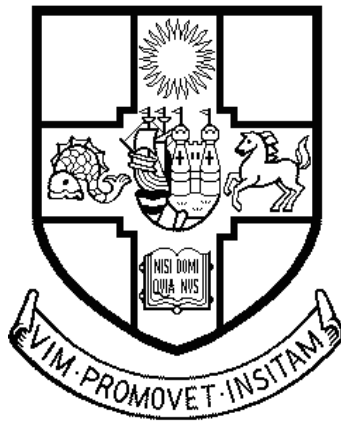


UNIVERSITY OF BRISTOL

# DEPARTMENT OF ENGINEERING MATHEMATICS



## A Simple Model of Biodiversity

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Project thesis submitted in support of the degree of

Bachelor of Engineering

June 2017

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## **Abstract**

This report proposes an IME model (Ignore, Make, and Eat) to model the food web to investigate the ecosystem biodiversity and understand what limits the number of coexisting species. Through applying two ecological rules, Competitive Exclusion and Not Eat in Cycle, the modeled food-web matrix will be close to the reality. The feasibility of IME model will be proved by comparing connectance of the model with connectance in nature. The connectance of the model is 0.28, and the range of nature connectance is 0.1 to 0.2. Although the result is in an acceptable range, IME model needs to be modified.

# Contents

<b>1</b>	<b>Introduction</b>	<b>5</b>
<b>2</b>	<b>Random Matrix to Represent the Food Web</b>	<b>7</b>
2.1	Three Basic Assumptions . . . . .	7
2.2	Two Ecological Rules . . . . .	7
2.3	Random Matrix . . . . .	8
<b>3</b>	<b>First Ecological Rule: Competitive Exclusion</b>	<b>10</b>
3.1	Apply Competitive Exclusion to the IME Model . . . . .	10
3.2	Theoretical expectation of the Competitive Exclusion . . . . .	12
<b>4</b>	<b>Second Ecological Rule: Not Eat in Cycle</b>	<b>13</b>
4.1	Two Methods to Apply Not Eat in Cycle . . . . .	13
4.1.1	First Method (Sorting Method) to Apply Not Eat in Cycle . . . . .	13
4.1.2	Second Method (Eigenvalue Method) to Apply Not Eat in Cycle . . . . .	14
4.2	Result after Applying Two Ecological Rules . . . . .	14
<b>5</b>	<b>Connectance of IME Model</b>	<b>16</b>
5.1	Definition of Connectance . . . . .	16
5.2	Double Counting . . . . .	16
5.2.1	What is double counting . . . . .	16
5.3	Two Methods to Calculate the Connectance . . . . .	17
5.3.1	First Method that is not affected by Double Counting . . . . .	17
5.3.2	Second Method that is Affected by Double Counting . . . . .	20
5.4	Compare the Connectance of Model with the Reality . . . . .	20
<b>6</b>	<b>Conclusion</b>	<b>22</b>

## List of Figures

1	Three-species food web with $P_E = 0.5$ . . . . .	9
2	Process to apply the Competitive Exclusion Rule . . . . .	10
3	The probability of randomly generating a feasible food web after applying the Competitive Exclusion Rule . . . . .	11
4	Process of sorting species in $3 \times 3$ matrix . . . . .	13
5	Process of sorting species in $4 \times 4$ matrix . . . . .	14
6	The proportion of feasible matrices in two methods after applying Not Eat in Cycle Rule	15
7	The proportion of feasible matrices after applying two ecological rules . . . . .	15
8	All combinations of the different matrices . . . . .	17
9	The food web of No.7 matrix and No. 10 Matrix . . . . .	17
10	Feasibility and Number of Links of all combinations . . . . .	18
11	Distribution of $X_K$ . . . . .	19
12	Distribution of $Y_K$ . . . . .	19
13	Distribution of $Z_K$ . . . . .	19
14	Trend of Connectance . . . . .	19
15	Estimated distribution in nature, when $N = 6$ . . . . .	20
16	Trend of connectance . . . . .	20

# 1 Introduction

Ecology has profited from a long history of research, a central question guiding ecological research is “Why are there so many species?” [1]. The main principle that limits the number of species is the competitive exclusion principle, which states if there are two species that have to share the same resources, one of them will extinct [2]. The competitive exclusion principle will also control the dynamics of ecosystems. Although in nature, resources in some situations are limited, these resources can still unexpectedly support many species. For instance, in the ocean, the only limiting resources are sunlight, nitrogen, carbon, iron, and phosphorus. Yet there are still hundreds of species of plankton. This phenomenon is called the “Paradox of the Plankton.” A solution to the puzzle is that species themselves can act as resources. So every species that we add acts as a resource again. So the competitive exclusion principle would allow food chains of infinite length. But they are not possible because the energy flow along the chain cannot sustain predators beyond a certain size.

To find which factor will affect biodiversity, an ecosystem model is developed. This model simulates a food web, which can describe the interactions between populations. This interaction transmits energy between species, and species have a direct or indirect relationship with each other [3]. Most species, in fact, have more than one food source; as a result, the food web could be intertwined. Therefore, the food web is a complex network. The energy flow can be described in the ecosystem through using stable isotopes [4], because the food web is a picture of the creature links between each other.

A simple food-web model needs to be produced to investigate what limits the number of coexisting species. The food webs are typically modelled as systems of differential equations where the population density of each species is described by one variable. The body size is the single biological trait subject to evolution. And the population dynamic of species with biomass and body size is modelled by differential equations [5]. In this report, a simple food-web model is provided, which is ANIME model. There are five elements that represent the interactions between each species. The five symbols are Avoid (A), Need (N), Ignore (I), Make (M), and Eat (E). However, in this report, we only consider trophic interaction (E), reproduction (M), and no interaction (I). Ignore means that the two species do not interact. Make denotes the reproduction process of a species. Moreover, Eat means that one species predate other species. To investigate what food webs can exist, an ensemble of random food webs is produced. The food web model consists of a random  $N \times N$  matrix that describes the interactions between  $N$  species.

The aim of this study is to explore whether the three constraints applied above are already sufficient

to produce realistic food webs structures. To this end, in section 2, we create an ensemble of food webs that obey these constraints and check whether they meet ecological expectations. In section 3 and sections 4, through applying two ecological rules, Competitive Exclusion and Not Eat in Cycle, the food web is studied. Competitive Exclusion means there cannot be two species that have the same niches [3]. Not Eat in Cycle means low trophic level species cannot eat high trophic level species. The main test is to compare whether the food webs created by the model have a connectivity that is comparable to the connectivity found in nature. Connectance is the actual food web interactions between species compared to the total possible number; usually expressed as a fraction. Realistic values are in the range of 0.1 to 0.2, with occasional outliers. Also, through comparing the connectance in nature, limits of the model are discussed, and the corresponding improvements will be provided.

## 2 Random Matrix to Represent the Food Web

In this section, there are three constraints that the IME model is based on. Also, the foundation of modelling the food web through mathematical method will be introduced.

### 2.1 Three Basic Assumptions

The first constraint is that every species needs to eat. Since every species needs to ingest food to maintain their life, the model compulsorily stipulates that every species needs to eat. However, in the food web, there is a basic resource. At the first trophic level, there are primary producers, which are typically plants and algae. These species do not usually eat others, but they usually absorb nutrients from soil or ocean. Therefore, in the food web, except the primary producer, other species need to eat.

The second constraint is that the length of the food chain is limited. The first level of the food chain is constituted by the autotroph, which is also called the producer (mainly plants). And species that feed on producers are at the second trophic level, as herbivorous trophic level [6]. The third trophic level includes all carnivores that depend on the herbivores. So the other levels could be deduced by this pattern. However, the energy flow through the trophic level would be significantly reduced, and about 10% of the energy in the food is available for next trophic level [7]. Therefore, the food chain and trophic level generally are with four or five levels, very rarely does it reach six levels. Since this reason, the model investigated in this report is based on six species.

The third constraint is that every species makes itself. In reality, evolution and gene exchange cause the diversity of species. Evolution in biology refers to the genetic traits that have been changed between generations [8]. The new trait will be transferred due to the migration of the species or the level of gene between the species. Hence the gene is transmitted in the population. When these genetic variants are affected by non-random natural selection becomes more common or no longer rare; the evolution has occurred [9]. Gene exchange is the combination of genes from multiple species. Gene level transfer is not only confined to microbes, but also plays an important role in many creatures, and possibly even all zoogenesis. However, in this report, these two aspects should be ignored to simplify the model, which means each species in the model should make itself, and there do not exist the evolution or gene exchange.

### 2.2 Two Ecological Rules

The first ecological rule is Competitive Exclusion. The competitive exclusion principle refers to that complete competitor cannot coexist. If there are two species that take in same food, provided if they are in the same territory, and if the propagation coefficient of species A is larger than the that of species

B, then species A will completely replace species B. Species B will become extinct [2]. Therefore, two populations cannot have the same resource. The competitive exclusion could contribute to the adaptive radiation, which could increase the diversity of species [2]. Under competitive exclusion, in order to continue to survive, the species will change their habitats or habits, such as becoming nocturnal animals.

The second rule is Not Eat in Cycle. This rule means species in low trophic level cannot eat the high-level species. The reason is that the energy transfers from producer to an apex predator. For instance, producers, first trophic level species, do not eat other species. They obtain energy from the sun by photosynthesis [6]. The second level species predate the first trophic level species. Other level species obey in the same pattern. Moreover, apex predator, which at the top of food chain, has no predator. On the other hand, low trophic level species do not have the ability to prey on organisms in high level. In order to eat another species, the predator has to be physically superior in interactions. Intuitively the predator must be able to kill the prey. Individuals of two species that could kill each other would rather avoid each other as the risks of being killed in an interaction would be greater than the possible gain of just one meal. Thus the predator can typically kill the prey without much risk, which implies that the prey cannot kill the predator, and thus the prey cannot be a predator of the predator. This shows that there can be no directed cycles of length 2 and by extension to more species, no directed cycles at all. This principle is even more pronounced in aquatic systems where the predators typically feed on prey that fits in their mouth in one piece. Thus in aquatic systems, a predator typically needs to have three times the body length of its prey.

### 2.3 Random Matrix

A food web can be represented by the matrix, and there are three relationships between species (Make (M=2), Eat (E=1) and Ignore (I=0)). Moreover, the probability that appears Eat ( $P_E$ ) is changing. Since the model is based on six species, hence the size of the matrix is  $6 \times 6$ . Based on the assumptions, there is a primary producer in the food web; therefore, the first row is 0(Ignore). Also, the diagonal is 2(Make) because all species make themselves. Other positions in the matrix should be either 0(Ignore) or 1(Eat). Firstly, these positions should be auto-filled with a random decimal number from zero to one. Then, the auto-filled number should compare with the  $P_E$ . If the value is less than  $P_E$ , the position should be 1. And if the value is larger than  $P_E$ , then the position should be 0. For instance, Figure 1 is a simple three-species food web with  $P_E = 0.5$ . It is clear that species A is the primary producer, so it cannot eat others. And species B predate the species C, and species C feeds on primary producer. The diagonal means every species makes itself. And the food web in the Figure 1 is corresponds to the matrix.



	<i>A</i>	<i>B</i>	<i>C</i>	
<i>A</i>	2	0	0	<i>B</i> ↑
<i>B</i>	0	2	1	<i>C</i> ↑
<i>C</i>	1	0	2	<i>A</i>

Figure 1: Matrix representation of a three-species food chain. An example of a  $3 \times 3$  interaction matrix is shown (left). The rows and columns of this matrix are labelled with the species (*A*, *B*, *C*). The respective elements indicate how the species interact. Every species makes itself (entry 2). Species *B* eats *C* and species *C* eats *A* (entry 1), otherwise the species ignore each other (entry 0). The network represented by this matrix is thus a food chain in which a predator *B* feeds upon a grazer *C*, which feeds on an autotroph *A*. This can also be represented by a simple diagram (right) where arrows indicate biomass flow.

### 3 First Ecological Rule: Competitive Exclusion

This section will apply the Competitive Exclusion to the model. Trough utilizing the numerical method to obtain the trend of feasibility that changes with probability that appears  $E(P_E)$ . Moreover, theoretical expectation  $P_E$  will be presented.

#### 3.1 Apply Competitive Exclusion to the IME Model

In this model, the effect of competitive exclusion is that there should be no two identical rows in the matrix. Given an interaction matrix  $M$ , two species  $i, j$  are at the risk of competitive exclusion if their interaction is symmetrical and if they interact in the same way with every other species  $k$  that is not  $i$  or  $j$ . We can write these conditions as  $M_{ij} = M_{ji}$  and  $M_{ik} = M_{jk}$  (for  $k$  is other species). In order for a food web to be feasible there can be no pair  $i, j$  that meets these conditions. In Figure 2, there is the process of applying the competitive exclusion rule.

$$\begin{array}{ll}
 \text{First Row} & 2 \quad 0 \quad 0 \quad 0 \\
 \text{Second Row} & 0 \quad 2 \quad 1 \quad 0 \\
 \text{Third Row} & 1 \quad 0 \quad 2 \quad 1 \\
 \text{Fourth Row} & 1 \quad 0 \quad 0 \quad 2
 \end{array} \tag{1}$$

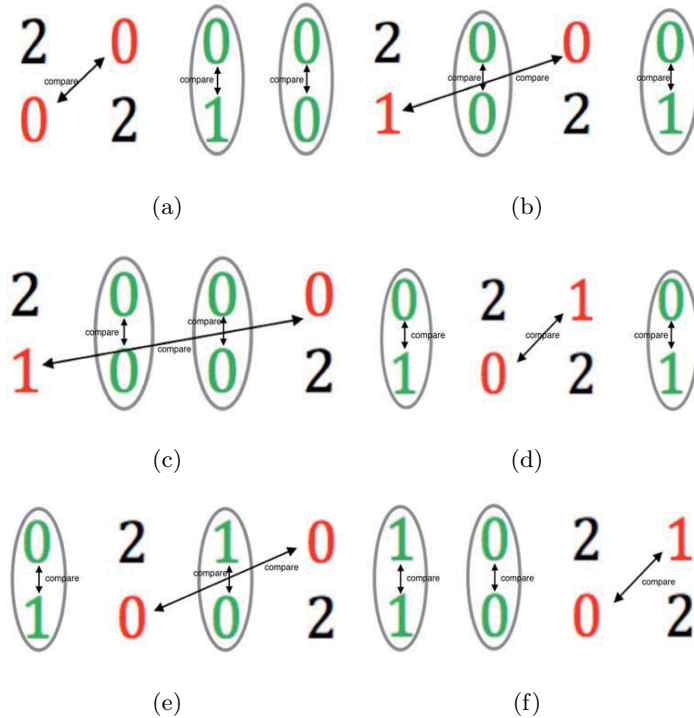


Figure 2: In Equation 1, there is a  $4 \times 4$  matrix, which represents the interactions between 4 species. In (a) to (g), it explains how to apply the competitive exclusion. (a) shows the process that compares the

first row with the second row, except for corresponding positions of **2**, other two positions should compare correspondingly (labeled green). And the corresponding positions of **2** in two rows should use cross-comparison (labeled red). After comparing the first and second rows, the third row will be compared through using the same method, as shown in (b). From (c) to (g), there are other four times comparisons. If competitive exclusion is applied, there will be  $\frac{N \times (N-1)}{2}$  times comparisons (N is the number of species).

Figure 3 shows the probability of a randomly generated food web being feasible. While calculating numerical values, the probability of appearing Eat is equally divided into 100 values. Under each probability, there will be 10,000 random matrices that are produced. And the number of valid matrices can be recorded. The probability of generating a feasible food web strongly depends on the probability with which an "eats" interaction is selected. Figure 3 shows that feasible webs are most likely, if 'eats' interactions are chosen with 50% probability. The trends of two curves are similar. Therefore, the result obtained from the numerical method is the same as  $P_{feasible}$ . In conclusion, the validity of probability of valid matrix is proven. The trend of validity is similar to a normal distribution. When probability of appearing Eat 1 is at 0.5, the maximum value of proportion of valid matrix is approximately 60%. Therefore, after applying competitive exclusion, the maximum validity is 60%.

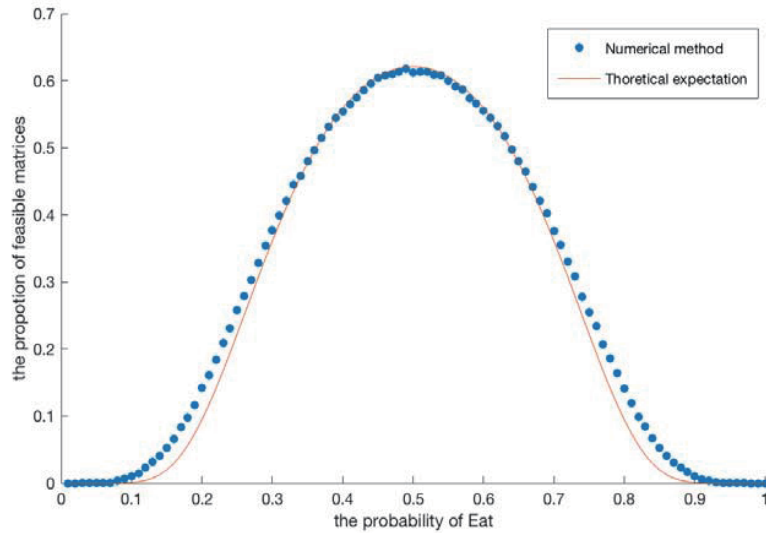


Figure 3: The probability of randomly generating a feasible food web with changing probability of appearing Eat. Red line shows the theoretical expectation, and the blue dotted line shows the numerical values for the probability of generating a feasible food web.

### 3.2 Theoretical expectation of the Competitive Exclusion

The probability of a randomly generated food web being feasible will be calculated in the theoretical method, which means there are no two identical rows in an  $N \times N$  matrix. Assume there are  $N$  species, and the probability of appearing Eat is  $p$ . If two species are taken, there will be  $N - 1$  comparisons. The reason of  $N-1$  comparisons is the position that has “2” cannot be compared. The species in first row is in the primary trophic level, and it eats nothing. Hence, the first row is fixed. Firstly, the probability that the first row meets the competitive exclusion condition with another one of the  $N - 1$  other species will be calculated. For two species (first species and one in other  $N - 1$  species), there are  $N - 1$  number of comparisons. Equation  $1 \times p = p$  shows the probability of a random comparison being different. The first row is fixed; therefore, the probability of appearing 0 in the first row is 1. The probability for one different comparison is  $p$ . In equation  $p^{N-1}$ , the probability that two species are different is obtained. For two species, there are  $N - 1$  comparisons that need to be performed. Hence, the probability of two different species is  $p^{N-1}$ . To ensure the first row is different from other  $N - 1$  rows, the first row will have to be compared for  $N-1$  times. Therefore, equation  $p^{N-1}$  will be repeated for  $N-1$  times. Therefore, the probability that all pairs are different ( $P_1$ ) is  $p^{(N-1)^2}$ .

The next step is to ensure other  $N-1$  rows are different. Firstly, the probability of two randomly selected species being identical needs to be obtained. In equation  $p^2 + (1 - p)(1 - p) = p^2 + \bar{p}^2$ , shows the probability that one comparison of two species is identical. The situation that one comparison is identical, when they are either both 0 or 1. And there are  $N-1$  comparisons for two species. Therefore, the probability that two species are identical is  $(p^2 + \bar{p}^2)^{N-1}$ . There can be two outcomes for comparison between two rows. The first one is that they are identical, and the second one is that they are different. Therefore, the probability that two species are different is  $1 - (p^2 + \bar{p}^2)^{(N-1)}$ . To ensure all  $N-1$  species are different,  $\frac{(N-1)(N-2)}{2}$  number of comparisons are needed to compare all rows. In equation  $P_2 = (1 - (p^2 + \bar{p}^2)^{N-1})^{\frac{(N-1)(N-2)}{2}}$ , the probability that all pairs are different ( $P_2$ ) is represented. The total probability of feasible food web is the sum of the probability that first row is different with other  $N-1$  rows ( $P_1$ ) and the probability of other  $N-1$  rows that are different ( $P_2$ ). ( $P_{feasible} = P_1 \times P_2$ )

## 4 Second Ecological Rule: Not Eat in Cycle

This section will discuss Not Eat in Cycle, and through two methods to find the validity. Results from two methods will be compared, and the final validity will be obtained.

### 4.1 Two Methods to Apply Not Eat in Cycle

In this section, there are two methods will be introduced to apply the rule. The first method is the sorting method. And the second method is to calculate the eigenvalues.

#### 4.1.1 First Method (Sorting Method) to Apply Not Eat in Cycle

Every matrix that obeys the rule can be sorted such that it becomes a lower trigonal matrix (all entries in the upper triangle are 0). The first method is to examine whether the values in upper diagonal part are all zero. If all upper diagonal are zero, the matrix will obey the second rule. However, before examining the upper diagonal part, species need to be sorted. In Figure 4, there is a  $3 \times 3$  random matrix, and this matrix will be sorted from low-level species to high-level species, but the order of the matrix will have no effect on the food web represented. Bubble sort method will be applied. And in this case, the lowest level is species B and the highest level is species C. In the upper diagonal part, there are all zeros. Therefore, the matrix in Figure 4 obeys the rule. In Figure 5(a), there is a  $4 \times 4$  matrix, and from Figure 5(b) and Figure 5(f) are the process of sorting. In Figure 5(e), since species A and species D have no relationship, these two species do not need to be sort. Also, species B and species C have no relationship. The meaning of matrix in Figure 5(f) is equivalent to the original matrix. After sorting, the upper diagonal part could be examined. In Figure 5(f), there is a 0 in the upper diagonal part. Hence, this  $4 \times 4$  matrix breaks the Not Eat in Cycle rule.

	I	II	III		I	II	III		II	I	III
<i>Species A</i>	2	1	0	<i>Species B</i>	0	2	0	<i>Species A</i>	2	0	0
<i>Species B</i>	0	2	0	<i>Species A</i>	2	1	0	<i>Species B</i>	1	2	0
<i>Species C</i>	1	0	2	<i>Species C</i>	1	0	2	<i>Species C</i>	0	1	2
(a)				(b)				(c)			

Figure 4: This is the process of sorting species in  $3 \times 3$  matrix. Firstly, species A and species B will be compared. The species A predate species B (labelled red in (a)); therefore, the rows of these two species should be swapped, as shown in (b). And the relationship between two species should be the same. In two rows (species A and species B for this case), columns that contain **2** (column I and column II for this case) should be switched. The matrix after the first sort is represented in (c). Then the species A and species C should contrast. In (c), species A is the food of species C; therefore, the sort is finished.

	I	II	III	IV		I	II	III	IV			II	I	III	IV
Species A	2	1	1	0	Species B	0	2	0	0	Species B	2	0	0	0	0
Species B	0	2	0	0	Species A	2	1	1	0	Species A	1	2	1	0	0
Species C	1	0	2	0	Species C	1	0	2	0	Species C	0	1	2	0	0
Species D	0	0	1	2	Species D	0	0	1	2	Species D	0	0	1	2	0

(a)

	I	II	III	IV		I	II	III	IV			II	I	III	IV
Species A	2	1	1	0	Species B	0	2	0	0	Species B	2	0	0	0	0
Species B	0	2	0	0	Species A	2	1	1	0	Species A	1	2	1	0	0
Species C	1	0	2	0	Species C	1	0	2	0	Species C	0	1	2	0	0
Species D	0	0	1	2	Species D	0	0	1	2	Species D	0	0	1	2	0

(b)

	II	I	III	IV		II	I	III	IV			II	I	III	IV
Species B	2	0	0	0	Species B	2	0	0	0	Species B	2	0	0	0	0
Species C	0	1	2	0	Species C	0	2	1	0	Species A	1	2	1	0	0
Species A	1	2	1	0	Species A	1	1	2	0	Species C	0	1	2	0	0
Species D	0	0	1	2	Species D	0	1	0	2	Species D	0	0	1	2	0

(c)

	II	III	I	IV		II	III	I	IV			II	III	I	IV
Species B	2	0	0	0	Species B	2	0	0	0	Species B	2	0	0	0	0
Species C	0	1	2	0	Species C	0	2	1	0	Species A	1	2	1	0	0
Species A	1	2	1	0	Species A	1	1	2	0	Species C	0	1	2	0	0
Species D	0	0	1	2	Species D	0	1	0	2	Species D	0	0	1	2	0

(d)

	II	III	I	IV		II	III	I	IV			II	III	I	IV
Species B	2	0	0	0	Species B	2	0	0	0	Species B	2	0	0	0	0
Species C	0	1	2	0	Species C	0	2	1	0	Species A	1	2	1	0	0
Species A	1	2	1	0	Species A	1	1	2	0	Species C	0	1	2	0	0
Species D	0	0	1	2	Species D	0	1	0	2	Species D	0	0	1	2	0

(e)

	II	III	I	IV		II	III	I	IV			II	III	I	IV
Species B	2	0	0	0	Species B	2	0	0	0	Species B	2	0	0	0	0
Species C	0	1	2	0	Species C	0	2	1	0	Species A	1	2	1	0	0
Species A	1	2	1	0	Species A	1	1	2	0	Species C	0	1	2	0	0
Species D	0	0	1	2	Species D	0	1	0	2	Species D	0	0	1	2	0

(f)

Figure 5: Process of sorting species in  $4 \times 4$  matrix

#### 4.1.2 Second Method (Eigenvalue Method) to Apply Not Eat in Cycle

The second method is to calculate eigenvalues of matrices. In a lower triangular matrix, the eigenvalues are the entries on the diagonal. So in our case the entries should all be two. Sorting may destroy the triangular structure, but it should not change the eigenvalues. If the matrix obeyed the rule, all eigenvalues should still be 2. And if the real part of an eigenvalue is larger than 2, the Not Eat in Cycle rule will be broken. The reason that the threshold value is 2 is that values on the diagonal line are 2 and the matrix is not uniform. The eigenvalues of matrix in Figure 5 are  $\lambda_1 = 1$ ,  $\lambda_2 = 2$  and  $\lambda_3 = 3$ . Since there is an eigenvalue larger than 2, this matrix does not obey the rule. Also, the result from eigenvalue method is same as the result from sorting method. The matrix in Figure 5 breaks the rule.

#### 4.2 Result after Applying Two Ecological Rules

Figure 6 shows trends after applying the ecological rule, Not Eat in Cycle. The results obtained from two methods are consistent. At each probability, there are 5,000 random matrices that are utilized. Then the number of valid matrices are recorded. With the increasing probability of Eat, the value of validity decreases gradually. When the probability is about 0.5, the value of validity approaches zero. Figure 7 shows the result that the IME model is applied to two ecological rules. The maximum value of validity is about 1.8%, when the probability of Eat is at 0.33. When “Eat” interactions are chosen 33% probability, there is the largest number of the feasible food web. Link is the pairwise interaction. And in IME model, link means Eat. In  $6 \times 6$  matrix, since the values first row and the diagonal line are fixed, there are 25 positions that could be filled. In this case, for the  $6 \times 6$  matrix, when the number of the link is about 8 ( $25 \times 0.33 \approx 8$ ), there will be a maximum value of the valid matrix.

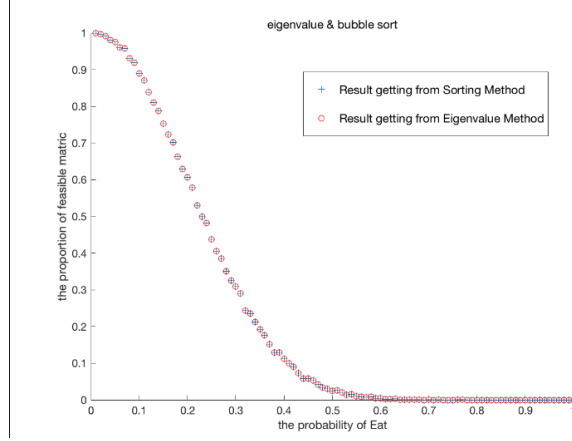


Figure 6: the proportion of valid matrix changing with the probability of Eat in two methods after applying Not Eat in Cycle Rule

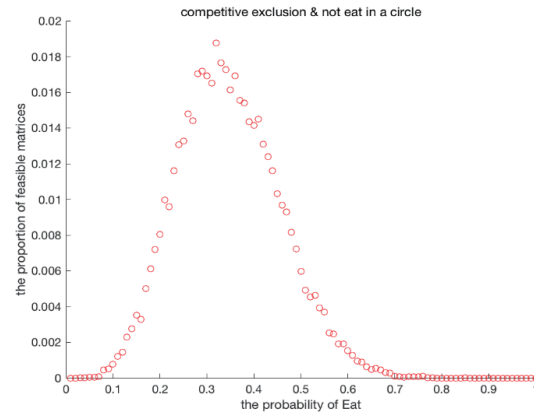


Figure 7: the proportion of valid matrix changing with the probability of Eat after applying two ecological rules

## 5 Connectance of IME Model

This section will introduce connectance, which is a crucial indicator to judge a food web. Before calculating connectance, the double counting phenomenon will be discussed. Finally, the calculated connectance will compare with the connectance in reality.

### 5.1 Definition of Connectance

Connectance ( $C$ ) is defined as the number of trophic links in food web divided by the total number of interactions. Connectance can be calculated as  $C = \frac{E}{N^2}$  [10]. In this equation,  $E$  represents the number of links, and  $N$  denotes the number of species in food web. Connectance plays an important role in determining the real food web [11]. For example, connectance can influence some properties of communities, such as the length of food chain [12]. Also, connectance could reflect the stability population dynamic. If there is a high connectance, the instability of population dynamics will appear [13]. Meanwhile, the high connectance could lead to a community that possesses lower probability to be feasible, and the recovery rate after small perturbations will be lower [14]. Therefore, connectance could reflect the property of food-web matrix.

### 5.2 Double Counting

#### 5.2.1 What is double counting

Before calculating connectance, the total number of different webs should be obtained, because the estimated distribution is based on feasibility and number of different food webs. Meanwhile, the estimated  $E$  could be obtained from estimated distribution. Therefore, finding the total number of different food webs is crucial. However, when food web is counted, there are some matrices that are repeatedly counted. The following example explains what is double counting. Take a  $3 \times 3$  matrix as an example:

$$\begin{array}{ccc} 2 & 0 & 0 \\ A & 2 & B \\ C & D & 2 \end{array}$$

A, B, C and D are four positions that will appear 1. In Figure 8, there is a table to list all possible combinations and the validity of the matrix.



	A	B	C	D	Feasibility
No.1	0	0	0	0	Miss E
No.2	0	0	0	1	Miss E
No.3	0	0	1	0	Miss E
No.4	0	0	1	1	Miss E
No.5	0	1	0	0	Miss E
No.6	0	1	0	1	Cycle
No.7	0	1	1	0	Ok
No.8	0	1	1	1	Cycle
No.9	1	0	0	0	Miss E
No.10	1	0	0	1	Ok
No.11	1	0	1	0	Com.Ex.
No.12	1	0	1	1	Ok
No.13	1	1	0	0	Miss E
No.14	1	1	0	1	Cycle
No.15	1	1	1	0	Ok
No.16	1	1	1	1	Cycle

Figure 8: All combinations of the matrix is shown. ‘Miss E’ means that there are some species that do not eat anything. ‘Cycle’ means that the Not eat in cycle rule is broken. And ‘Com. Ex.’ means that the competitive exclusion is broken. ‘Ok’ means that the matrix represents a feasible food web.

If the combination method is applied to calculate the number of different webs, there will be 16 different webs. However, in these 16 matrices, there exist some equal matrices. As shown in the example, No.7 matrix and No.10 matrix are same, as well as No.12 matrix and No.15 matrix. In Figure 9, it shows the corresponding food webs of No.7 and No.10. Although the positions of species 2 and that of species 3 exchange in these two food webs, the structures of two food webs have no difference. Therefore, there should be 14 different matrices. Since this reason, the combination method cannot be applied to calculate the number of different webs.

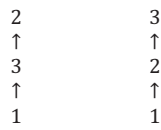


Figure 9: The food web of No.7 matrix and No.10 matrix

### 5.3 Two Methods to Calculate the Connectance

In this section there are two methods will be introduced to calculate the connectance. The first method is not affected by double counting, and the second method will be affected. Moreover, the results from these two methods will be compared.

#### 5.3.1 First Method that is not affected by Double Counting

In this method, the estimated E is the mean of the number of links in feasible food webs. Therefore, the estimated E is based on the probability that a random food web has K links (defined as  $Z_K$ ). Double counting will not affect the final result. There are two parameters which  $Z_K$  depends on.  $X_K$

is the probability that a randomly generated network has  $K$  links. The calculating method is shown in equation 2. In equation 2,  $N$  means that the largest link number can be reached.  $Y_K$  is the probability that a network with  $K$  links is feasible. The equation 3 represents the calculation method. And the equation to calculate  $Z_K$  is  $Z_K = \frac{X_K Y_K}{\Sigma_K X_K Y_K}$ .

$$X_k = \frac{\text{the number of network that has } K \text{ link}}{\text{total number of different networks}} \quad K = 1, 2, 3, \dots, N \quad (2)$$

$$Y_k = \frac{\text{the number of feasible network that has } K \text{ link}}{\text{total number of network that has } K \text{ link}} \quad K = 1, 2, 3, \dots, N \quad (3)$$

Take  $3 \times 3$  matrix in Figure 8 as an example to display the process to get connectance. In Figure 10, the number of links ( $K$ ) in each matrix is labeled. With the increase of  $K$ ,  $X_K$  can be calculated by using the method shown in equation 2. The result is  $X_K = (\frac{1}{16}, \frac{4}{16}, \frac{6}{16}, \frac{4}{16}, \frac{1}{16})$ , as shown in Figure 11. And  $Y_K = (0, 0, \frac{1}{3}, \frac{2}{4}, 0)$  shows in Figure 12. Before calculating  $Z_K$ , the  $\Sigma_K X_K Y_K$  should be obtained.  $\Sigma_K X_K Y_K = 0 + 0 + \frac{1}{8} + \frac{1}{8} + 0 = \frac{1}{4}$ . And Figure 13 shows the tendency of  $Z_K$ . ( $Z_K = (0, 0, \frac{1}{2}, \frac{1}{2}, 0)$ ) Connectance for  $3 \times 3$  matrix is  $C = \frac{K}{N^2} = \frac{2 \times 0.5 + 3 \times 0.5}{3^2} = 0.28$ . And the connectance with other different number of species should be calculated with the same method. And the pattern of connectance is shown in Figure 14. And the trend of connectance is approximate to  $\frac{K}{N^2} = 0.28$ . (labeled in red curve)

	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>	<i>Feasibility</i>	<i>Number of Link(K)</i>
<i>No.1</i>	0	0	0	0	<i>Miss E</i>	0
<i>No.2</i>	0	0	0	1	<i>Miss E</i>	1
<i>No.3</i>	0	0	1	0	<i>Miss E</i>	1
<i>No.4</i>	0	0	1	1	<i>Miss E</i>	2
<i>No.5</i>	0	1	0	0	<i>Miss E</i>	1
<i>No.6</i>	0	1	0	1	<i>Cycle</i>	2
<i>No.7</i>	0	1	1	0	<i>Ok</i>	2
<i>No.8</i>	0	1	1	1	<i>Cycle</i>	3
<i>No.9</i>	1	0	0	0	<i>Miss E</i>	1
<i>No.10</i>	1	0	0	1	<i>Ok</i>	2
<i>No.11</i>	1	0	1	0	<i>Com.Ex.</i>	2
<i>No.12</i>	1	0	1	1	<i>Ok</i>	3
<i>No.13</i>	1	1	0	0	<i>Miss E</i>	2
<i>No.14</i>	1	1	0	1	<i>Cycle</i>	3
<i>No.15</i>	1	1	1	0	<i>Ok</i>	3
<i>No.16</i>	1	1	1	1	<i>Cycle</i>	4

Figure 10: Feasibility and Number of Links of all combinations

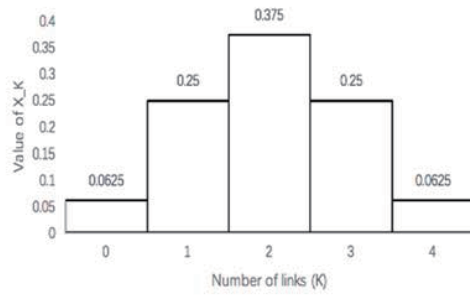


Figure 11: Distribution of  $X_K$

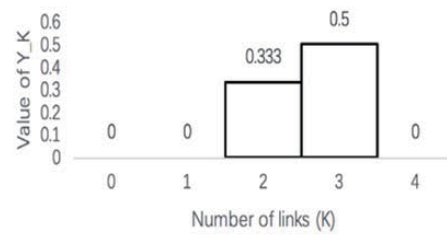


Figure 12: Distribution of  $Y_K$

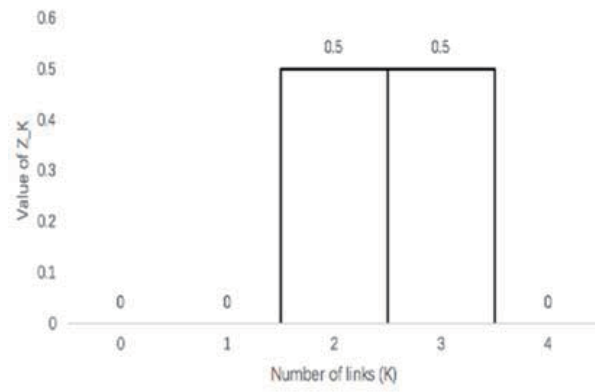


Figure 13: Distribution of  $Z_K$

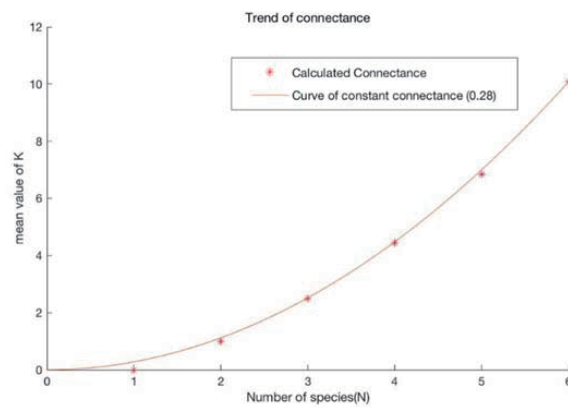


Figure 14: Trend of Connectance

### 5.3.2 Second Method that is Affected by Double Counting

This method is to find estimated distribution in nature, which is the product of feasibility and number of different food webs. However, double counting has not been taken into account. And the number of different food webs will use combination method to calculate. In Figure 15, it is the tendency of the estimated distribution, when the number of species is six. And the estimated  $E$  is the mean of the number of links in the estimated distribution. Figure 16 is the trend of connectance. In Figure 16, the value of connectance is not affected by double counting from one species to four species; it is about 0.28. However, when the number of species changes to five and six, there is a huge gap between calculated connectance and correlation line. Therefore, double counting has a significant influence on the number of species reaching five.

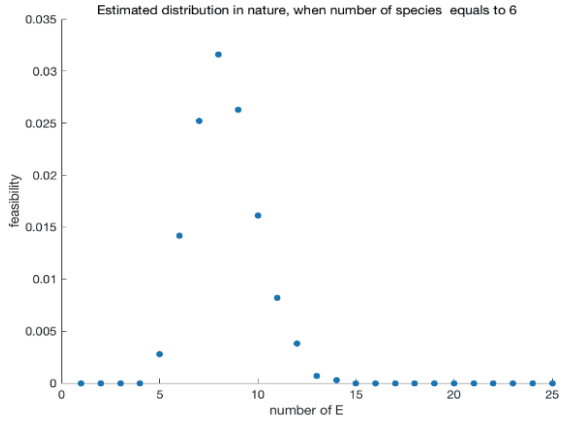


Figure 15: Estimated distribution in nature, when  $N = 6$

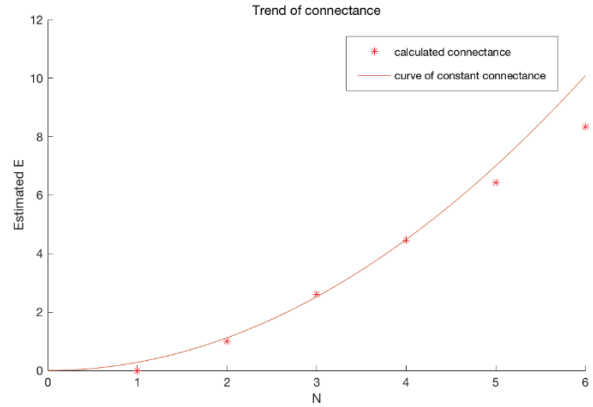


Figure 16: Trend of connectance

## 5.4 Compare the Connectance of Model with the Reality

There is an experiment to survey the value of connectance. The experiment is based on 16 high-quality food webs, which are in a wide range of species number, taxa and habitat types. The range of size of the 16 food webs is from 25 to 172 species. Finally, connectance range for these 16 food webs is from 0.026 to 0.315, and the average connectance is 0.11 [13]. Therefore, the normal connectance range should be between 0.1 and 0.2. And the estimated connectance is about 0.28. So our value is at the top end of the plausible range but within the range of values found in real nets. There is a slight difference between these two data. The first reason of the difference is that the size of the food web in IME model is smaller than the food web size in the experiment. Since the small food web size, the accuracy of calculating connectance will be reduced. The second reason is that the IME model solely applies two important ecological rules, competitive exclusion and not eat in cycle; however, there are other ecological rules in reality, such as resource partitioning and interspecies competition. These ignored

rules are less crucial than applied rules, but these ignored rules will affect the feasibility of food-web matrix to some extent. Therefore, the calculated connectance will higher than connectance in reality.

## 6 Conclusion

This model is to establish a food web model to find which factor that will affect the biodiversity. Through applying competitive exclusion and not eat in cycle, the model will be more realistic. Moreover, the connectance of the model is 0.28. This value is at the top end of the plausible range, but within the range of values found in real nets. Therefore, the feasibility of IME model is proved. And the feasible web will be most likely, when the probability of appearing “Eat” interaction at 0.33. In another word, when the number of links is about 8 in the model, there will be a maximum feasible web.

However, this model faces some challenges. The key challenge for IME model is to detect the connectance for large species number. In the model, the species number is less than six. However, in reality, species number in food web will far more than six. If the species number in IME model exceeds six, the feasibility of model will be difficult to proof. For the present IME model, connectance is the only method to prove the feasibility of model. However, when calculating connectance in the model, all possible combinations of different matrices are considered. For instance, for six species model, there are approximate 44,000,000 different matrices. It will take a large amount time to prove the feasibility of the model. Therefore, the method that calculates connectance needs to be modified to fit a large scale of species numbers. And there should be other methods to test the feasibility of model.

Before starting to focus on further work, the method of calculating connectance needs to be improved to prove the feasibility of IME model with a large scale of species number. Further work may need to focus on ANIME model, which has two more parameters (Avoid (A), Need (N)). These two parameters represent other two relationships between species. For instance, since bird needs a tree to nest, in the row of the food-web matrix that corresponds to “Bird,” we would have ‘N’ in the column that corresponds to “Oak.” “Oak” occludes the sun and therefore other most “Other Plants” cannot grow under “Oak.” They need to avoid the “Oak.” There should be relationship ‘A’ in the row that corresponds to “Oak” and “Other Plants.” Through these five parameters, food web could be modeled better. Another thing to look at would be other network matrices. We considered only connectance, but there are many other metrics. For instance, natural food webs have a characteristic ratio of prey species per predator.

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