The Effect of Different Definitions of Community Matrix on the Stability of Ecological Networks

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Abstract

Network models are used to analyse the stability of ecological communities. In this research we used the competitive Lotka-Volterra model for a community of two, three and four species to demonstrate the relationship between complexity and stability in ecological networks. We have based this on four different matrix methods for analysing the interaction data. The data set represents the interaction among species, which we generated from random normal distributions with different standard deviations. The four matrix methods used are Jacobian, Interaction strength (Alpha), Encounter and Competition matrix. The results highlight the different complexity-stability relationships emerging from the four different definitions of the community matrix.

يتم استخدام نماذج الشبكات في تحليل مدي إستقرار مجتمع ما. لقد قمنا في هذا البحث بإستخدام نموذج لوتكا فولتيرا لمجتمعات تحتوى علي اثنان، ثلاثة او اربعة عنصار تتنافس علي نفس المورد. البيانات المستخدمة في التحليل تم إستخراجها عشوائيا من التوزيع الطبيعي حيث، الصفر هو متوسط البيانات مقابل اي إنحراف معياري يتم اختياره. تم استخدام أربعة أنواع من المصفوفات و التي عادة ماتسخدم في تحليل الاستقرار بالنسبة مجتمع ما. المصفوفات المستخدمة هي مصفوفة الجاكوبيان، مصفوفة الفا، مصفوفة المنافسة و مصفوفة المواجهة.

Declaration

I, the undersigned, hereby declare that the work contained in this research project is my original work, and that any work done by others or by myself previously has been acknowledged and referenced accordingly.

Asmaa Omer Tiraab Tbaeen, 18 May 2017

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1. Introduction

One of the major problems in ecological studies is how to understand the stability of ecological communities, and how the stability affected by the structural properties (community size or diversity, strength of interactions, etc.) particular to each community [Landi et al. (2017)]. The growth and decline of each species in the network is influenced by self interactions, interactions with other species and with its constantly-changing environment. This movement induces a different response for each species in the community, which in turn affects both the environment and the other members of the community. Large real world communities are highly complex and interconnected. May showed in (1972) that such communities tend to be unstable [May (1972)].

The rate at which species go extinct does not appear to be very high in real world communities. Whenever there is a shift in species density, it will affect the stability state of the ecological community [May (1972)]. We will study the stability of populations using a competitive Lotka-Volterra model of ecological population dynamics considering n interacting species in the community. Lotka-Volterra model describes the ecological network using a system of differential equations. The matrices used to analyse the network structure are quite different both in their mathematical construction and in their ecological motivation. We use random number generation for the interaction strength and we will show the variation in these matrices and their corresponding stability results in our modelled network [Novak et al. (2016)].

The Jacobian (community) matrix is one of the most popular methods used to determine the stability of dynamic models. May's [May (1971)] work relies on random matrices. He studies the stability of the non-linear differential equations using the Jacobian method, to examine a large number of interacting species in a community [May (1972)]. May's argument is that large communities may not be stable [May (1972)] contrary to previous work by [Gardner and Ashby (1970)]. For maintaining ecological networks, the interactions between the members of the community are very important. There are few strong interactions in the real networks, where most of the interactions are weak [Berlow (1999)]. In this research, we assume that all pairs of the species in the community have at least some level of interaction between them. Also we consider models with two, three or four species' in the community. And the stability criteria is dependent on the sign of the largest real part of the eigenvalues of the matrix. The empirical analysis is based on 100 randomly-generated communities, with interaction strengths sampled from a normal random distribution with different standard deviations. To analyse the data we used theoretical investigation and python.

We start by introducing some terminologies of ecological networks and dynamic systems in Chapter 2. In Chapter 3 we define the matrices that have been used for the stability analysis, and in Chapter 4 we summarise the numerical result.

2. Ecological Networks

2.1 Ecological Network Dynamics

An ecological network, also known as a trophic web, usually starts with primary producers such as plants. They make up the first level of the network. In the next level are the herbivores, which are animals that eat plants, such as cows, sheep and caterpillars. The third level consists of predators, such as lions, and in the last levels are carnivores or apex predators e.g, snakes such as anacondas. The ecological network structures vary through time. The interactions between the species very important to maintain natural ecosystem diversity. These dynamics change the state of the network (species abundance and the connectivity between the species). Each species has a population dependent per capita growth rate. In this case we can describe the population dynamics using a system of differential equations of the form

$$\frac{dN_i}{dt} = F_i(N_1, N_2, ..., N_n, t), \qquad i = 1, 2, ..., n, \tag{2.1.1}$$

where:

- $N_i \equiv$ the density of species i in the ecological Community.

2.1.1 The Interactions Classification in the Ecological Networks. In an ecological network, each organism interacts with its environment and with other organisms in the community. There are several types of interactions between species that live as a community(ecosystem), as it shown in Table 2.1.

Interactions type	Specie 1	Specie 2
mutualism	$+$	$+$
competition	$-$	$-$
commensalism	$+$	0
parasitism, predation	$+$	$-$

Table 2.1: The different interaction types. Positive sign indicates a benefit to the species, while the negative sign indicates a suffering species.

In mutualistic interactions (such as plants and pollinating insects) both species are benefiting from their relationship, so the interaction coefficients of both are positive. On the other hand, in competition interactions (for example rabbits and sheep competing for food) both species are suffering from the interaction (for the sheep it is better to forage without rabbits present) and the interaction coefficients are negative for both species (see Table 2.1).

In this research, we focus on competition interactions representing two or more species competing for the same resources. We use the Lotka-Volterra model as a case study to see how the diversity of the network can effect the network stability (see Chapter 3).

2.1.2 Ecological Networks. An ecological networks, used to model the interactions between species in a biological community. An ecological network is characterised by a set of n node representing species and a set of L links representing the interactions between species. The description of the ecological network can be simplified as a square $n \times n$ matrix. We focus on specific examples of these matrices, the Jacobian matrix, interaction strength (Alpha) matrix, Encounter matrix and Competition matrix. The interaction matrix elements characterise the relationship between each pair of species, with a_{ij}

representing the effect of species i on species j. The strengths of the interactions can be weighted, unweighted (uniform), directed (one-way) or undirected in the network. The interaction strength matrix is symmetric when the network is undirected (i.e, $a_{i,j} = a_{j,i}$), as shown in Figure 2.2. Symmetric can be weighted or unweighted.

2.1.1 Example. The interaction strengths in Figure 2.1 are directed and unweighted; we denote the relation between each pair species by (present $= 1$, absent $= 0$). In this case the elements of the community matrix are 0 or 1 and we can construct the interaction strength matrix from the network.

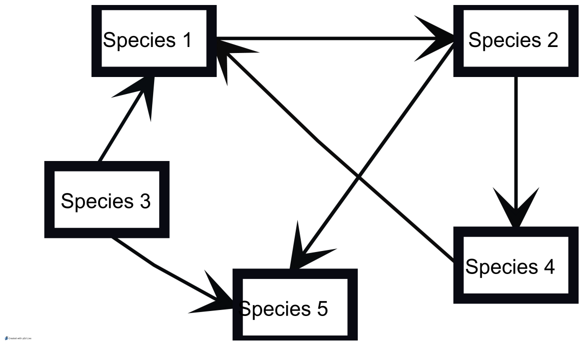

Figure 2.1: Community of 5 interacting species. The species' has direct relation between each pair of species, and the network is unweighted.

The matrix that represents this network is given by the following:

$$M_{5,5} = \begin{bmatrix} 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 \\ 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}.$$

2.1.2 Example. The interaction strengths in Figure 2.2 are undirected and unweighted; we denote the relation between each pair of species as in the previous network by (present $= 1$, absent $= 0$). The

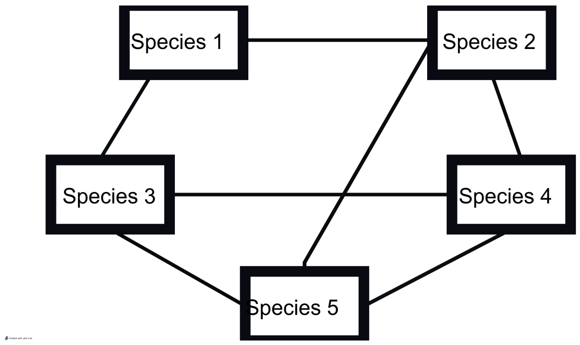

Figure 2.2: Community of 5 interacting species with undirected and unweighted relationship between each pair of species.

matrix elements are $(0, 1)$ and we can construct the matrix from the network as follows:

$$M_{5,5} = \begin{bmatrix} 0 & 1 & 1 & 0 & 0 \\ 1 & 0 & 0 & 1 & 1 \\ 1 & 0 & 0 & 1 & 1 \\ 0 & 1 & 1 & 0 & 1 \\ 0 & 1 & 1 & 1 & 0 \end{bmatrix}.$$

2.1.3 Example. In the last example we consider 4 interacting species and the interaction strengths in Figure 2.3 form a directed weighted network. We denote the relation between each pair species by the amount of interaction of the species i on the species j. Thus the matrix formulation for this network is:

$$M_{4,4} = \begin{bmatrix} 0 & 0.05 & 0.65 & 1.05 \\ 0.8 & 0 & 1.02 & 0 \\ 0 & 0.3 & 0 & 0 \\ 0.15 & 0 & 0 & 0 \end{bmatrix}.$$

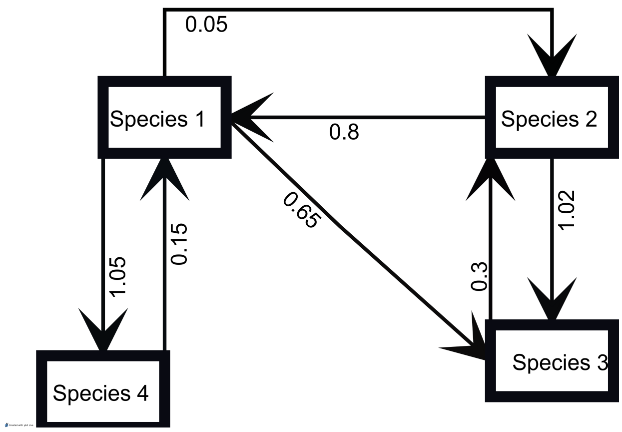

Figure 2.3: Community of 4 interacting species. Where each pair of species relationship is directed and weighted.

2.2 Fixed Points

2.2.1 Definition. The fixed points are equilibrium solutions of the differential equations that represent the rate of change in the density of each species in the ecological community. In general, a fixed point is a mapping function of set differential equations to some object (N_0). This mapping gives a constant solution of the given dynamic network in time t, and we can determine the behaviour of the network equations at this point. An equilibrium solution of this system of equations is a set of points $\{N_1, N_2, ...N_n\}$ such that:

$$\frac{dN_i}{dt} = 0, \quad \forall i \in \{1, 2, ..., n\}$$

i.e, $\frac{dN_1}{dt} = 0, \frac{dN_2}{dt} = 0, ..., \frac{dN_n}{dt} = 0, \quad i = 1, 2, 3, ..., n.$

2.3 Eigenvalues

2.3.1 Definition. Let us consider $\boldsymbol{A}$ to be an $n \times n$ matrix of real numbers. The eigenvalues of the matrix $\boldsymbol{A}$ are stored in the vector λ, where $\{\lambda_i, i = 1, 2, ..., n\}$ is a real or complex numbers i.e, $\{\lambda = \lambda_1, \lambda_2, ..., \lambda_n\}$. The stability classification of the fixed points is determined by the sign of the leading eigenvalue in the matrix. this show how every species in the network behaves and responds to the dynamics that could happen. To calculate the eigenvalues mathematically we set the equation $A\underline{N}$ equal to $\underline{N}$ which is given by:

$$\boldsymbol{A}\underline{N} = \lambda \underline{N}, \tag{2.3.1}$$

consider the population densities matrix that consist of all the information on the interactions among species in the community. We use the eigenvalues of the matrix to obtain the stability criteria for the network, in general λ is an eigenvalue such that:

$$|\boldsymbol{A} - \lambda \boldsymbol{I}| = 0. \tag{2.3.2}$$

2.4 Stability of Ecological Networks

Consider the equations of the population dynamics:

$$\frac{dN_i}{dt} = F_i(\underline{N}, t), \quad \text{where } N_i \in \mathbb{R}^n, t \in \mathbb{R}, \tag{2.4.1}$$

the continuous vector function F_i is mapped as follows [Kuznetsov (2008)]:

$$F_i : \mathbb{R}^n \times \mathbb{R} \longrightarrow \mathbb{R},$$

we can represent Equation (2.4.1) as the following discrete system:

$$N_i(t+1) = F_i(\underline{N}, t), \qquad N_i \in \mathbb{R}^n \text{ and } t \in \mathbb{Z}, \tag{2.4.2}$$

$$F_i : \mathbb{R}^n \times \mathbb{Z} \longrightarrow \mathbb{R}, \tag{2.4.3}$$

the solution $N_i(t_0)$ of this system should exist and be unique at a given time interval [Kuznetsov (2008)]. The point $N_i(t_0)$ is said to be stable if there exist small positive number δ such that:

$$|\widehat{N_i}(t) - N_i(t_0)| < \delta, \quad \forall t \geq t_0, \tag{2.4.4}$$

where:

- $N_i(t_0) \equiv$ fixed point.
- $\widehat{N_i} \equiv$ is small perturbation from the fixed point.

To understand the ecological network stability we can take as an example a group of connected balls. If we move any one of them it will affect the next ball and then the next one and so on until it reaches the last one. The structure of the ecological network is similar to this group. For example, changes in the growth rate of any species will affect the interactions between the species themselves and other species.

This in turn affects the network stability. In this research we consider the competition interaction among species, and the strength of this interaction differs depending on a growth rate of the population as well as the resource availability. There are different matrices used to obtain the stability of the ecological networks [Novak et al. (2016)]. Using these matrices, we consider the coexistence of the species at equilibria and find the dominant eigenvalues to obtain the stability. In general the stability of the network shows the qualitative behaviour of the network. In other words, the small perturbations from the initial conditions in the network can stabilize (back to equilibrium) or destabilize (move far from the equilibrium).

The leading eigenvalue determines the state of the network [May (1971)] and we are using the non-zero fixed points of the differential equations that describe the rate of change in the ecological network. Moreover, the largest eigenvalue provides a measure of how small changes in the ecological network structure reflect the influence (for example, connections between species) on the ecological network. We determine the stability, or the behaviour of the network structure near the equilibrium positions by specifying the sign of real part for the leading eigenvalue. We assumed that:

- The leading eigenvalue $\lambda^* = x + iy$, forms network stability as follows:
  - $Re(\lambda^*) < 0$, the ecological network is stable, i.e, a small changes around the fixed point will return toward the equilibria [May (1971)].
  - $Re(\lambda^*) > 0$, it shows that the ecological network is unstable, i.e, any small change around the fixed points changes the state of the network to be unstable [May (1971)].

The evolution of the species affects the stability of the network, The rate of change in the species population depends on the current population, population growth rate and interaction with other species.

May suggests that the large complex ecological networks are unstable [May (1971)], but if we divide the network in to blocks then the stability will raise in the community. This analysis is completely different from the previous analysis of [Gardner and Ashby (1970)] which expected large complex networks to be stable at such points. We measure the complexity of a network using the average interaction strengths and connectedness in the network.

2.5 Competitive Lotka-Volterra Model

2.5.1 Definition. The Lotka–Volterra model is a mathematical model developed to describe the network structure [Boccara (2010)]. The model is a system of first-order non linear differential equations of n interacting species in an ecological community discovered independently by Alfred Lotka, an American biophysicist in 1925, and Vito Volterra, an Italian mathematician in 1926 [Boccara (2010)]. These equations are used to describe the dynamics of biological network communities for any number of interacting species. For example, this set of equations can be used to describe competition or predation in the network, depending on the values of the $\alpha_{i,j}$'s and r_i's in the equations. The populations are changing through time and the general formula that describes these dynamic is shown in the following equation:

$$\frac{dN_i}{dt} = r_i N_i (1 - \sum_{j=1}^{n} \alpha_{i,j} N_j), \tag{2.5.1}$$

where:

- N_i is the density of species i in the community.
- n is the number of interacting species in the community.
- r_i is the intrinsic growth rate of the species i in the community.
- $\alpha_{i,j}$ is the effect of species j on the growth rate of the species i.

2.5.1 Example.

Consider a biological network of two interacting species, the Lotka-Volterra equations describing the dynamics in this community are given by:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \sum_{j=1}^{2} \alpha_{1,j} N_j), \tag{2.5.2}$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \sum_{j=1}^{2} \alpha_{2,j} N_j), \tag{2.5.3}$$

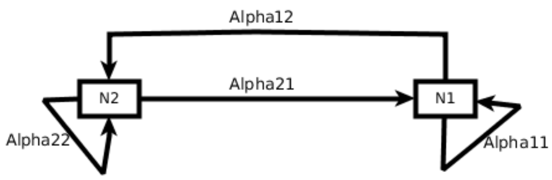

Figure 2.4: A network of two interacting species.

to find the non zero fixed points of the system, we compute the steady state at:

$$\frac{dN_1}{dt} = 0 \quad \text{and} \quad \frac{dN_2}{dt} = 0, \tag{2.5.4}$$

using Equation (2.5.2) and Equation (2.5.3), the system becomes:

$$r_1 N_1 (1 - (\alpha_{1,1} N_1 + \alpha_{1,2} N_2) = 0, \tag{2.5.5}$$

$$r_2 N_2 (1 - (\alpha_{2,1} N_1 + \alpha_{2,2} N_2) = 0, \tag{2.5.6}$$

we will assume that each species overlaps with itself completely in per capita species, in other words $\alpha_{i,i} = 1$. By solving the system of linear equations, we find the fixed points depend on the α's value (N_1^*, N_2^*) located at:

$$(N_1^*, N_2^*) = (\frac{(1 - \alpha_{1,2})}{1 - \alpha_{1,2}\alpha_{2,1}}, \frac{(1 - \alpha_{2,1})}{1 - \alpha_{2,1}\alpha_{1,2}}). \tag{2.5.7}$$

The analytical solution (Equation (2.5.7)) of the system is difficult to compute when the system is linear with large numbers of interacting species, and we used the python programming language for solving this system numerically.

3. Matrix methods

3.1 General Formulation

In the second chapter we constructed the interaction matrix from the ecological network structure. There are a number of different matrices used to examine how the interaction affects the community dynamics in an ecological networks. Here we define these matrices and provide some motivation for their form, we use numerical approximation to investigate the stability properties implied by each of this matrix methods.

3.2 Jacobian Matrix

A Jacobian, or a community matrix is a square matrix of first-order partial derivatives of the rates of change of each species' density in the system with respect to other species' densities [Novak et al. (2016)]. The determinant of the Jacobian matrix is a fundamental representation of the transformation when we zoom in near a specific point. The Jacobian linearises the non linear system, and when evaluated at the equilibrium points tell us about the behaviour or the nature near to the equilibria [Boccara (2010)]. The Jacobian matrix is used by the mathematicians to predict the behaviour of dynamic systems, using the equations that explain the system the Jacobian matrix form is given by:

$$\frac{\partial(\frac{dN_i}{dt})}{\partial N_j} = \frac{\partial F_i(N_1, N_2, ..., N_n)}{\partial N_j} = \boldsymbol{J_{i,j}} \qquad i,j = 1,2,...n, \tag{3.2.1}$$

This equation illustrates the fact that the flow near a point in the system is governed by the direct dependence of the rate of change of each species on its own density and on the population densities of the other species in the community [Landi et al. (2017)].

$$\boldsymbol{J} = \begin{pmatrix} \frac{\partial F_1}{\partial N_1} & \frac{\partial F_1}{\partial N_2} & \cdots & \frac{\partial F_1}{\partial N_n} \\ \frac{\partial F_2}{\partial N_1} & \frac{\partial F_2}{\partial N_2} & \cdots & \frac{\partial F_2}{\partial N_n} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial F_n}{\partial N_1} & \frac{\partial F_n}{\partial N_2} & \cdots & \frac{\partial F_n}{\partial N_n} \end{pmatrix}.$$

3.2.1 Example. We consider a community of three interacting species in an ecological network, with network dynamics described by the Lotka-Volterra competition model:

$$\frac{dN_i}{dt} = r_i N_i (1 - \sum_{j=1}^{3} \alpha_{i,j} N_j), \qquad i,j = 1,2,3, \tag{3.2.2}$$

to define the Jacobian, we know that the equilibrium point of the network is N^* and since we are considering the neighbourhood of the equilibrium [Boccara (2010)], our new state of the species' densities can be written:

$$N_1 = \widehat{N_1} + N_1^*,$$
$$N_2 = \widehat{N_2} + N_2^*,$$
$$N_3 = \widehat{N_3} + N_3^*,$$

where:

- $\widehat{N_i} \equiv$ small perturbation.

the Jacobian is evaluated at this point, given by a small perturbation $(\widehat{N_1}, \widehat{N_2}, \widehat{N_3})$ from the equilibrium point $N^* = (N_1^*, N_2^*, N_3^*)$. Since the system is in a steady state at the equilibrium point:

$$\frac{d\widehat{N_1}}{dt} = \frac{dN_1}{dt} = F_1(N_1, N_2, N_3), \tag{3.2.3}$$
$$\frac{d\widehat{N_2}}{dt} = \frac{dN_2}{dt} = F_2(N_1, N_2, N_3), \tag{3.2.4}$$
$$\frac{d\widehat{N_3}}{dt} = \frac{dN_3}{dt} = F_3(N_1, N_2, N_3), \tag{3.2.5}$$

using the Taylor series expansion[Boccara (2010)], we can represent this perturbation as:

$$\frac{d\widehat{N_1}}{dt} = F_1(N_1^*, N_2^*, N_3^*) + \frac{\partial F_1(N^*)}{\partial N_1}\widehat{N_1} + \frac{\partial F_1(N^*)}{\partial N_2}\widehat{N_2} + \frac{\partial F_1(N^*)}{\partial N_3}\widehat{N_3} + ..., \tag{3.2.6}$$
$$\frac{d\widehat{N_2}}{dt} = F_2(N_1^*, N_2^*, N_3^*) + \frac{\partial F_2(N^*)}{\partial N_1}\widehat{N_1} + \frac{\partial F_2(N^*)}{\partial N_2}\widehat{N_2} + \frac{\partial F_2(N^*)}{\partial N_3}\widehat{N_3} + ..., \tag{3.2.7}$$
$$\frac{d\widehat{N_3}}{dt} = F_3(N_1^*, N_2^*, N_3^*) + \frac{\partial F_3(N^*)}{\partial N_1}\widehat{N_1} + \frac{\partial F_3(N^*)}{\partial N_2}\widehat{N_2} + \frac{\partial F_3(N^*)}{\partial N_3}\widehat{N_3} + ..., \tag{3.2.8}$$

since we have that $F_i(N_1^*, N_2^*, N_3^*) = 0$, the Jacobian matrix transformation from for this system is given by:

$$\boldsymbol{J} = \begin{pmatrix} \frac{\partial F_1(N^*)}{\partial N_1} & \frac{\partial F_1(N^*)}{\partial N_2} & \frac{\partial F_1(N^*)}{\partial N_3} \\ \frac{\partial F_2(N^*)}{\partial N_1} & \frac{\partial F_2(N^*)}{\partial N_2} & \frac{\partial F_2(N^*)}{\partial N_3} \\ \frac{\partial F_3(N^*)}{\partial N_1} & \frac{\partial F_3(N^*)}{\partial N_2} & \frac{\partial F_3(N^*)}{\partial N_3} \end{pmatrix} =$$

$$\begin{pmatrix} -2r_1N_1^* + r_1(1 - \alpha_{1,2}N_2^* - \alpha_{1,3}N_3^*) & -\alpha_{1,2}r_1N_1^* & -\alpha_{1,3}r_1N_1^* \\ -\alpha_{2,1}r_2N_2^* & -2r_2N_2^* + r_2(1 - \alpha_{2,1}N_1^* - \alpha_{2,3}N_3^*) & -\alpha_{2,3}r_2N_2^* \\ -\alpha_{3,1}r_3N_3^* & -\alpha_{3,2}r_3N_3^* & -2r_3N_3^* + r_3(1 - \alpha_{3,1}N_1^* - \alpha_{3,2}N_2^*) \end{pmatrix},$$

we use the equilibrium point (N_1^*, N_2^*, N_3^*), computed from the system of equations, to study the behaviour of the network with different values of the system parameters i.e. $\{r_i, \alpha_{i,j}\}$. In short, the fixed point (N_1^*, N_2^*, N_3^*) is stable if real part of the eigenvalue with largest real part is negative [May (1971)], otherwise it will be unstable.

3.3 Alpha or Interaction Strength Matrix

The interaction strength matrix represents the magnitude of the effect of the density of each species on the other species densities in the network community [Novak et al. (2016)]. We generate the interactions strength matrix by sampling from a random normal distribution with zero mean and a variety of standard deviation (σ) values to see how the numbers of species and the connectivity influence the network stability. Each species' density is dependent on its own growth rate, other species growth rates and the environment of the community. We assumed that the species overlap with themselves and their interactions strength (the magnitude) are all set to be $\alpha_{i,i} = 1$ as May's assumption [May (1972)] while the off-diagonal $\alpha_{i,j}$ elements of α matrix represent interspecific interaction, therefore the interaction matrix has the form:

$$\frac{\partial(\frac{1}{N_i}\frac{dN_i}{dt})}{\partial N_j} = [\alpha_{i,j}], \quad \{i,j\} = 1, 2, ..., n, \tag{3.3.1}$$

The interaction matrix has the form :

$$\boldsymbol{\alpha_{i,j}} = \begin{pmatrix} -1 & -\alpha_{1,2} & \cdots & -\alpha_{1,n} \\ -\alpha_{2,1} & -1 & \cdots & -\alpha_{2,n} \\ \vdots & \vdots & \ddots & \vdots \\ -\alpha_{n,1} & -\alpha_{N,2} & \cdots & -1 \end{pmatrix}, \quad i,j = 1, 2, ..., n,$$

3.3.1 Example. In this example we will consider three interacting species in a community, the interaction matrix from this network is given by :

$$\boldsymbol{\alpha} = \begin{pmatrix} -1 & -\alpha_{1,2} & -\alpha_{1,3} \\ -\alpha_{2,1} & -1 & -\alpha_{2,3} \\ -\alpha_{3,1} & -\alpha_{3,2} & -1 \end{pmatrix}, \quad i,j = 1, 2, 3.$$

3.4 Encounter Matrix

The encounter matrix form is:

$$\boldsymbol{E_{i,j}} = \begin{pmatrix} -N_1^2 & -N_1N_2 & \cdots & -N_1N_n \\ -N_2N_1 & -N_2^2 & \cdots & -N_2N_n \\ \vdots & \vdots & \ddots & \vdots \\ -N_nN_1 & -N_nN_2 & \cdots & -N_n^2 \end{pmatrix}, \quad i,j = 1, 2, ..., n.$$

3.4.1 Example. Consider an ecological network with two competing species, the encounter matrix of this community is given by:

$$\boldsymbol{E} = \begin{pmatrix} -N_1^2 & -N_1N_2 \\ \\ -N_2N_1 & -N_2^2 \end{pmatrix}, \quad i,j = 1,2,$$

Since we already computed the non zero equilibrium point for Equation (2.5.7) in Chapter.2, when we have two species which is $(\frac{(1-\alpha_{1,2})}{1-\alpha_{1,2}\alpha 2,1}, \frac{(1-\alpha_{2,1})}{1-\alpha_{2,1}\alpha 1,2})$, the encounter matrix representation for this system is given by:

$$\boldsymbol{E} = \begin{pmatrix} -(\frac{(1-\alpha_{1,2})}{1-\alpha_{1,2}\alpha 2,1})^2 & -\frac{(1-\alpha_{1,2})(1-\alpha_{2,1})}{1-\alpha_{1,2}\alpha 2,1} \\ \\ -\frac{(1-\alpha_{2,1})(1-\alpha_{1,2})}{1-\alpha_{2,1}\alpha 1,2} & -(\frac{(1-\alpha_{2,1})}{1-\alpha_{2,1}\alpha 1,2})^2 \end{pmatrix}.$$

3.5 Interaction (Competition) Matrix

In a competitive network of n interacting species, the competition matrix is a matrix which is containing the interspecific competition interaction parameters, including the species interactions with themselves and with the initial abundance of both competing species. The competition matrix form is:

$$\boldsymbol{I_{i,j}} = \begin{pmatrix} -\alpha_{1,1}N_1^2 & -\alpha_{1,2}N_1N_2 & \cdots & -\alpha_{1,n}N_1N_n \\ \\ -\alpha_{2,1}N_2N_1 & -\alpha_{2,2}N_2^2 & \cdots & -\alpha_{2,n}N_2N_n \\ \\ \vdots & \vdots & \ddots & \vdots \\ \\ -\alpha_{n,1}N_nN_1 & -\alpha_{n,2}N_nN_2 & \cdots & -\alpha_{n,n}N_n^2 \end{pmatrix},$$

3.5.1 Example. Consider an ecological network with two competing species, the competition matrix of this community is given by:

$$\boldsymbol{I} = \begin{pmatrix} -\alpha_{1,1}N_1^2 & -\alpha_{1,2}N_1N_2 \\ \\ -\alpha_{2,1}N_2N_1 & -\alpha_{2,2}N_2^2 \end{pmatrix}, \quad i,j = 1,2,$$

Since we already computed the non zero equilibrium point in Equation (2.5.7) in Chapter 2 for two species which is $(\frac{(1-\alpha_{1,2})}{1-\alpha_{1,2}\alpha 2,1}, \frac{(1-\alpha_{2,1})}{1-\alpha_{2,1}\alpha 1,2})$, the encounter matrix representation for this system is given by:

$$\boldsymbol{I} = \begin{pmatrix} -\alpha_{1,1}(\frac{(1-\alpha_{1,2})}{1-\alpha_{1,2}\alpha 2,1})^2 & -\alpha_{1,2}\frac{(1-\alpha_{1,2})(1-\alpha_{2,1})}{1-\alpha_{1,2}\alpha 2,1} \\ \\ -\alpha_{2,1}\frac{(1-\alpha_{2,1})(1-\alpha_{1,2})}{1-\alpha_{2,1}\alpha 1,2} & -\alpha_{2,2}(\frac{(1-\alpha_{2,1})}{1-\alpha_{2,1}\alpha 1,2})^2 \end{pmatrix}.$$

4. Assumptions and Results

4.1 Assumptions

The dynamics of ecological networks are governed by the growth rates of the species and the interaction strengths between them. Real world measurements of these parameters are based on estimations using statistical approaches. These estimations are often difficult to accurately compute. For example with large measurement areas or with large numbers of interactions (connections) between species. However these estimations need to be accurate in order to be useful for making good predictions, as small changes in the parameters can make a huge difference to the network dynamics and network structure (e.g. species extinction) [Logofet (2005)].

The simulations in this research use interaction parameters $\alpha_{i,j}$ based on random numbers. We perform random number generation to generate the interaction coefficients. We extracted the interaction coefficients from normal distribution $[\alpha_{i,j} \sim N(0, \sigma^2)]$ with zero mean and different values of standard deviation σ. The normal distribution is often used to study network stability [Logofet (2005)]. The diagonal elements are set to be one (the overlap of species with it self) and the off-diagonal elements are positive numbers, and since the interaction is competition the sign of all alpha matrix inters will be negative. We compute the positive equilibrium point (species' densities in a coexist point). Moreover, we use the equilibrium points to normalise near to the steady state of the interactions coefficient in the matrices entries [Allesina and Tang (2012)].

In this analysis we use 100 random matrices to represent the ecological network community, using python program to compute the eigenvalues for each matrix and determine the dominant eigenvalues. We can infer the network stability from the sign of leading eigenvalue in each matrix. In Table 4.1 we show the eigenvalues domain and the numbers of the negative eigenvalues in each 100 random matrix selection.

The measuring estimation of the parameters is very important to have good approximation. In fact a small change in the parameters can make huge difference in the network dynamics and network structure, such as species extinction.

We consider that:

- Growth rate parameter r_i to be 1.
- The interaction parameters $\alpha_{i,j}$ we selected them randomly from normal distribution.
- Carry capacity as $K_i = 1, \quad i = 1, 2, ..., n.$
- The stranded deviation of the interaction parameters we choose it to be $\sigma = (1, 0.5, 0.1)$.

4.2 The Stability Result for Two Interacting Species

We summarise the result of our testing data set when we have two interacting species in the ecological community.

Two interacting species						
Matrix	domain when $\sigma = 1$	Neg-E	domain when $\sigma = 0.5$	Neg-E	domain when $\sigma = 0.1$	Neg-E
Alpha	$[-1, 1.2]$	81	$[-1, -.3]$	100	$[-1, -.9]$	100
Jacobian	$[-.8, 1]$	41	$[-.9, .9]$	41	$[-.4, .4]$	50
Encounter	$[-.001, .01]$	19	$[-.001, .01]$	20	$[-.001, .01]$	24
Competition	$[-.1, 0]$	100	$[-.01, 0]$	100	$[-.06, -.05]$	100

Table 4.1: We summarise the domain and the number of negative eigenvalues for all matrices when we have two interacting species in the community.

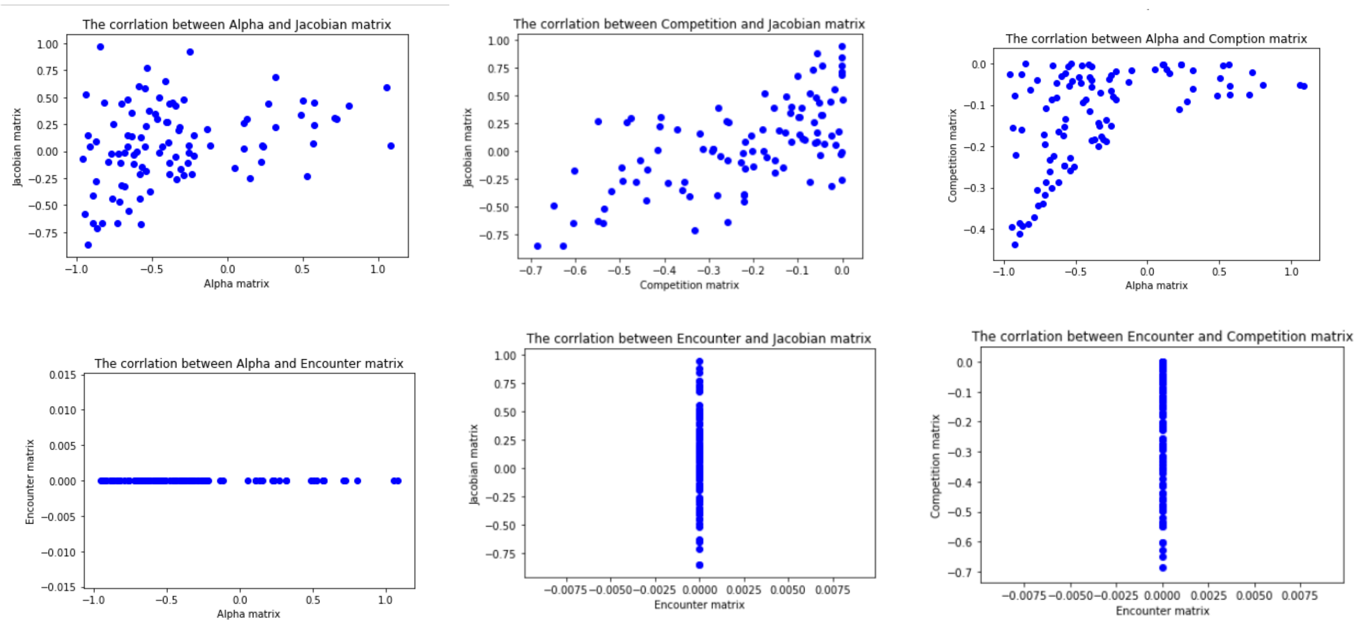

Figure 4.1: The correlation of the eigenvalues for all pairs of the matrices. The weakest negative correlation is between the eigenvalues of alpha and encounter matrix (correlation coefficient $r = -0.07$), and there is moderate negative correlation between the eigenvalues of alpha and competition matrix($r = -0.5$). The standard deviation for the data set is 1.

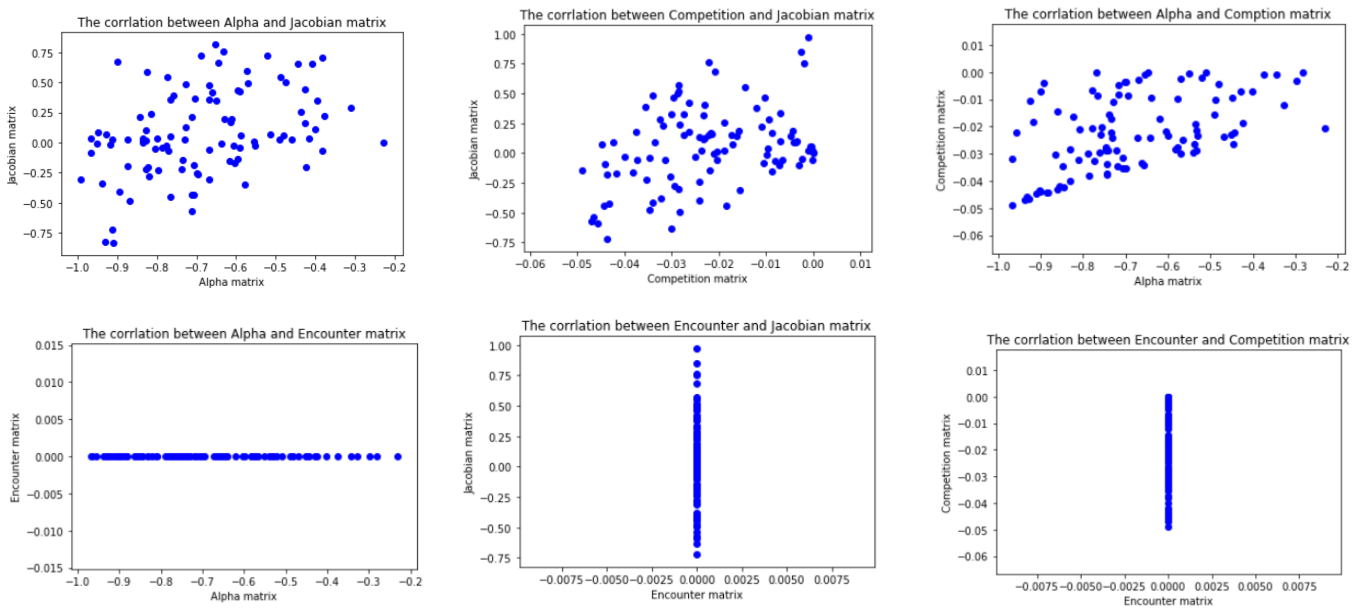

Figure 4.2: The correlation of all six pairs of eigenvalues of all matrices. The weakest negative correlation is between the eigenvalues of Jacobian and encounter matrix, and correlation coefficient is $r = -0.2$. There is a moderate positive correlation between all three pairs alpha and competition , alpha and Jacobian and competition and Jacobian matrix, the correlation coefficient approximately $r = 0.6$. The standard deviation for the data set is 0.5.

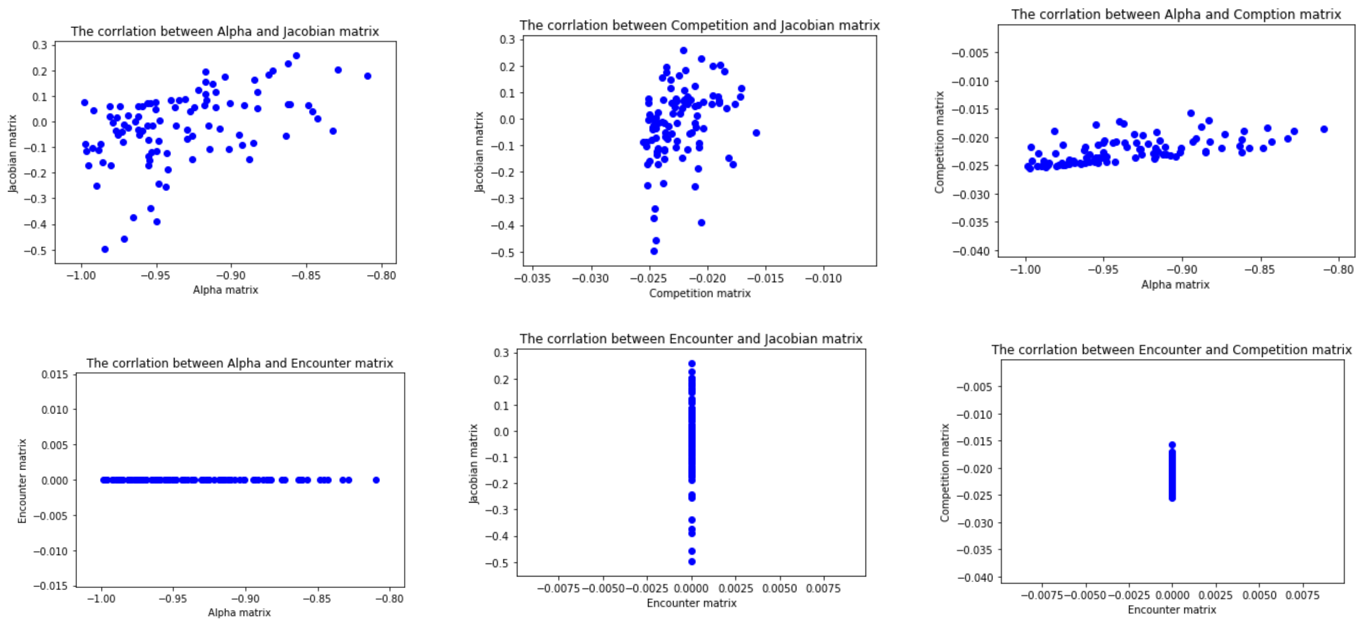

Figure 4.3: The weakest negative correlation is between the eigenvalues of alpha and encounter and Jacobian and encounter matrix which is $r = -0.01$, and there is strong positive correlation between all three pairs alpha and competition , alpha and Jacobian and competition and Jacobian matrix which have correlation coefficient approximately $r = 0.7$. The standard deviation for the data set is 0.1.

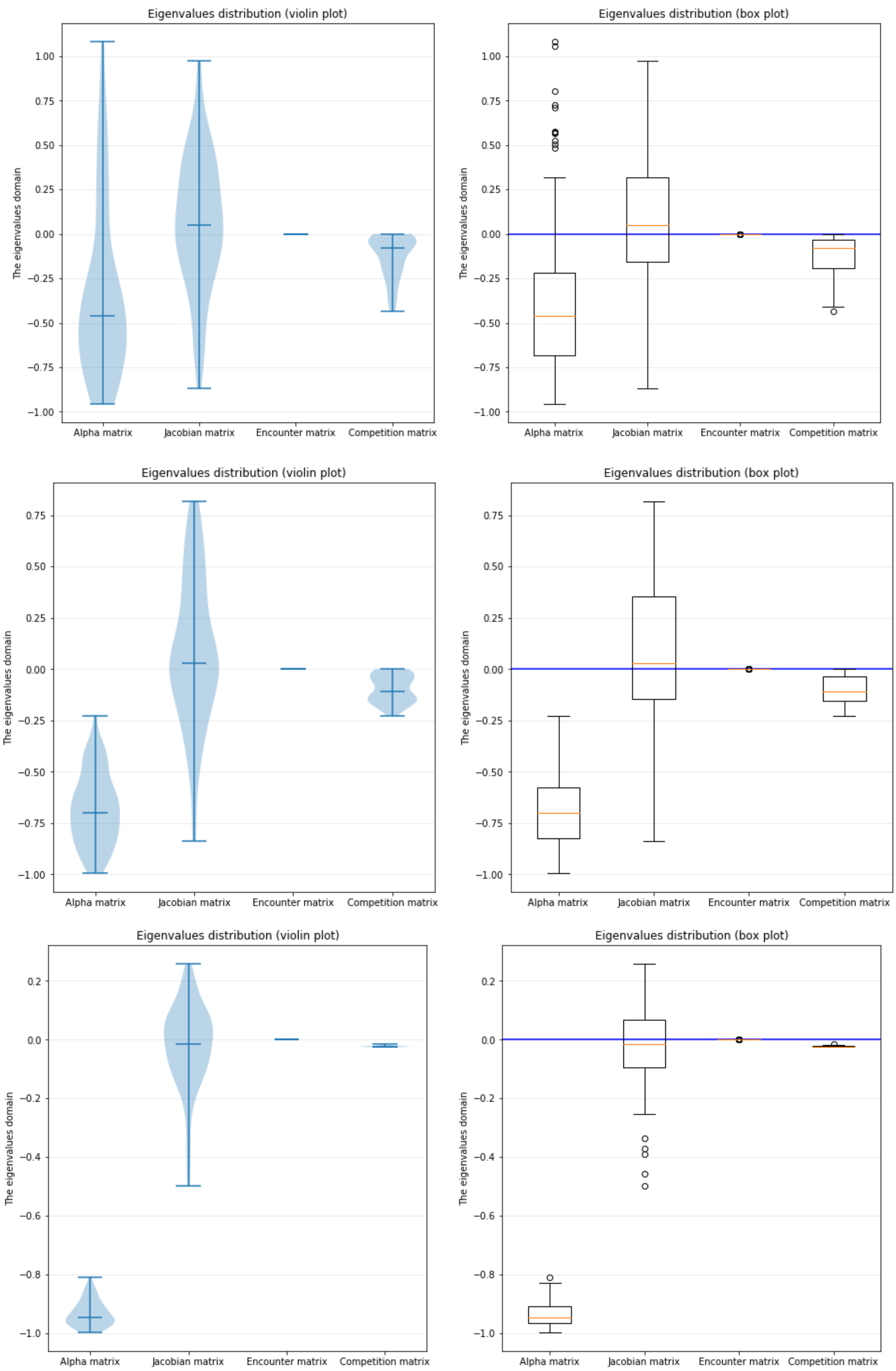

Figure 4.4: The violin and box plots of the eigenvalue distributions for different values of the interaction parameters $\alpha_{i,j}$ and standard deviations σ, when we have two interacting species in the community.

4.3 The Stability Result for Three Interacting Species

We summarise the result of our testing data set when we have three interacting species in the ecological community.

Three interacting species						
Matrix	domain when $\sigma = 1$	Neg-E	domain when $\sigma = 0.5$	Neg-E	domain when $\sigma = 0.1$	Neg-E
Alpha	$[-.83, 1.5]$	57	$[-.9, -.2]$	100	$[-1.3, -.8]$	100
Jacobian	$[-.98, .8]$	62	$[-1.1, .7]$	87	$[-.1.3, -.9]$	100
Encounter	$[-.001, .001]$	11	$[-.001, .001]$	11	$[-.001, .01]$	15
Competition	$[-.27, 0]$	100	$[-.4, 0]$	100	$[-.8, -.2]$	100

Table 4.2: We are summarising the negative eigenvalues and the domain for all matrices for three interacting species in the community.

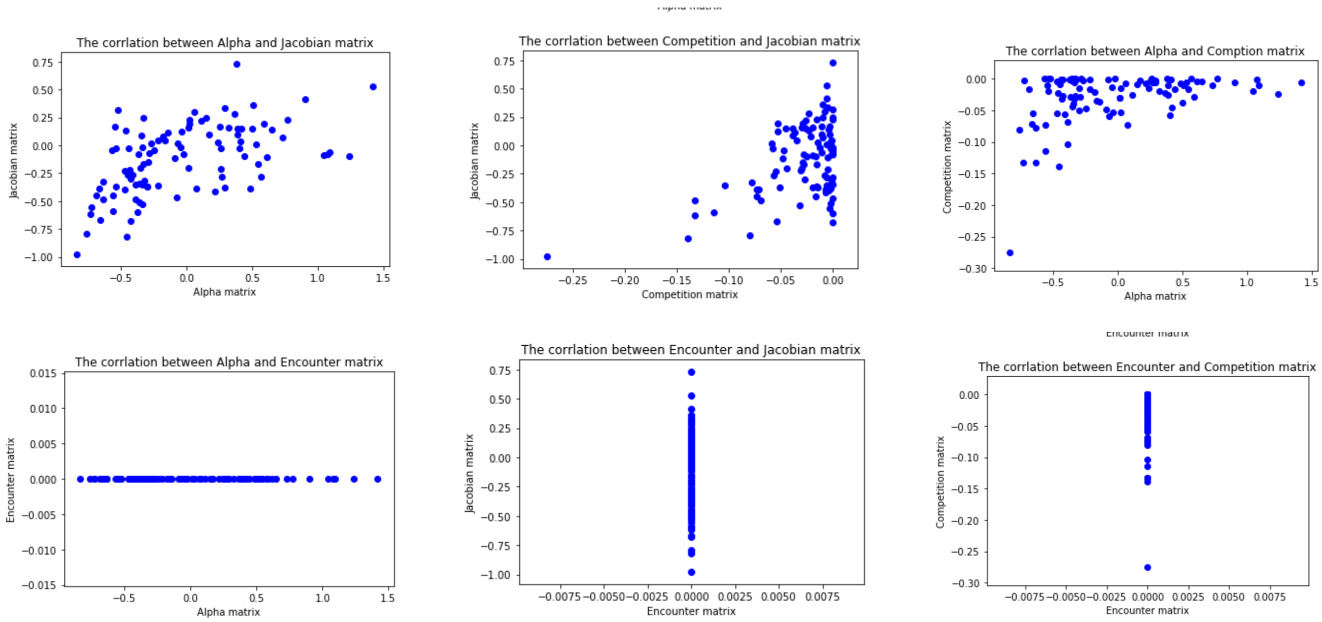

Figure 4.5: The weakest positive correlations are between the eigenvalues of alpha and encounter and alpha and competition matrix, which is $r = 0.03$. And there is a moderate positive correlation between alpha and Jacobian matrix, the correlation coefficient approximately $r = 0.5$. The standard deviation for the data set is 1.

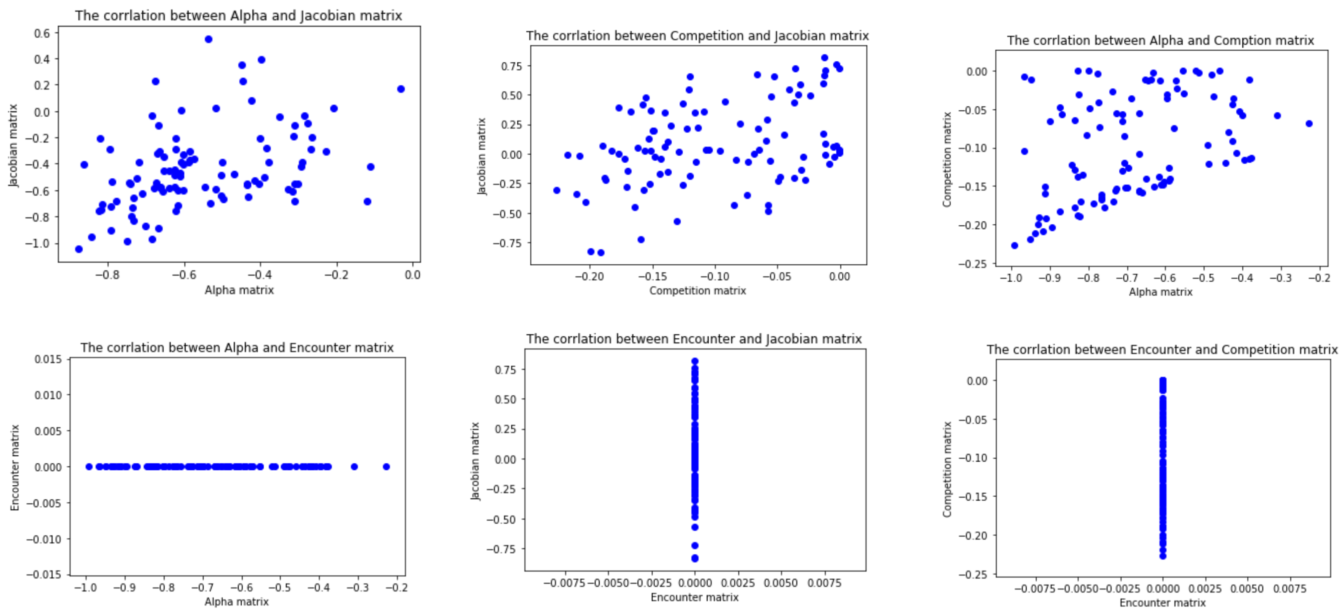

Figure 4.6: The weakest negative correlation is between the eigenvalues of alpha and encounter and Jacobian and encounter matrix which is $r = -0.01$, and there is strong positive correlation between all three pairs alpha and competition , alpha and Jacobian and competition and Jacobian matrix. The correlation coefficient approximately is $r = 0.7$. The standard deviation for the data set is 0.5.

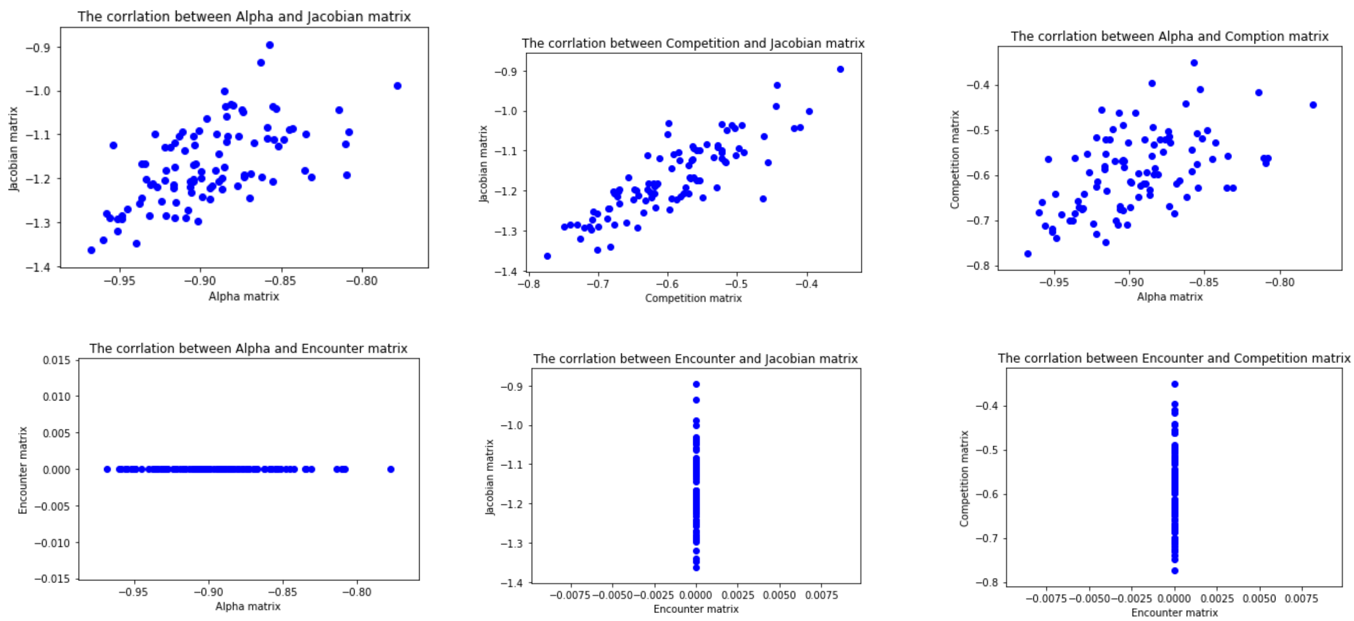

Figure 4.7: The strongest positive correlation is between the eigenvalues of the Jacobian and competition matrix ($r = 0.88$), and also there is strong positive correlation between two pairs alpha and competition and alpha and Jacobian matrix. The correlation coefficient approximately $r = 0.7$. The weakest correlation is between the eigenvalues of the encounter and competition matrix $r = -05$. The standard deviation for the data set is 0.1.

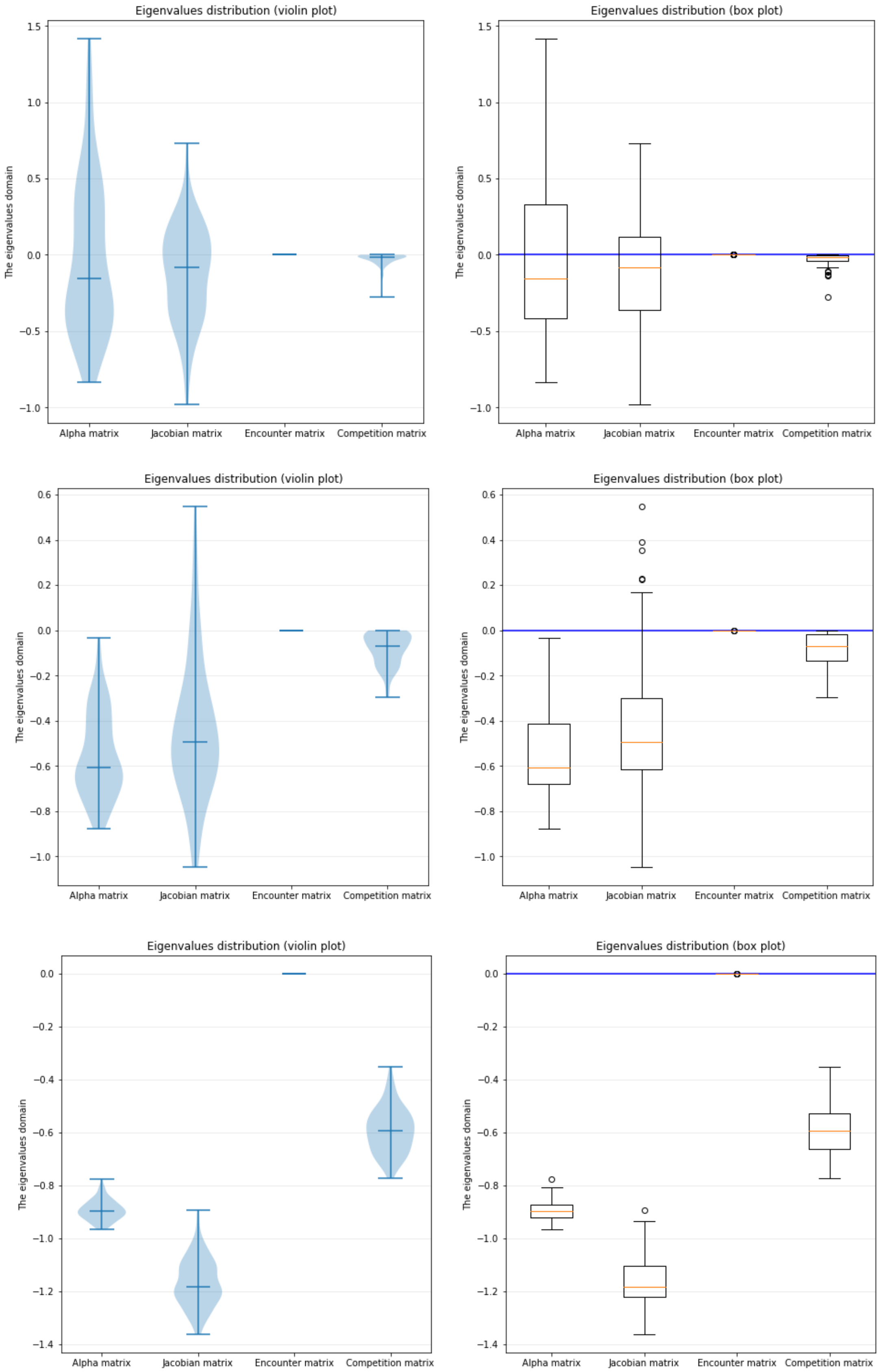

Figure 4.8: The violin and box plots of the eigenvalue distributions for different values of the interaction parameters $\alpha_{i,j}$ and standard deviations σ, when we have three interacting species in the community.

4.4 The Stability Result for Four Interacting Species

We summarise the result of our testing data set when we have four interacting species in the ecological community.

Four interacting species						
Matrix	domain when $\sigma = 1$	Neg-E	domain when $\sigma = 0.5$	Neg-E	domain when $\sigma = 0.1$	Neg-E
Alpha	$[-.5, 1.5]$	40	$[-.8, .2]$	98	$[-.95, -.7]$	100
Jacobian	$[-., .4]$	10	$[-.1, .4]$	1	$[.3, .5]$	0
Encounter	$[-.01, .01]$	2	$[-.001, .001]$	6	$[-.001, .001]$	6
Competition	$[-.02, .08]$	76	$[-.2, 0]$	100	$[-.6, -.2]$	100

Table 4.3: Summary of the negative eigenvalues and the domain for the eigenvalues of the matrices. We have four interacting species in the community.

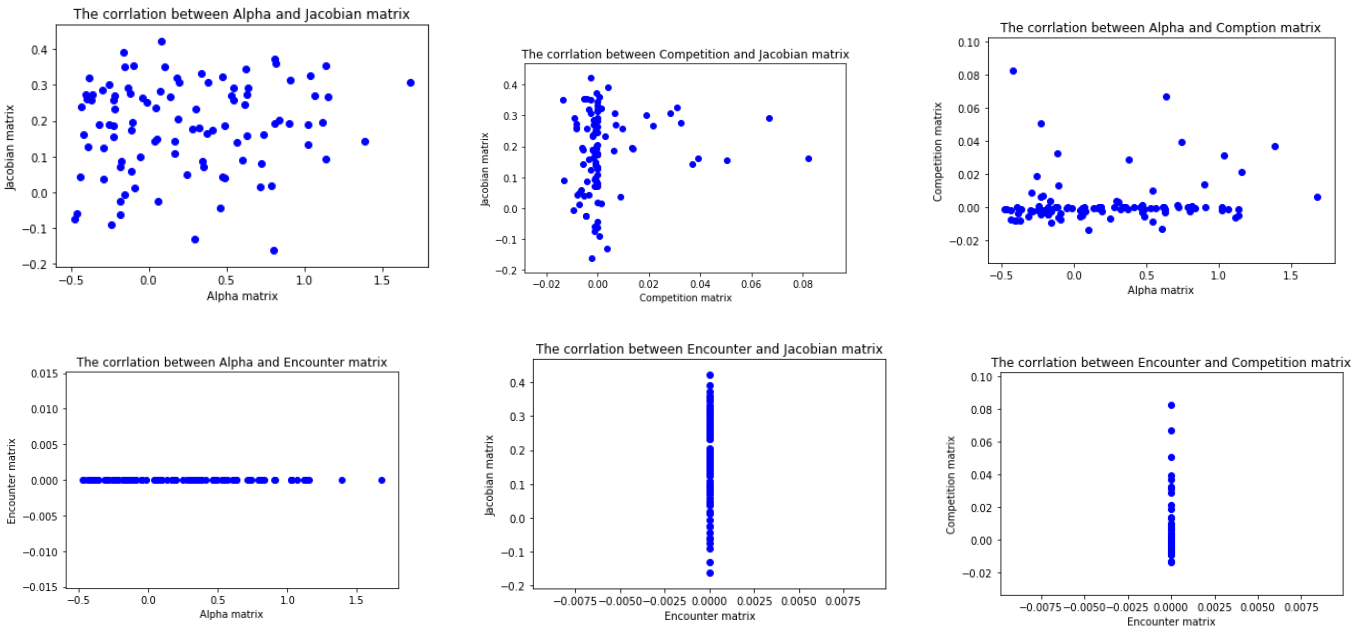

Figure 4.9: In this plot we set the standard deviation of the data sets to be 1. The weakest negative correlation is between the eigenvalues of competition and encounter, and encounter and alpha matrix which is $r = -0.08, -0.09$ respectively.

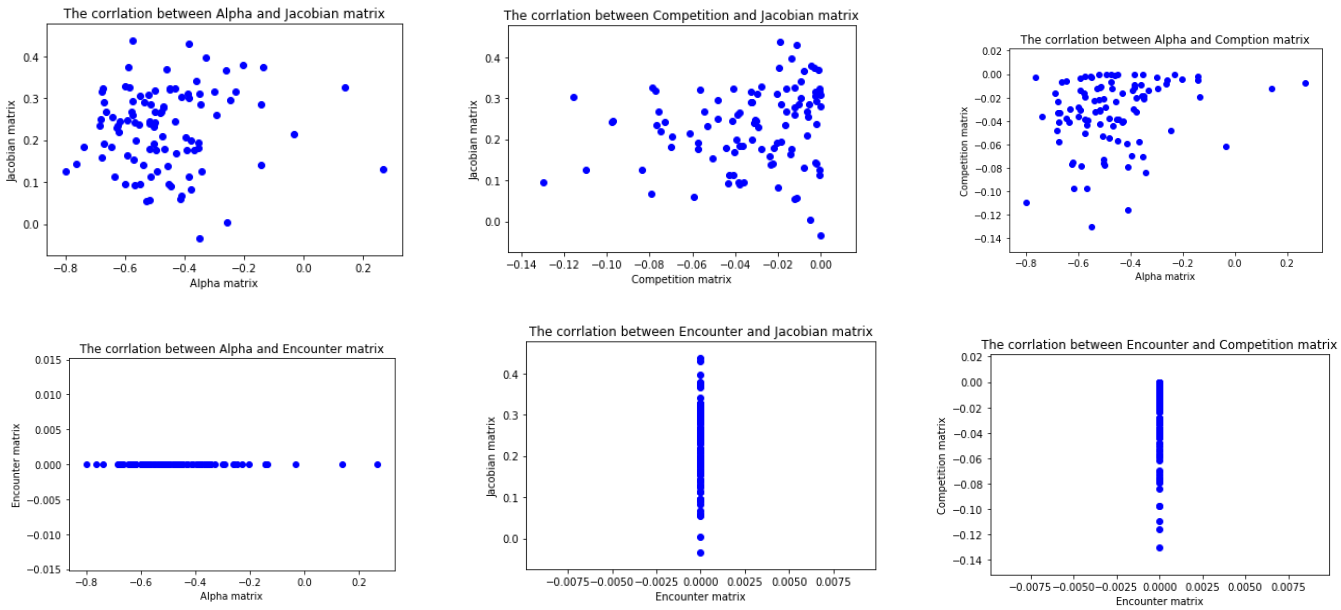

Figure 4.10: We set the standard deviation of the data sets to be 0.5. The weakest negative correlation is between the eigenvalues of competition and encounter and encounter and Jacobian matrix which is $r = -0.07, -0.08$ respectively. There is weak positive correlation between alpha and competition, alpha and Jacobian and competition and Jacobian matrix) the correlation coefficient approximately $r = 0.3$.

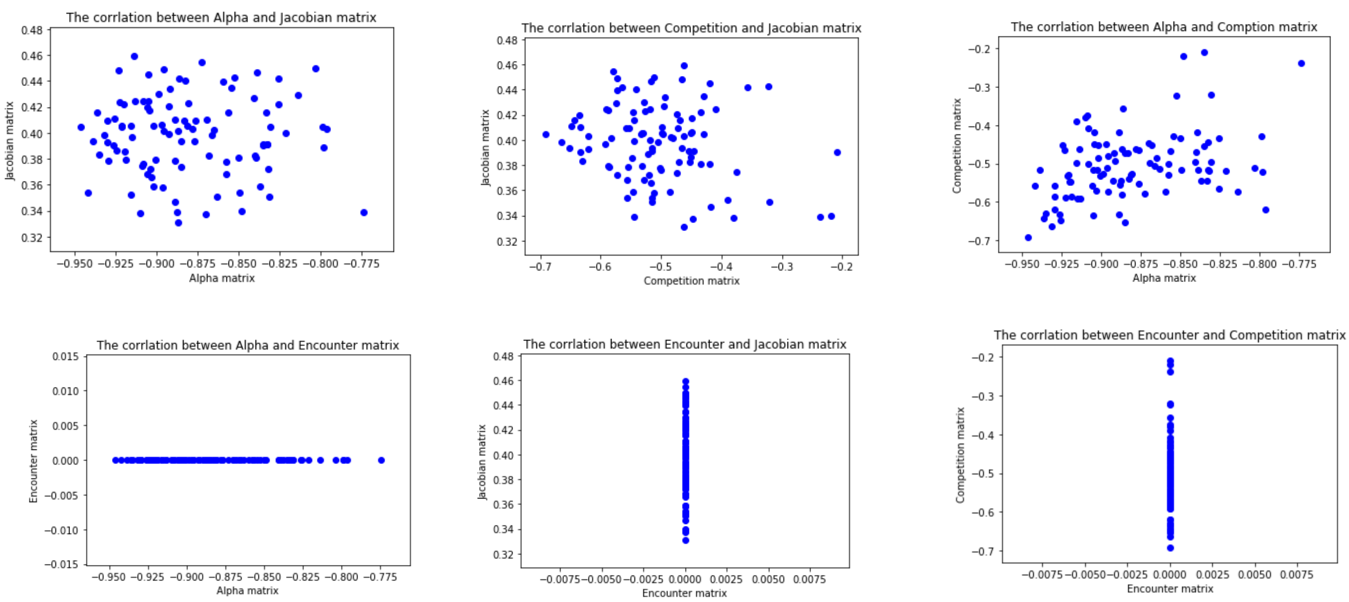

Figure 4.11: All the correlations are weak. The standard deviation of the random data sets is set to be 0.1.

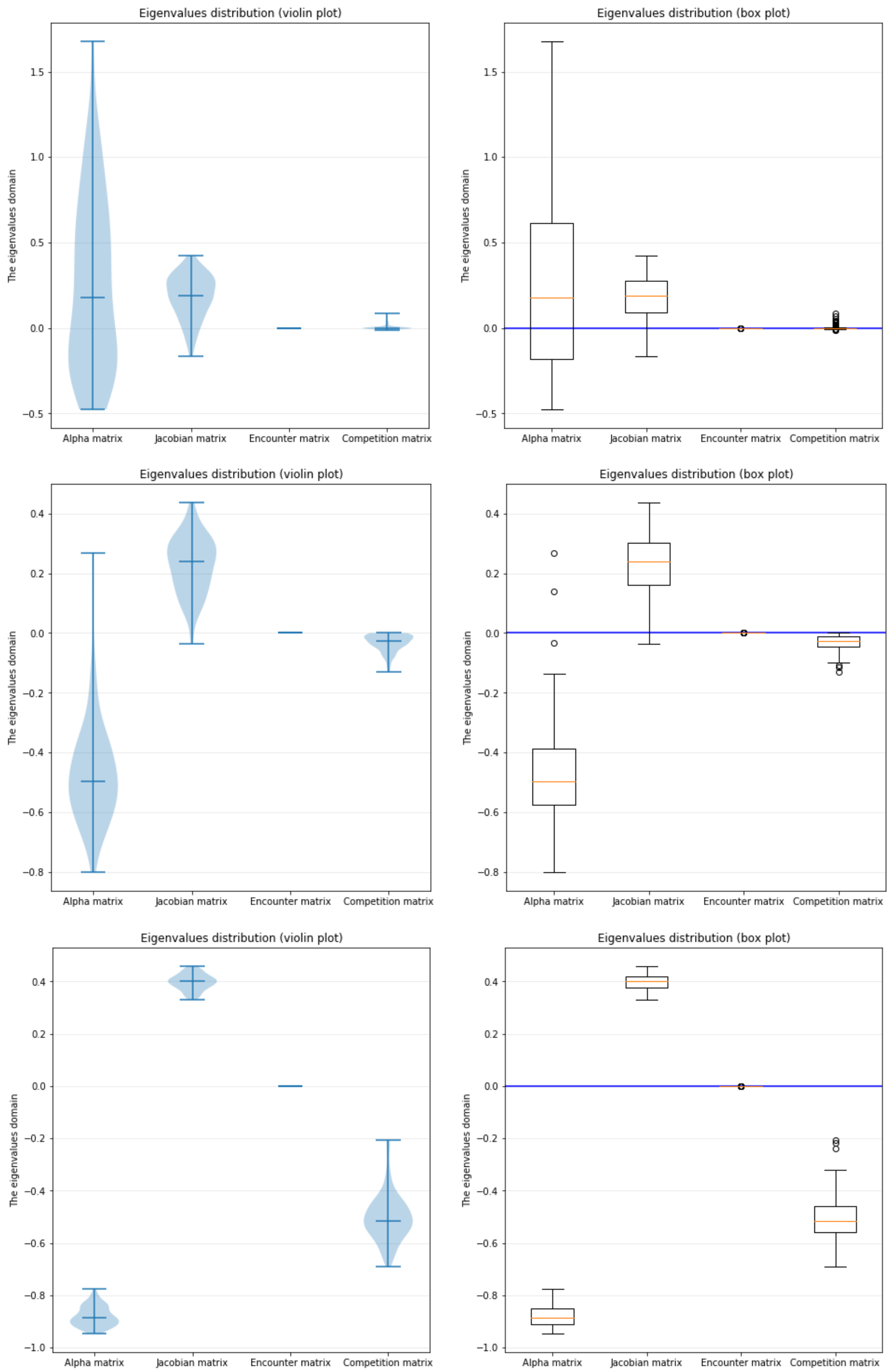

Figure 4.12: The violin and box plots of the eigenvalue distributions for different values of the interaction parameters $\alpha_{i,j}$ and standard deviations σ, when we have four interacting species in the community.

4.5 Statistical Analysis (T-test)

In this t-test, the statisticians are comparing between the t-value which we calculated from the data set that we test, with the t-test value that we compute it from the t-table. We will get the t-test result as follows:

1 Calculated t-value $<$ t-test value, then the comparison of the pair of the matrices eigenvalues are not sufficiently different.

2 Calculated t-value $>$ t-test value, then the comparison of the pair of the matrices eigenvalues are sufficiently different.

4.5.1 We will use the following statistical formulas.

$$M_i = \frac{\sum_1^{100} N_i}{100} \qquad i = 1, 2, .., 4, \tag{4.5.1}$$

$$s_i^2 = \frac{\sum_1^{n} (N_i - \overline{N_i})^2}{n} \qquad i = 1, 2, ..., 4, \tag{4.5.2}$$

$$SE_{i,j} = \sqrt{\frac{s_i^2}{n_i} + \frac{s_j^2}{n_j}} \qquad i, j = 1, 2, ..., 6 \quad \text{and} \quad i \neq j, \tag{4.5.3}$$

$$t - test = \frac{\overline{N_i} - \overline{N_j}}{SE_{i,j}} \qquad i = 1, 2, ..., n, \tag{4.5.4}$$

$$df_i = \frac{[\frac{s_i^2}{n_i} + \frac{s_j^2}{n_j}]^2}{\frac{(\frac{s_i^2}{n_i})^2}{(n_i-1)} + \frac{(\frac{s_j^2}{n_j})^2}{(n_j-1)}}, \tag{4.5.5}$$

where :

- $n \equiv$ The matrices number that we test.
- $M_i \equiv$The mean of the eigenvalues.
- $SE_{i,j} \equiv$The standard error of each pair of the data sets.
- $N_i \equiv$The magnitude of each eigenvalue.
- $s_i^2 \equiv$The variance of the eigenvalues.
- $s_i \equiv$The standard deviation of the eigenvalues.
- $df_i \equiv$ degrees of freedom.

4.5.1 Example. In this example we consider three interacting species with a random data sets of the interaction coefficients. The interaction coefficient are generated with zero mean and $\sigma = 1$. The off-diagonal elements are basically the parameters $\alpha_{i,j}$'s values. Using the data set to preform a t-test to see if the eigenvalues for each pair are significantly different or not. The hypothesises that we used for the t-test they are as follows:

H_0 : The eigenvalues of the matrices are significantly different,
H_1 : The eigenvalues of the matrices are not significantly different.

Calculations for the t-value

The calculations that we will use it to compute the t-value for the test are:

Alpha matrix calculations
$n_1 = 100$
$M_1 = -0.031$
$s_1^2 = 24.6$
Jacobian matrix calculations
$n_2 : 100$
$M_2 = -0.12$
$s_2^2 = 9.7$

Encounter matrix calculations
$n_3 = 100.$
$M_3 = 3.6e^{-17} \approx 0.$
$s_3^2 = 3.996e^{-33} \approx 0.$
Competition matrix calculations
$n_4 = 100.$
$M_4 = -0.029.$
$s_4^2 = 0.16.$

Alpha and Jacobian matrix t-value
T-value Calculation:
$SE_1 = 0.059$
$M_1 = -0.031$
$M_2 = -0.121$
$\alpha = 0.01$
$df_1 = 166$
$t = \frac{(M_1 - M_2)}{SE_1} = \frac{-0.031+0.12}{0.059} = 1.5383$
The calculated t-value $= 1.5383$
t-test $= \pm 2.60577034$
$1.5383 < 2.60577034$
calculated t-value $<$ t-test
The two matrices are not significantly different.

Competition and Jacobian matrix t-value
T-value Calculation :
$SE_4 = 0.0315.$
$M_2 = -0.121.$
$M_4 = -0.029.$
$\alpha = 0.01$
$df_4 = 102$
$t = \frac{(M_2 - M_4)}{SE_4} = \frac{-0.121+0.029}{0.0315} = 3.8426$
The calculated t-value $= 3.8426$
t-test $= \pm 2.62489148$
$3.8426 > +2.62489148$
calculated t-value $>$ t-test
The two matrices are significantly different.

Alpha and encounter matrix t-value
T-value Calculation:
$SE_2 = 0.0499$
$M_1 = -0.031$
$M_3 = 0$
$\alpha = 0.01$
$df_2 = 99$
$t = \frac{(M_1 - M_3)}{SE_2} = \frac{-0.031-0}{0.0499} = -0.61245$
The calculated t-value $= -0.61245$
t-test $= \pm 2.62640546$
$-0.61245 > -2.62640546$
$\Rightarrow 0.61245 < 2.62640546$
calculated t-value $<$ t-test
The two matrices are not significantly different.

Encounter and Jacobian matrix t-value
T-value Calculation:
$SE_5 = 0.0.03124$
$M_2 = -0.121$
$M_3 = 0$
$\alpha = 0.01$
$df_5 = 99$
$t = \frac{(M_2 - M_3)}{SE_5} = \frac{-0.121-0}{0.03124} = -2.9562$
The calculated t-value $= -2.9562$
t-test $= \pm 2.62640546$
$-2.9562 < -2.62640546$
$\Rightarrow 2.9562 > 2.62640546$
calculated t-value $>$ t-test
The two matrices are significantly different.

Alpha and Competition matrix t-value
T-value Calculation:
$SE_3 = 0.05$
$M_1 = -0.031$
$M_4 = -0.029$
$\alpha = 0.01$
$df_3 = 100$
$t = \frac{(M_1 - M_4)}{SE_3} = \frac{-0.031+0.029}{0.05} = -0.03712$
The calculated t-value $= -0.03712$
t-test $= \pm 2.62589052$
$-0.03712 > -2.62589052$
$\Rightarrow 0.03712 < 2.62589052$
calculated t-value $<$ t-test
The two matrices are not significantly different.

Encounter and competition matrix t-value
T-value Calculation:
$SE_6 = 0.0.004$
$M_3 = 0$
$M_4 = -0.029$
$\alpha = 0.01$
$df_6 = 99$
$t = \frac{(M_3 - M_4)}{SE_6} = \frac{0+0.029}{0.004} = 7.161$
The calculated t-value $= 7.161$
t-test $= \pm 2.62640546$
$7.161 > +2.62640546$
calculated t-value $>$ t-test
The two matrices are significantly different.

From this result of the t-test we can conclude

In these t-test we are trying to generalise the results from the sampling data sets to all populations, and to see if there any significant differences between the mean of the data sets. In our case we trying to find out about the stability of the network system. In other words, the behaviour of the network wither it stable or not. Looking to our t-test result, the data set of competition and encounter matrices are significantly different as well as competition and Jacobian, and encounter and Jacobian matrices. This implies different results in the network stability. The competition matrix gives a positive result (the network is stable), while the encounter matrix show that the network is not stable. The other combinations that we have are:

- Alpha and Jacobian matrix.
- Alpha and Competition matrix.
- Alpha and Encounter matrix.

In the t-test analysis they are not significantly different, that mean each pair of this combination have same result for network stability. They all imply the stability when we have three interacting species' in the network community.

4.6 Results and Discussion

Throughout the analysis with different standard deviations σ and number of species, there are some common patterns:

- The encounter matrix shows a majority of positive small eigenvalues with small variability.
- The competition matrix shows a vast majority of negative eigenvalues.
- The alpha matrix tends to display higher stability (larger fraction of negative eigenvalues) with decreasing standard deviation value (σ).
- The Jacobian matrix tends to display higher stability with odd numbers (three species in the community), versus lower stability with even numbers (two and four species in the community).

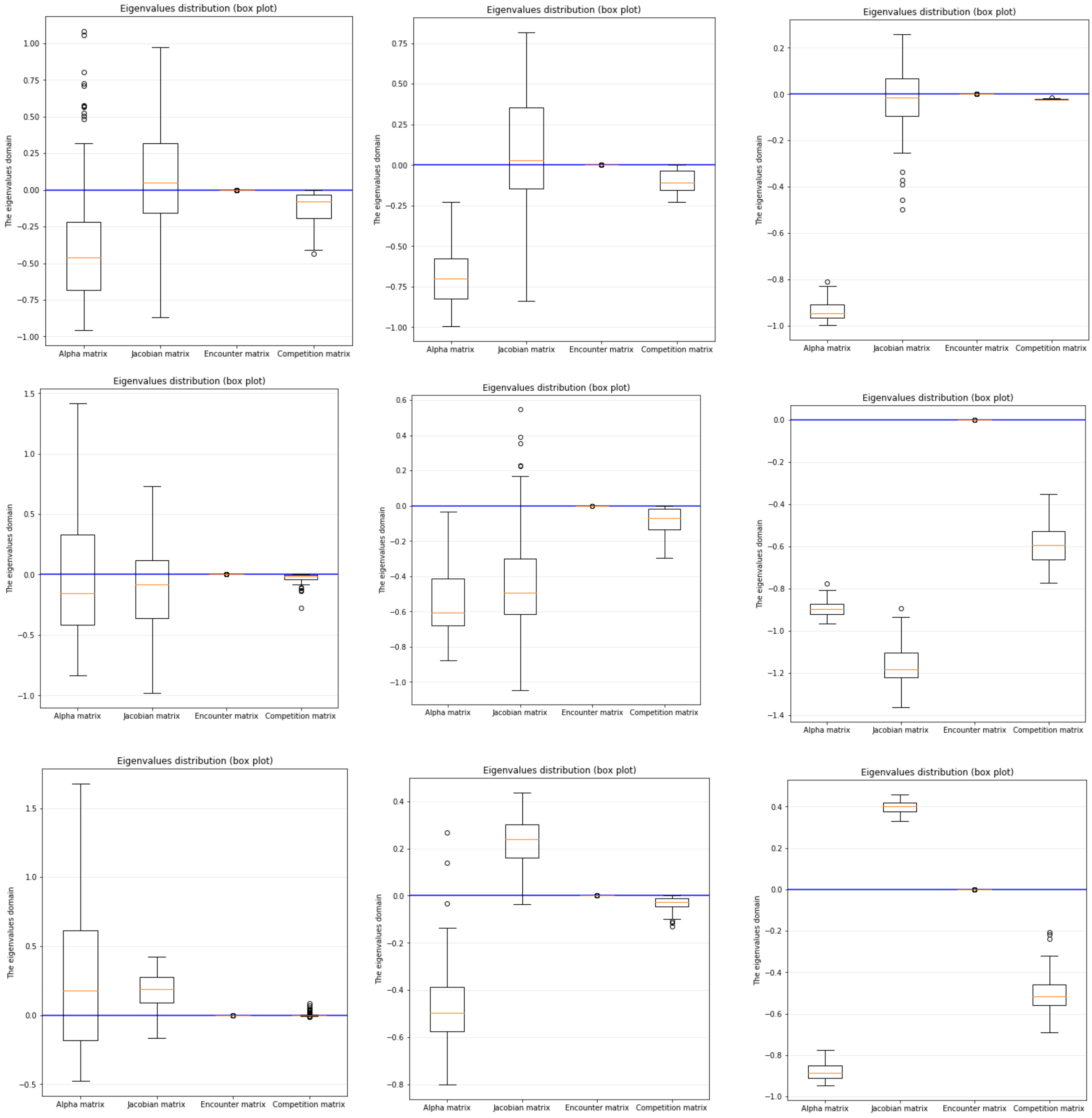

Figure 4.13: The box plot for all species of a 100 communities that we consider. Each community have two, three or four species, with different standard deviation.

By comparing the results in Table 4.1 for the numbers of the negative eigenvalues, we can observe that the stability in the community increases when we reduce the standard deviation of the sampling data sets - we observe the same in Table 4.2. The comparison is when we have more species in the network community, according to the results we find the stability of the network influence when we have more species in the community.

Four species case, the stability of the Jacobian matrix decreased when we decreased the standard deviation values (see Table 4.3).This contrasts with the two and three species case, when the stability implied by the results in the Jacobian increased with the degreasing standard deviation.

In the box plots we can see that the overlap between the leading eigenvalues of all the matrices is decreasing with small value of standard deviation, that means the result in the stability will differ in each matrix analysis until we find a reverse result as in Figure 4.13. The mean comparison is between the alpha matrix and the Jacobian matrix and we find that the outcome of the stability analysis is disparity from almost the same result in two species in the community and start to differ when we have three and four species.

In the t-test Example 4.5.1, three combinations from the pair groups combination of the eigenvalues are not significantly different, that means all these matrices overlap with each other. The other pair groups combinations of the eigenvalues are significantly different, and that means all these matrices not overlap with each other. That means they didn't have the same stability state for the network structure.

4.7 Conclusion

In previous sections, we saw the influence of the number of competing species in the community on the stability state of the ecological network community. In addition to the effect of changing interaction parameters in the networks, and according to the results from the analysis for each matrix we can conclude that if there any small perturbation in the network structure can effect the stability state of the network. Every species has a different way to respond to this perturbation, looking to the all tables and figures in the above section we can see the variety in the number of negative eigenvalues of each matrix which decreases when we have more species or when we decrease the values of parameters $r_i$andσ. From an ecological perspective that means the persistence probability of the network community decreases with more number of the species in the network [May (1972)]. This analysis supports May's argument about the persistence in large complex communities, he argued that the large communities have small persistence than the simple ones [May (1972)].

4.8 Future Directions

In this research we analyse data sets of all probability of the interaction between all species in the community. We assume that all the species interacts with each other. In real ecological networks the interaction strength has a probability less than 1. We suggest that, in future work we consider this probability. Also we just analyse the competition interaction in the network and the effect of the complicity in the network stability, next we can consider all possible interactions between species.

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