros and infinities). We have shown how to create a feasibility table (i.e., matrix) whose columns are the individual feasibility conditions of the model. We have then provided a minimization process that can combine feasibility conditions into fewer ones and remove redundant quantities. Of course, the expressions involved in the inequality are complicated, nevertheless, they can be significantly simplified by sophisticated factorization.

Additionally, we have shown how to provide feasibility conditions under parameter restrictions. We have shown that by restricting parameters, the feasibility domain can be described by a single inequality only. In recent years, the topic of feasibility has been focused on relationships between parameters while maintaining feasibility [61]. Using simulations (i.e., solving for the location of the isocline equations numerically then checking for the feasibility of roots) one can plot the feasibility domain for one, two, or three parameters at most while fixing the remaining ones. However, it is impossible to generate a four-dimensional plot that the human eye can capture. Also, it is impossible to find an analytical expression of the feasibility domain using numerical simulations. Of course, someone can find an approximate formula of the feasibility domain, nevertheless, there is no unique formula and different approximations may lead to different interpretations of how parameters are linked while maintaining feasibility. Following our proposed methodology, we can determine mathematically how any number of parameters are linked by describ-

ing polynomial inequalities that are functions of those free-parameters while maintaining feasibility: a task that is impossible to perform with simulations. This is an important property to consider in ecological modeling given that mathematical expressions are frequently formed assuming that parameters are independent of each other. However, once one imposes mechanisms or constraints, such as feasibility, these parameters can be linked and break the conclusions based on independent parameters [101].

Our methodology provides a fast method for plotting feasibility domains, computing the number of feasible roots, and displaying feasibility conditions. For example, for our 3-species example with higher-order interactions, plotting the feasibility domain by solving the isocline equations numerically using the software package PHCLab [93] took more than 1.5 hours to compute the number of feasible points with  $2^{16}$  trials. Instead, using our methodology (and code which involves a naive implementation of our methodology without parallelization), it took less than 11.5 minutes to run the analysis, and a few seconds to plot the feasibility domain for different ranges of the free parameters using the same number of trials. Moreover, when we change the ranges of our free parameters  $a_{21}$  and  $b_3$ , we only need a few seconds to run our code, whereas we need to repeat the entire 1.5 hours with the traditional numerical technique. With a clever implementation of the methodology and parallelizing the code (since the entire methodology can be parallelized), a faster computation of the feasibility domain/conditions and links between parameters can be achieved.

One significant drawback of the methodology is that it requires the handling of large symbolic expressions. Thus, careful implementation is required to run a successful code using the presented methodology. For example, when we created the generating function  $G$ , we did not multiply the determinant of the eliminant  $T$  and the determinant of the Jacobian of the isocline equations  $J$ , divided them by the product of all resultants, and took the series expansion of the final polynomial quotient. Instead, we took the series expansion of each resultant reciprocal separately, wrote  $TJ$  as multivariate polynomial in species abundances, found the coefficients of each term, and multiplied it by a single appropriate term in the series expansion of each resultant reciprocal to find the  $\Sigma$ 's. However, it is always possible to handle such large expressions as the entire methodology can be parallelized. The second drawback of the methodology is its susceptibility to numerical errors. In our 3-species application example, our code gives as output non-integer values of the number

of feasible roots in the system. Nevertheless, in our example we rectified it quickly by assigning non-integer values to their closest integers (see section 4.4.2). Remember that the methodology requires only checking signs of large symbolic expressions, and we do not need them to be computed accurately. Nevertheless, such quantities can be computed more accurately by following several techniques such as increasing precision of numeric calculations. Similarly, cancellation errors can be reduced by combining positive numbers and negative ones together, and then performing a single subtraction. Round-off and truncation errors can also be avoided when ratios are computed. For example, instead of computing  $(10^{90} - 10^{91})/10^{90}$  by computing  $(10^{90} - 10^{91})$  then dividing the result by  $10^{90}$ , it is better to add  $10^{90}/10^{90} = 1$  with  $-10^{91}/10^{90} = -10$  as the latter reduces round-off errors in large computations [121]. Of course, there are other techniques to reduce such errors, nevertheless, it is important to think about numerical errors in the implementation process.

In sum, the contribution of this theoretical work is that it provides a foundation for important ecological concepts such as species coexistence, stability, and permanence. Indeed, it has been shown that the existence of a feasible solution is a necessary condition for persistence and permanence in dynamical models of the form  $dN_i/dt = N_i f_i(\mathbf{N})/q_i(\mathbf{N})$  [41, 51]. Similarly, it has been proved that this type of models cannot have bounded orbits in the feasibility domain without a feasible free-equilibrium point [41]. In fact, we cannot talk about asymptotic or local stability without the existence of a feasible equilibrium point [115]. Hence, coexistence, stability, or permanence domains are subsets of the feasibility domain and their conditions are effectively the feasibility conditions obtained in this work plus some added conditions. Thus, this work unlocks the opportunity to increase our systematic understanding of multispecies coexistence.





# Chapter 5

## Conclusions and Future Work

### 5.1 Conclusions

Lotka-Volterra (LV) models have been a pillar in the field of ecology [18, 30]. Yet, these models are first-order approximations that do not fully encapsulate the complex dynamics of ecological systems, such as the existence of multiple equilibria or alternative states [33, 49, 81]. This is attributed to the fact that the number of free-equilibrium points of LV models is always one regardless of the dimension of the system, making it a limited yet tractable model [53]. Recent work has shown that higher-order terms in population dynamics models can increase stability, promote diversity, and better explain the dynamics of ecological systems [43–46]. While it has been speculated that these perceived benefits come from an increasing number of alternative solutions given by the nature of multivariate polynomials, this mathematical advantage had not been formally quantified. In the Chapter 2 of this thesis, we have developed a general method to quantify the mathematical consequences of adding higher-order terms in ecological models based on the number of *free-equilibrium* points that can emerge in a system. These equilibria can be feasible or unfeasible as a function of model parameters. For a generic choice of parameters, the number of free-equilibrium points is independent of model parameters. Thus, this number (which is parameter-free) is a suitable measure of modeling complexity and advantages for LV models with higher-order interactions since higher-order parameters are seldom restricted (or known). We have applied this method to calculate the number of free-equilibrium points in LV dynamics analytically. While it is known that LV models without higher-order in-

interactions have only one free-equilibrium point regardless of the number of parameters [53], we find that by adding higher-order terms, this number increases exponentially with the dimension of the system. Hence, we have shown that the number of free-equilibrium points can be used to compare more fairly between ecological models. Our results suggest that while adding higher-order interactions in ecological models may be suitable for prediction purposes, they cannot provide additional explanatory power of ecological dynamics if model parameters are not ecologically restricted or if results are not compared against random expectations. That is, our results do not invalidate complex models, but provides a clear roadmap and best practices for ecological modeling.

Due to the simplicity of LV models, studies have embedded more mechanisms into them for the premise of adding realism and dynamical richness [11]. Nevertheless, finding a compromise between tractability and realism has not been easy [77–79]. The introduction of nonlinear functional responses in 2-species models has reconciled part of this compromise [10, 11, 35, 48]. However, it had remained unclear whether this compromise could be extended to multispecies models [72, 81]. Yet, answering this question was necessary to differentiate whether the explanatory power of a model comes from the general form of its polynomial or a more realistic description of multispecies systems. In the Chapter 3 of this thesis, we have studied the probability of feasibility (the existence of at least one positive real equilibrium) in complex models by adding higher-order interactions and nonlinear functional responses to the linear LV model. We characterize complexity by the number of free-equilibrium points generated by a model, a function of the polynomial degree, and the system’s dimension. We have shown that the probability of generating a feasible system in a model is an increasing function of its complexity, regardless of the specific mechanism invoked and whether parameters are restricted or not. Furthermore, we find that the probability of feasibility in a model will exceed that of the linear LV model when a minimum level of complexity is reached. Significantly, this minimum level is modulated by parameter restrictions but can always be exceeded via increasing the polynomial degree or system’s dimension. These results confirm our results from Chapter 2, showing that conclusions regarding the relevance of mechanisms embedded in complex models must be evaluated against the expected explanatory power of their polynomial form.

Nevertheless, when an ecological model is constructed, understanding its behavior in full (e.g., analytically) remains one of the significant challenges in ecological research [10–12].

Most ecological systems are coupled polynomial ordinary differential equations, which are generally unsolvable and challenging to analyze, except for particular cases that simplify the model [122–124]. Without the availability of such solutions, extracting the set of conditions compatible with the coexistence of such species remains a big mathematical challenge [49, 61]. Even at the 2-species level, there is currently no general methodology that can provide us with a complete analytical understanding of feasibility conditions (i.e., necessary conditions for species coexistence in equilibrium dynamics) for any given model. Knowledge of feasibility is essential as feasibility is a necessary condition for coexistence in equilibrium dynamics, stability, and permanence [41, 119]. Traditionally, feasibility conditions are found by solving the isocline equations analytically for species abundances (equilibrium points) before imposing a positivity of at least one equilibrium point [61]. However, solving the location of equilibrium points analytically is impossible if the isocline equations have five or more roots, which is a consequence of Abel’s impossibility theorem [112, 113]. In Chapter 4 of this thesis, we have strayed away from this traditional approach and use tools from algebraic geometry to identify and separate feasibility conditions that guarantee exactly  $k$  feasible equilibrium points for any value  $k$  of a model system. We show that these feasibility conditions are always represented by polynomial inequalities in species abundances. We demonstrate that feasibility and infeasibility conditions are represented by identical polynomial expressions, whose signs determine the number of feasible equilibrium points in the system. We have shown a general methodology to express the derived feasibility conditions into the smallest minimal mathematical expressions to easily (as much as possible) analyze them. Additionally, we have illustrated the power of our methodology by showing how it is possible to derive mathematical relationships between model parameters while maintaining feasibility in modified LV models with functional responses and higher-order interactions (model systems with at least five equilibrium points)—a task that is impossible to do with simulations. Note that exact relationships between parameters is a necessary condition to know in order to reach a more mechanistic or causative knowledge of ecological systems. These results unlock a previous impossible analytic task towards our understanding of species coexistence. Overall, we hope these contributions can serve as a guideline for a more comprehensive use of ecological modeling and the advancement of mathematical ecology in general.

## 5.2 Future Work

In this thesis, we borrowed tools from algebraic geometry to study polynomial ecological dynamical systems. The main goal of this work has been directed towards understanding the conditions leading to species coexistence. In particular, we have studied the necessary conditions: feasibility. The necessary and sufficient conditions (feasibility and stability) have not been addressed in this thesis. Indeed, finding the sets of conditions that guarantee the stability of at least one free-equilibrium point remains an open problem. For LV models, as mentioned in the introduction section of Chapter 4, feasibility conditions are known and can be attained analytically in closed-form. However, for the linear Lotka-Volterra model with a single free-equilibrium point, necessary and sufficient conditions for asymptotic stability are unknown [125]. Since feasibility is a necessary condition for asymptotic stability, the stability domain must be contained in the feasibility domain. Therefore, stability conditions only require additional conditions to be placed on top of feasibility to obtain them. In this line, future work can focus on finding necessary and sufficient conditions for stability for LV models and extending the techniques to general polynomial ecological systems. On top of stability, permanence is one of the essential ecological concepts that has been studied in the literature. In permanence, starting from any initial condition, bounded abundances must be attained after a sufficiently large time, and that bound is independent of the initial value [126, 127]. However, conditions of permanence in ecological systems are unknown, and no link between stability and permanence has been studied either [127]. Therefore, it also remains to investigate conditions of permanence for the LV system, link it to the asymptotic stability of its unique free-equilibria, and extend the work for a general polynomial system.

Moreover, this thesis has focused on polynomial ecological dynamical systems with a finite number of free-equilibrium points. However, non-polynomial systems also appear in the ecological literature. For instance, stochastic Lotka-Volterra systems have square-root terms embedded into them, and exponential functions appear in less-popular functional responses. For example, it was demonstrated that stochasticity can provide a dynamical model with many marginally stable equilibrium points [128]. Nevertheless, when nonlinear functions are introduced, such as the exponential or trigonometric function, the number of free-equilibrium points can be infinite. This is evident by the infinite number of roots

of the function  $\sin(z)$  which are given by  $z = \pi n$  where  $n \in \mathbb{Z}$ . This phenomenon of an infinite number of roots cannot happen in polynomial systems. As a consequence, the feasibility table derived in Chapter 4 can be infinitely long when nonlinear functions are incorporated into ecological systems. Hence, the mathematical consequences that we have shown in this thesis for polynomial systems can be easily surpassed when non-monomials are added to ecological models. This could help us to rethink when and how this highly complex functions should be used. However, if such functions are believed to be an integral part of a model, then as future work, one can ask: how can we characterize the complexity of non-polynomial ecological systems, and how can we fairly compare between two non-polynomial models? Will it be possible to obtain the feasibility domains of such models? Dissecting these systems, which are currently treated as black boxes, will help us to use ecological models in a more rigorous and informative way.



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