SENSITIVITY OF SYSTEM-WIDE ECOSYSTEM MEASURES TO MODEL DATA

by

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(Under the direction of Caner Kazanci)

ABSTRACT

Ecological network measures are used to capture system-wide properties of ecosystems. The aim of this study is to investigate the sensitivity of flow-based ecological network measures to model perturbations. We characterize the patterns of these system-wide measure changes with respect to the network size and structural properties of the ecosystem. The method for creating a sequence of perturbations for steady-state flow modes also informs us about the minimum amount of flow data needed to build a full model that can predict certain system-wide network measures with reasonable accuracy. The results of this work improve our understanding of ecological network measures and also pose new open questions for future research.

INDEX WORDS: Ecological network analysis, Network model, System-wide measures

Sensitivity of system-wide ecosystem measures to model data

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DEDICATION

This dissertation is dedicated to my family.

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Chapter 1

Introduction

Ecological Network Analysis (ENA) [20, 6, 26] is a system-oriented methodology to analyze the transactions of energy, matter, and nutrients between compartments within ecosystem models. ENA provides various measures to capture different aspects of the ecosystem, such as link density, total system throughflow (TST), the ratio of indirect to direct effects (I/D) [19, 9], Finn's cycling index (FCI) [7], synergism [21], and mutualism [5]. These system-wide measures serve to uncover the complex relationships and influences among all compartments. For example, FCI [8] measures the proportion of total system throughflow (TST) generated by cycling (TST_c); and mutualism [5] represents the ratio of positive to negative interactions.

ENA relies on compartment models defined by nodes (vertices, compartments, components, storages, etc.) and connections between them (arcs, links, flows, etc.) that represent the ecosystem. A typical example is the intertidal oyster reef energy flow ecosystem model [3] as shown in Figure 1.1. This example demonstrates several properties. First, it is an open model since the environment is represented explicitly as directed edges that carry afferent and efferent flows from and to environmental sources and sinks [1]. Second, the links that connect compartments are weighted by a real number that quantifies the flow rate. Finally, the oyster reef model is at steady-state because the total inputs and outputs are equal for each compartment. Ecological networks are widely used to describe both biotic and abiotic interactions among species themselves, as well as interactions with their external environment. Based on the purpose of a particular model, compartments may represent species, a group of species with common properties (e.g., predatory fish) or even non-living parts of the ecosystem. Ecological network models can also be used to assess the stability of an ecosystem to perturbations (e.g., species extinction, climate change) which is defined as the propensity of an ecosystem returning to its functioning regime after a stress or a perturbation [15].

The primary purpose of this work is to investigate the sensitivity of system-wide ecological network measures to certain changes in the ecosystem model. The results inform us about the reliance of network measures in data accuracy, which is a common concern for any analysis based on empirical data. The secondary purpose of this work is to identify the minimum amount of empirical data needed to predict certain system-wide measures with reasonable accuracy. Given a model structure, certain amount of flows need to be quantified to build an ecosystem model at steady-state. For a given compartmental model, the minimum number of flows that needs to be quantified is equal to the difference between the number of flows and the number of compartments [12]. For example, for the Oyster reef model, this value is $19 - 6 = 13$. However, given that empirical measurements contain a certain amount of error, the number of empirical measurements necessary to compute a system-wide measure with reasonable accuracy may be significantly less. To achieve both goals simultaneously, we devise a sequence of model perturbations (chapter 2), and apply them to three real ecosystem models from literature (chapter 3), and our observations (chapters 3 and 4).

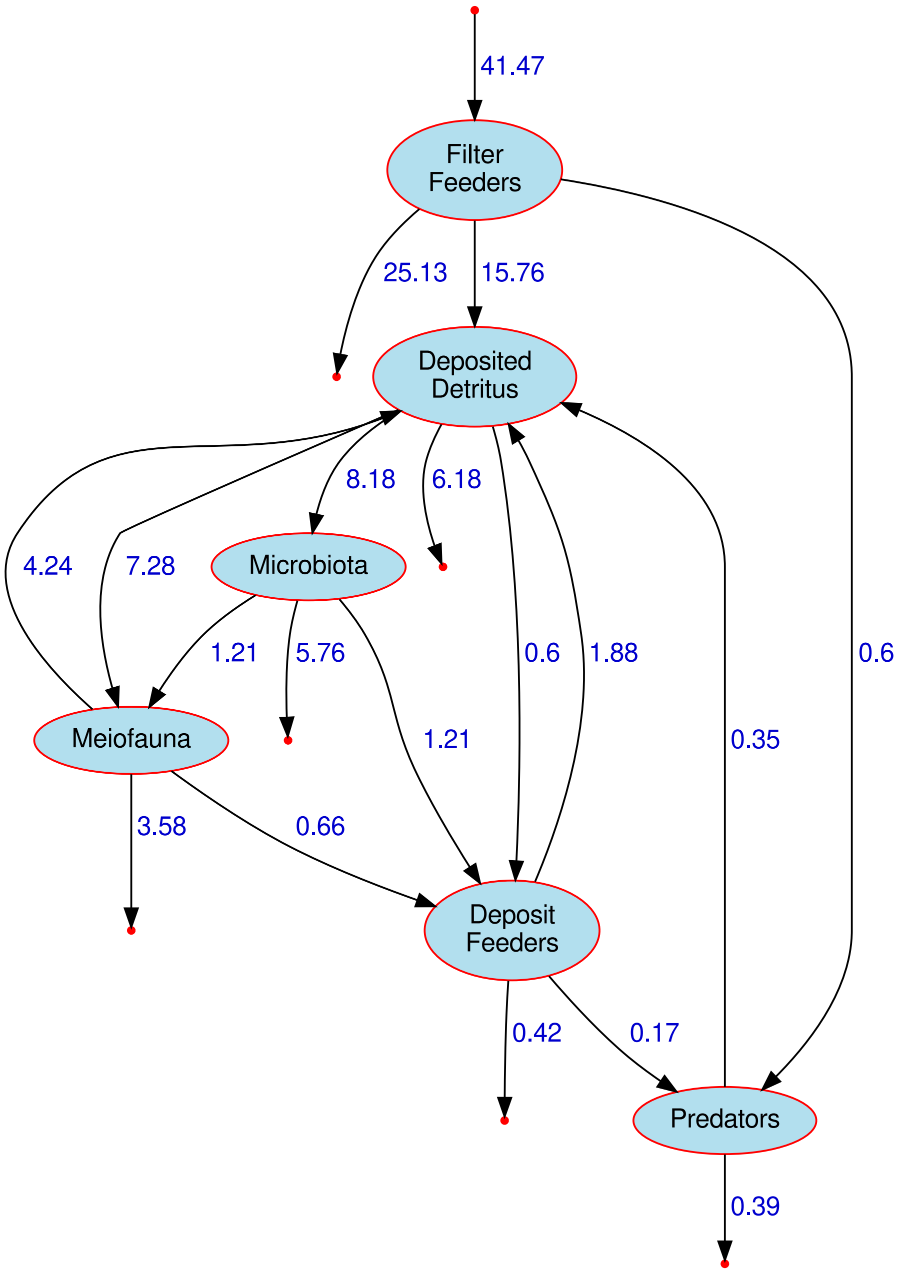


Figure 1.1: Network diagram of the intertidal oyster reef energy flow model [3] with six compartments and one environment input at Filter Feeders. Numbers beside the arrows indicate flow rate values from one compartment to another (or the environment). Flow rate unit is $Kcal/m^2$.

Chapter 2

Data and Method

2.1 Characterizing model perturbations

In order to measure the sensitivity of system-wide measures to changes in the model, we need to define these changes first. It is clear that significant changes to a model will probably cause large changes in most system-wide measures. Similarly, extremely small changes are likely to have no noticeable effect on system-wide measures. Therefore, it seems reasonable to define a sequence of perturbations that initially start small, and then increase in magnitude at each iteration, to determine at which point the system-wide measures start reacting to these changes. For a reasonably large model, eliminating a flow at each iteration, starting with the flow with the smallest value, may potentially serve as such a sequence of perturbations. However, the majority of the system-wide measures are only applicable to systems at steady-state. In order to investigate the effects of these perturbations on the system-wide measures, the model should still be at steady-state after the perturbation. In other words, all perturbations should preserve the steady-state condition. Unfortunately, any change to a single flow will disturb the balance of the ecosystem. Therefore, several flows need to be changed simultaneously to keep the model at balance. Then we need to identify the smallest change possible that would preserve the steady-state condition.

2.2 Fluxes

A *flux* is a sub-network with the property that each compartment has exactly one input and one output. Assuming all flow values are unity, a flux is at steady-state by definition. In a sense, fluxes are the “smallest” sub-networks of a model that can be at steady-state. This important property enables us to express any model at steady-state as a linear combination of its unique sets of fluxes [3, 17], as shown in Figure 2.1.

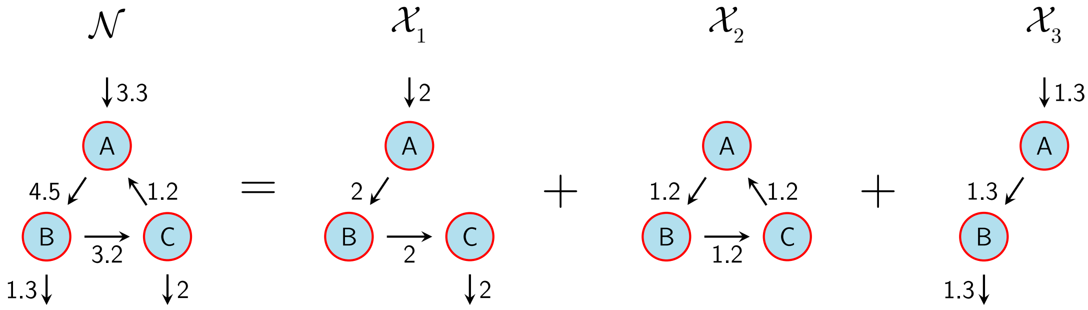


Figure 2.1: A three-compartment model N at steady-state is expressed as a linear combination of its fluxes as $\mathcal{N} = 2\mathcal{X}_1 + 1.2\mathcal{X}_2 + 1.3\mathcal{X}_3$. Numerical values on edges represent flow rates. The coefficients 2, 1.2, 1.3 are called flux rates, as they represent the amount of flow currency that passes through that flux per unit time. For example, the flow from A to B is 4.5 units/time. The flow $A \to B$ exists in all three fluxes. Then adding up all flux rates, we get $2 + 1.2 + 1.3 = 4.5$. On the other hand, the flow $C \to A$ only exists in the second flux $\mathcal{X}_2$. Then the flow rate of $C \to A$ equals the flux rate of $\mathcal{X}_2$.

This property makes fluxes an ideal perturbation tool for our purposes. Since a flux itself is a balanced system, when we deduct a flux from an ecosystem model, the remaining system is still at balance. Therefore, system-wide properties can still be computed if some of its fluxes are excluded. It is clear that the exclusion of fluxes will result in predictable changes in certain system-wide measures, such as a decrease in link density and TST. However, the effects of flux exclusion on other measures such as cycling, synergism and indirect effects are not clear, and has not been studied.

Fluxes are classified into two groups: (i) *chain fluxes* have one input from the environment, and one output back to the environment; (ii) *cycle fluxes* are interior, and have no

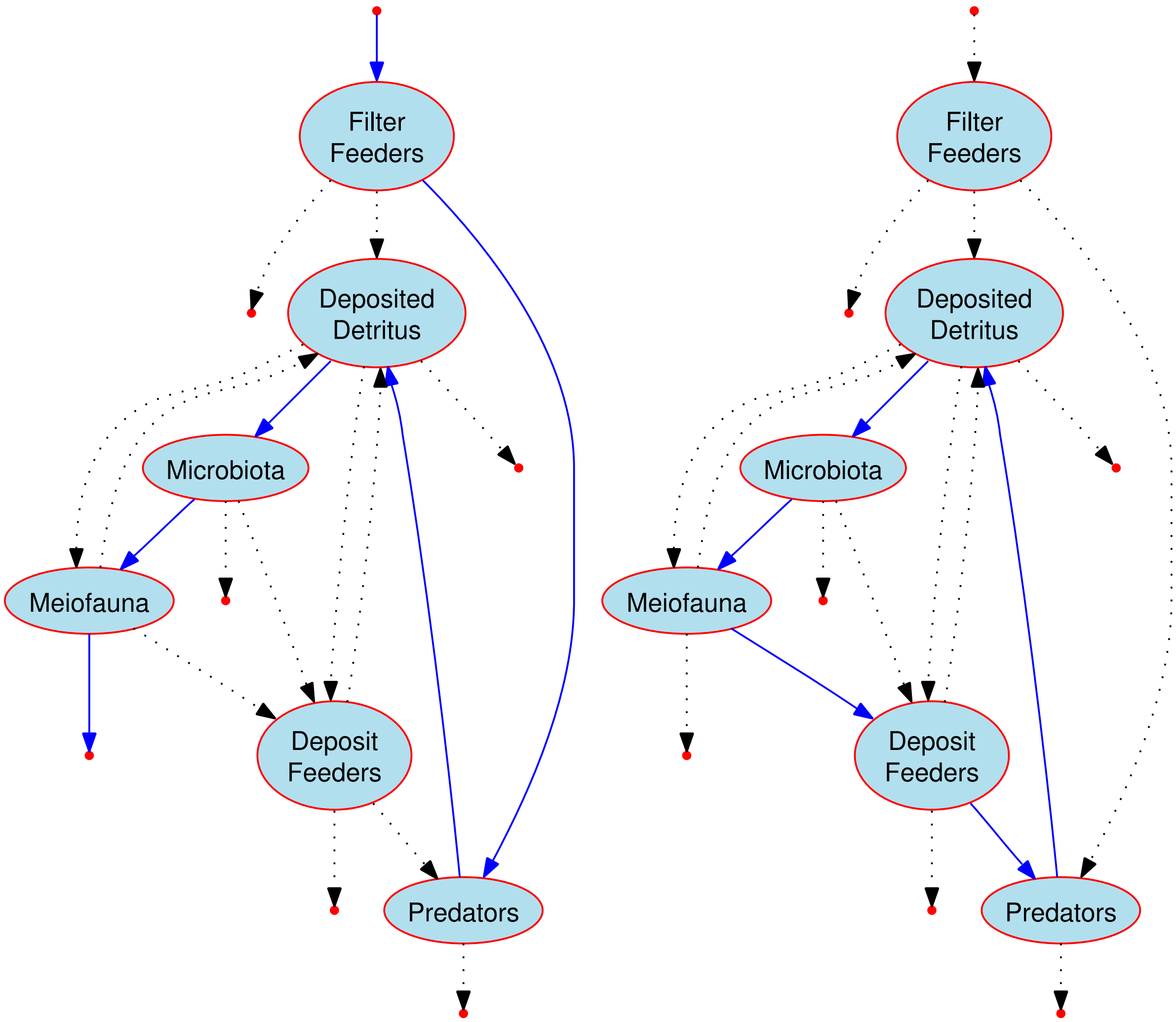


Figure 2.2: A chain flux (left) and a cycle flux (right) of the intertidal oyster reef model [3]. The diagrams are created by EcoNet [11, 23].

environmental inputs or outputs. Figure 2.2 shows a chain flux and a cycle flux of the intertidal oyster reef model. Based on their structural differences, chain and cycle fluxes may serve different functions for an ecosystem. Thus, a third goal of this study is to investigate the patterns of system-wide measure changes with respect to the type of flux (cycle or chain) loss.

2.3 Notation

An ecosystem model can be defined using matrices and vectors. For flux decomposition, we adopt the following notation:

1. Flow vector f, where f_i represents the flow rate of the i^{th} flow in the network. The f vector includes all of the non-zero intercompartmental flows, and environmental inputs and outputs for the focal system.

2. Stoichiometric matrix S, where S_{ij} represents how the j^{th} flow affects the i^{th} compartment:

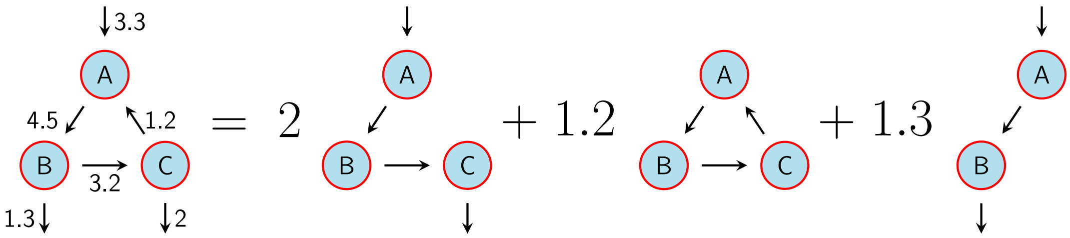
$$S_{ij} = \begin{cases} 1 & \text{if flow } j \text{ is to compartment } i \\ -1 & \text{if flow } j \text{ is from compartment } i \\ 0 & \text{neither} \end{cases}$$

3. Decomposition matrix X, where each column of X represents a different flux:

$$X_{ij} = \begin{cases} 1 & \text{if flow } i \text{ is part of flux } j \\ 0 & \text{otherwise} \end{cases}$$

4. Flux rate vector r, where r_i represents the rate of flux i.

For the simple three compartment model in Figure 2.1, these vectors and matrices are as follows:



$$f = \begin{bmatrix} 3.3 \\ 4.5 \\ 3.2 \\ 1.2 \\ 1.3 \\ 2 \end{bmatrix}, \; S = \begin{bmatrix} 1 & -1 & 0 & 1 & 0 & 0 \\ 0 & 1 & -1 & 0 & -1 & 0 \\ 0 & 0 & 1 & -1 & 0 & -1 \end{bmatrix}, \; X = \begin{bmatrix} 1 & 0 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \end{bmatrix}, \; r = \begin{bmatrix} 2 \\ 1.2 \\ 1.3 \end{bmatrix}$$

The decomposition matrix X can be used to express the flow values (f) using the flux rates (r),

$$f = Xr,$$

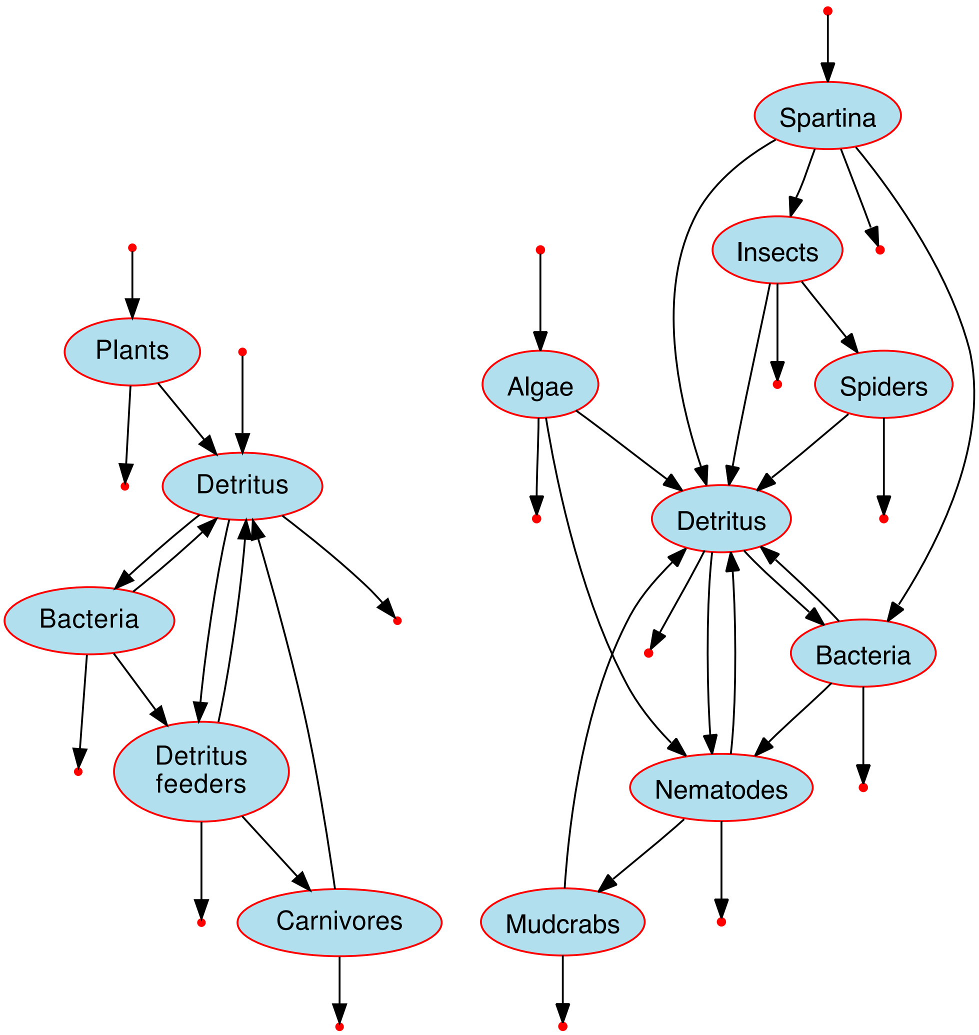
which is another way to express the linear combination shown in Figure 2.1. By definition, a flux is a sub-network where each compartment has exactly one input and one output. Then, if a certain amount of biomass or energy flows through a single flux, no change should occur on any of the compartment storage values. In other words, the dot product of the rows of S and the columns of X always equal zero,

$$SX = 0,$$

meaning that the columns of the flux decomposition matrix X belong to the null-space of the stoichiometric matrix S. This fact can be used to identify the fluxes of any given model.

2.4 Models

We use three steady-state ecosystem models in this study: (i) the intertidal oyster reef energy ecosystem model [3] shown in Figure 1.1; (ii) the Cone Spring ecosystem model [25] shown in Figure 2.3(a); and (iii) the Georgia salt marsh ecosystem model [24] shown in



(a) (b)

Figure 2.3: Network diagrams of the Cone Spring model (left) [25], and the Georgia salt marsh model (right) [24].

Figure 2.3(b). Table 2.1 provides the structural statistics of the three models. Analyzing three different models that vary in size and structure increases our chance of detecting exceptional situations as well as helps us identify similar changes or phenomena across all three models to achieve more reliable results.

2.5 Data Analysis Procedure

In this section, we describe the data analysis procedure that provides answers to the following three research goals mentioned earlier:

1. Investigate the sensitivity of system-wide ecological network measures to certain changes in the ecosystem model.
2. Identify the minimum amount of empirical data needed to predict certain system-wide measures with reasonable accuracy.
3. Investigate the patterns of system-wide measure changes with respect to the type of flux (cycle or chain) loss.

We use the intertidal oyster reef energy ecosystem model [3] as an example to represent our data analysis procedure. As shown in Figure 1.1, this model has 6 compartments, 19 flows, a single environmental input at the "Filter Feeders" compartment, and environmental outputs from all compartments. The software EcoNet [11] offers a convenient way to identify all 32 fluxes for the oyster reef ecosystem model (Table 2.2) with their corresponding figures. EcoNet analysis results also include compartmental properties, system-wide properties, the stoichiometric matrix (S), and the flux decomposition matrix (X). Using these matrices, the flux rates are computed and shown in Table 2.3.

Our model perturbation procedure creates a sequence of models starting with the original model, where a flux is removed from the model at each step. The difference between any two consecutive models in this sequence is a single flux with its associated rate. We eliminate

Ecosystem Model	**#compartments**	**#flows**	**#fluxes**
Cone spring	5	8	18 (13 chain, 5 cycle)
Oyster reef	6	19	32 (22 chain,10 cycle)
Georgia salt marsh	8	25	47 (42 chain, 5 cycle)

Table 2.1: Numbers of compartments, flows, and fluxes, as well as types of fluxes for the three ecosystem models used in this study.

```
* -> Filter_Feeders c= 41.4697
Filter_Feeders -> Deposited_Detritus c= 0.0079
Filter_Feeders -> Predators c= 0.0003
Deposited_Detritus -> Microbiota c= 0.0082
Deposited_Detritus -> Meiofauna c= 0.0073
Deposited_Detritus -> Deposit_Feeders c= 0.0006
Microbiota -> Meiofauna c= 0.5
Microbiota -> Deposit_Feeders c= 0.5
Meiofauna -> Deposited_Detritus c= 0.1758
Meiofauna -> Deposit_Feeders c= 0.0274
Deposit_Feeders -> Deposited_Detritus c= 0.1172
Deposit_Feeders -> Predators c= 0.0106
Predators -> Deposited_Detritus c= 0.0047
Filter_Feeders -> * c= 0.0126
Deposited_Detritus -> * c= 0.0062
Microbiota -> * c= 2.3880
Meiofauna -> * c= 0.1484
Deposit_Feeders -> * c= 0.0264
Predators -> * c= 0.0052
Filter_Feeders = 2000; Deposited_Detritus = 1000; Microbiota = 2.4121
Meiofauna = 24.121; Deposit_Feeders = 16.274; Predators = 69.237
```

Table 2.2: The intertidal oyster reef ecosystem model [3] in EcoNet format. Here "*" represents the environment, and "->" represents the flows among compartments. The initial storage value of each compartment is provided in the last two lines. This system is at steady-state.

fluxes starting with the ones with the lowest flux rate. For example, for the intertidal oyster reef ecosystem model, Table 2.3 indicates that the first flux (→1→6→2→3→4→5→, Figure 2.4) has the lowest flux rate of 0.0003 kcal/day·m^2, and hence, will be the first one to be removed.

Removal of a flux from a model consists of subtracting the flux rate value from all flows that make up that flux, including environmental inputs and outputs if it is a chain flux. For example, all flow rates before and after the elimination of the first flux (→1→6→2→3→4→5→) for the oyster reef model is shown in Table 2.3. The sum of the rates of all fluxes that include a particular flow equal the rate of that flow, therefore, as fluxes are deducted, the rates of flows involved in that flux are also decreased. This iterative process continues until a single flux is left in the system. By definition, this last flux has the highest flux rate,

Fluxes	Flux Rates
→1→6→2→3→4→5→	0.0003
→1→6→2→4→5→	0.0017
→1→6→2→5→	0.0018
2→3→4→5→6→2	0.0031
→1→2→3→4→5→6→	0.0033
→1→6→2→3→5→	0.0037
→1→6→2→3→4→	0.009
→1→2→3→4→5→	0.0158
2→4→5→6→2	0.0189
2→4→6→2	0.0199
→1→2→4→5→6→	0.0201
→1→2→5→6→	0.0212
2→3→5→6→2	0.0401
→1→2→3→5→6→	0.0428
→1→6→2→4→	0.0544
2→3→4→5→2	0.0715
→1→2→4→5→	0.0954
→1→2→5→	0.1006
→1→6→2→3→	0.102
→1→6→2→	0.1095
→1→2→3→5→	0.2029
→1→6→	0.3157
2→4→5→2	0.431
2→5→2	0.4546
→1→2→3→4→	0.5002
2→3→4→2	0.6032
2→3→5→2	0.9169
→1→2→4→	3.0172
2→4→2	3.6387
→1→2→3→	5.6597
→1→2→	6.0713
→1→	25.121

Table 2.3: Fluxes and their corresponding rates for the oyster reef model, sorted from lowest flux rate to the highest. Data is presented in two separate columns to save space. In flux descriptions, the numbers from one to six are used to represent the compartments: Filter Feeders (1), Deposited Detritus (2), Microbiota (3), Meiofauna (4), Deposit Feeders (5), and Predators (6). Fluxes that start and end with arrows are chain fluxes, whereas fluxes that start and end with the same compartment are cycle fluxes. Flux and flow rates have the same units, which is kcal/day·m^2 for this model. Flux rates are rounded to four decimal places to save space, in actual calculations we trace up to 15 decimal places. The flux in red fonts is later referred to in Section 3.6.

which is (→1→, see Figure 2.4) for the oyster reef model, as it has the highest rate of 25.121 kcal/day·m^2.

Note that a flux itself is a balanced sub-network, therefore the elimination of a flux from a model does not influence the steady-state property of the system. Therefore, all models created at each step according to this procedure are at steady-state, and the entire set of system-wide network analysis measures can be computed for each model. For this purpose, we used `NEA.m` [5], a MATLAB function which implements algorithms to calculate input and output environs and a wide range of system-wide measures. In order to investigate the effects of model perturbations, we applied `NEA.m` after each flux removal to perform Network Environ Analysis (NEA) [5, 20]. Among the many scalar, vector and matrix valued

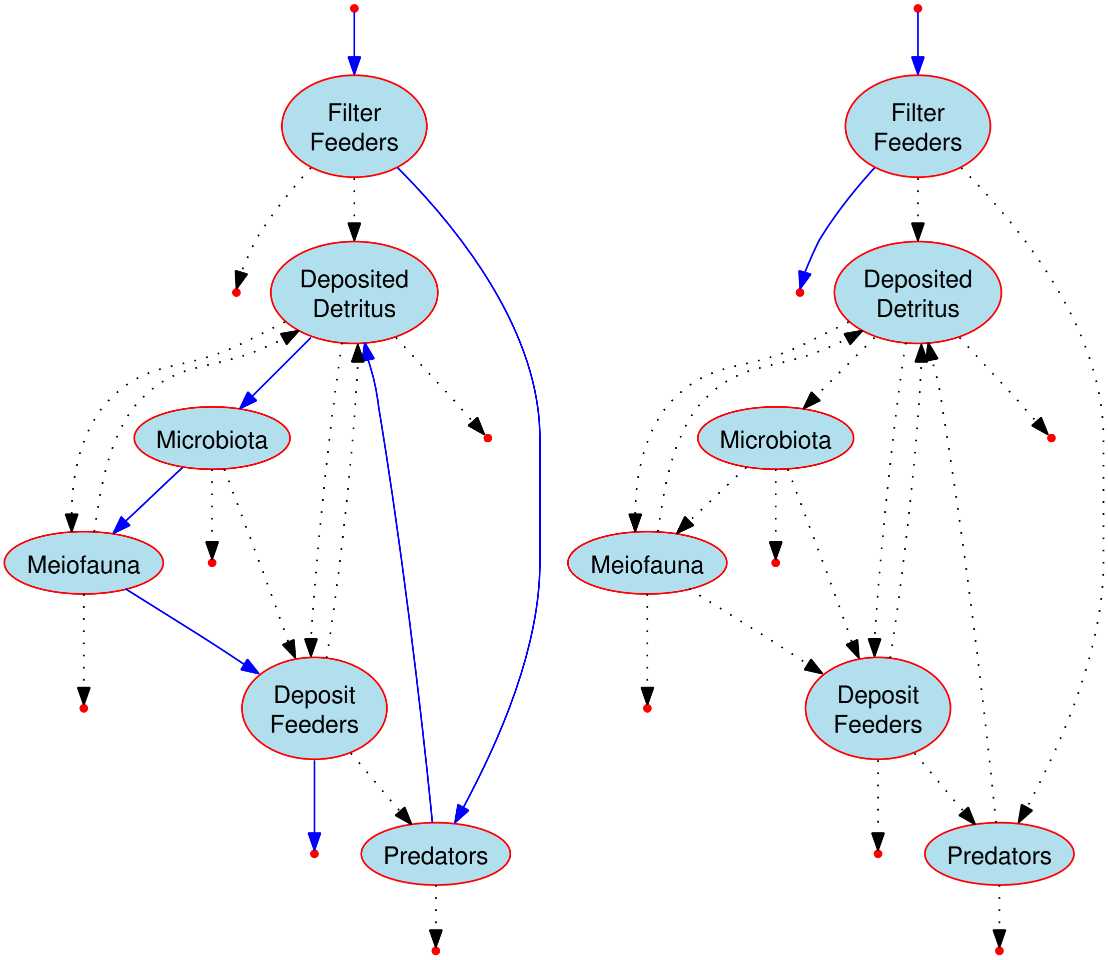


Figure 2.4: Network diagrams of the fluxes with the smallest (left) and largest (right) flux rates from the oyster reef ecosystem model [3].

measures computed by `NEA.m`, we chose to focus on a short list of measures provided on Table 2.5, which include both structure-based measures such as link density and connectance, as well as flow-based measures such as cycling index, indirect effects index, and synergism. In addition, we kept a record of the type and length of each eliminated flux, so we can study the correlation between the characteristics of a flux and the effects of its loss.

Flow	Flow rate before flux elimination	Flow rate after flux elimination	Difference
→1	41.4697	41.4694	0.0003
1→2	15.7505	15.7505	0
1→6	0.5981	0.5978	0.0003
2→3	8.1746	8.1743	0.0003
2→5	7.2773	7.2773	0
2→4	0.5981	0.5981	0
3→4	1.2064	1.2061	0.0003
3→5	1.2064	1.2064	0
4→2	4.2419	4.2419	0
4→5	0.6611	0.6608	0.0003
5→2	1.8740	1.8740	0
5→6	0.1695	0.1695	0
6→2	0.3644	0.3641	0.0003
1→	25.1210	25.1210	0
2→	6.1808	6.1808	0
3→	5.7618	5.7618	0
4→	3.5807	3.5807	0
5→	0.4221	0.4218	0.0003
6→	0.4031	0.4031	0

Table 2.4: Flow values before and after the flux (→1→6→2→3→4→5→) is eliminated are shown for the oyster reef model, including environmental inputs and outputs. Numbers from one to six are used to represent the compartments: Filter Feeders (1), Deposited Detritus (2), Microbiota (3), Meiofauna (4), Deposit Feeders (5), and Predators (6). Values are rounded to four decimal places to save space.

Measures	Description
n	# of compartments
L	# of direct flows
L/n^2	Connectance
L/n	Link density
TST	Total system throughflow
FCI	Finn's cycling index
IEI	Indirect effects index
$\text{IEI}_{\text{realized}}$	Realized IEI [2]
$\text{IEI}_{\text{revised}}$	Revised IEI [18]
Synergism	benefit-cost ratio
Mutualism	ratio of "+" to "−" interactions

Table 2.5: The basic structure-based and flow-based network system measures recorded in this study using the Matlab function NEA.m [5].

Chapter 3

Results

3.1 Structural changes associated with flux elimination

By definition, a flux is a sub-network of the ecosystem model; thus, the elimination of fluxes have an impact on the model structure. As more and more fluxes are removed from a model, eventually some flows will be lost as well. Similarly, if enough flows are lost, some compartments will be disconnected from the model, and they will no longer be part of the system. Figure 3.1 shows the numbers of compartments and flows in the model as the fluxes are eliminated according to the procedure described in Section 2.5. Because the rates of the fluxes that are eliminated initially are low, we do not see a significant change in the number of compartments or flows until a significant amount of fluxes are removed. we observe that the change in the number of compartments and flows become rapid and almost linear towards the very end, as the last few remaining fluxes are eliminated.

Towards the very end of the flux elimination procedure, as the last two remaining fluxes with the highest flux rates are being removed, there exist only one or two compartments and at most two flows left in the system. At this point, it makes little sense to quantify system-wide measures because limited or no interactions are left. Therefore, in our study, we stop computing system-wide measures after the third-to-last flux is eliminated in the oyster

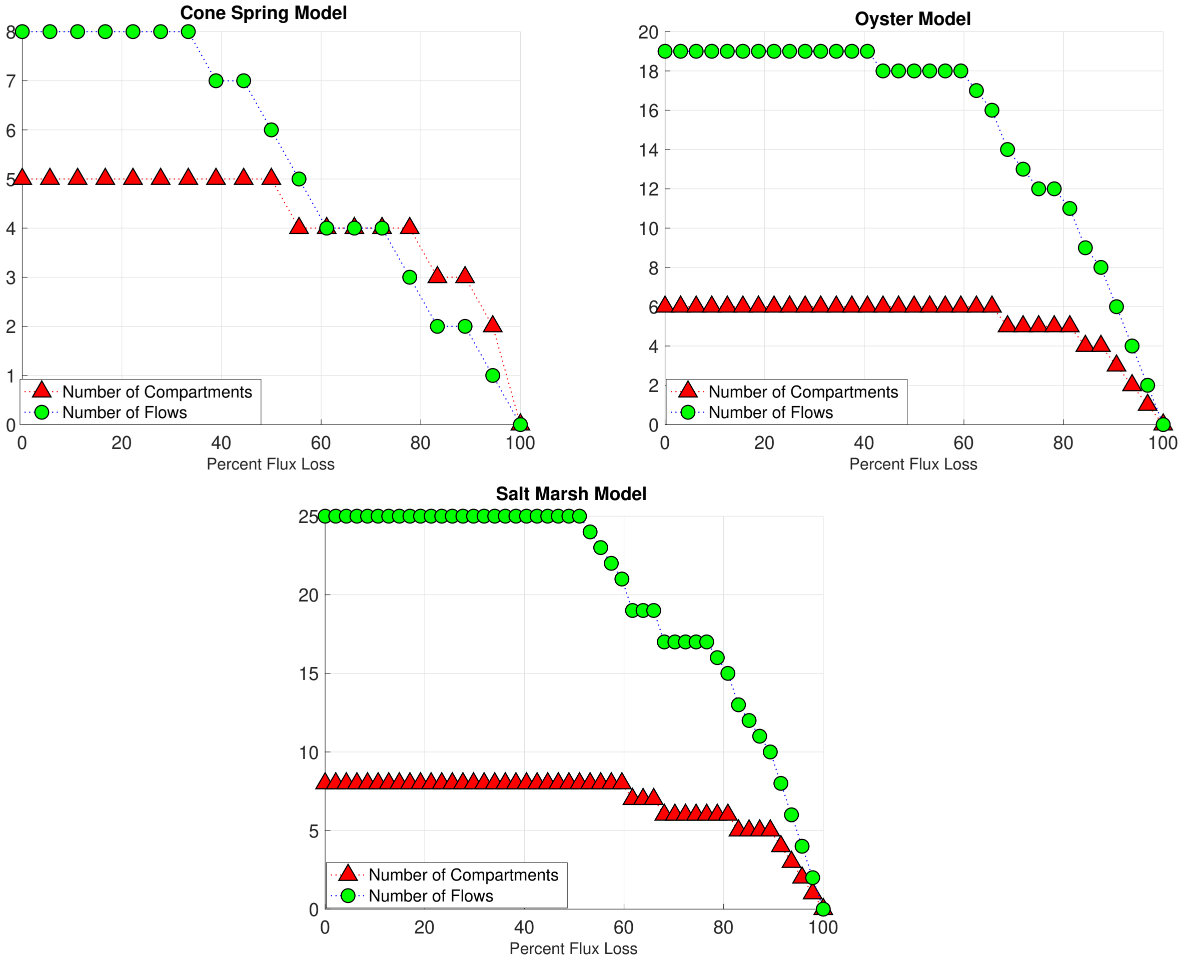


Figure 3.1: Numbers of compartments and flows remaining in the model as the fluxes are eliminated according to the procedure described in Section 2.5.

reef model [3] and the Georgia salt marsh model [24]. For the cone spring model [25], we compute the measures until the second from the last flux is eliminated.

3.2 Changes in TST associated with flux elimination

The compartmental throughflow T_i is a key networks property that measures the rate of flow through compartment i. The input throughflow T_i^{in} is defined as the sum of all flow rates into the i^{th} compartment from other compartments and environment. Similarly, the output throughflow T_i^{out} is defined as the sum of all flow rates from the i^{th} compartment to other compartments and the environment. In a steady-state ecosystem, the input throughflow

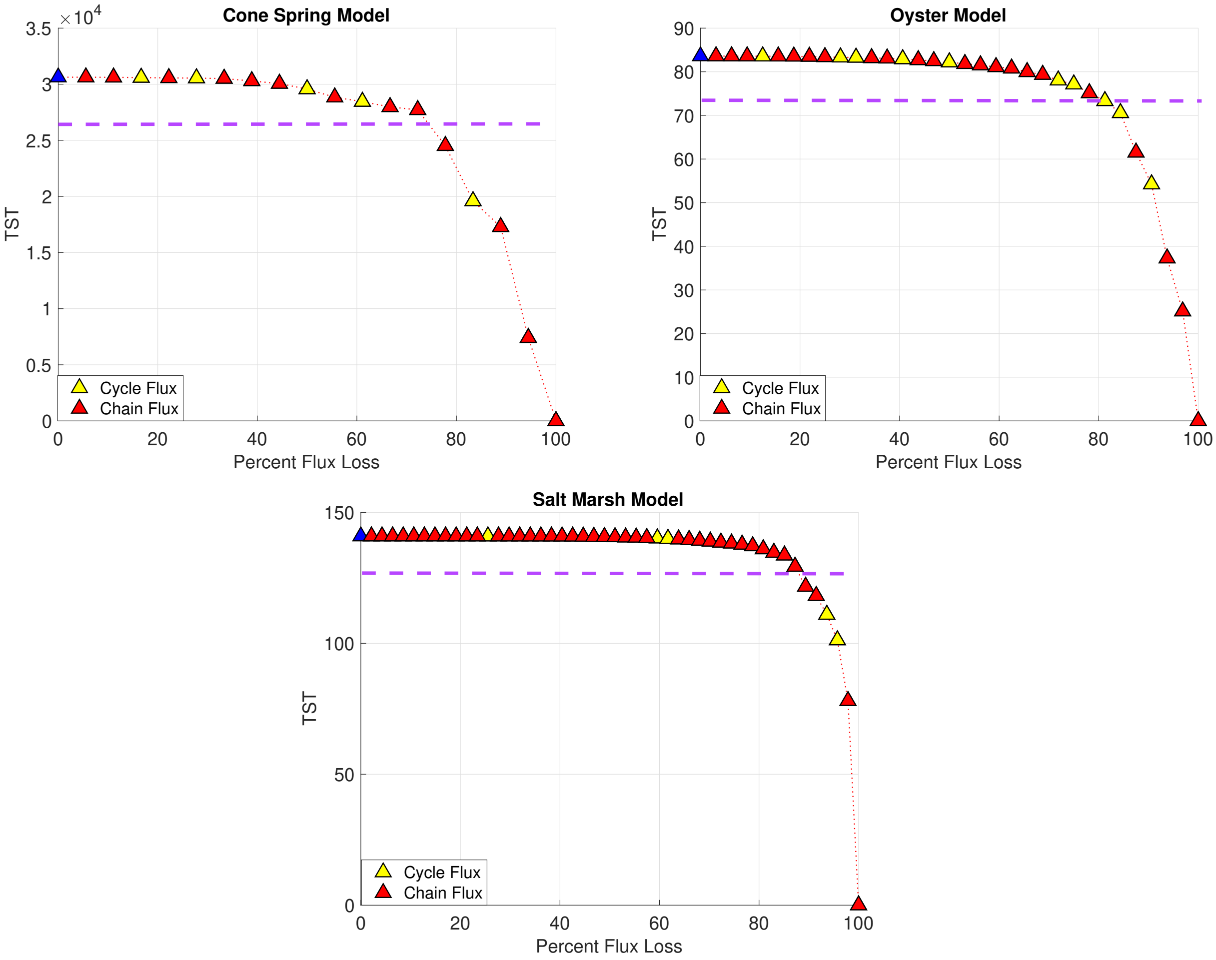


Figure 3.2: TST of the model as the fluxes are eliminated according to the procedure described in Section 2.5. The dashed line indicates the 90% of the original TST value of the model. Red and yellow markers indicate the type of flux removed. Blue marker indicates the original full model, before any fluxes are removed.

T_i^{in} is equal to the output throughflow T_i^{out} ($T_i = T_i^{in} = T_i^{out}$) at all times. In this study, we investigate the changes of total system throughflow (TST), defined as the sum of compartmental throughflows T_i of all compartments, in response to the changes in fluxes.

$$TST = \sum_{i=1}^{n} T_i$$

Figure 3.2 shows the changes in the total system throughflow (TST) with respect to the elimination of fluxes in three different ecosystems. As expected, TST decreases as its fluxes are removed from the model. Since the fluxes with the lowest rates are removed initially, the change in TST is almost negligible at first. TST keeps 90% of its original value until more than 75% of the fluxes are eliminated from the Cone Spring model, and even more for the oyster reef and the Georgia salt marsh ecosystem models. This difference indicates that the flux rates of the Cone Spring model have a more uniform distribution than the other two models. Furthermore, 90% of the total throughflow values in these models are represented by 5 out of the 18 total fluxes for the Cone Spring model. These numbers are 7 out of 32 for the oyster model; and 6 out of 47 for the Georgia salt marsh model. In other words, relatively few fluxes carry the majority of the energy transfer burden in these ecosystems. From a data accounting point of view, this is a significant reduction, especially considering the often higher than 10% error rate of most experimental methods.

3.3 Changes in indirect effects associated with flux elimination

Patten [20] defines the indirect to direct effect ratio (I/D) as a measure that quantifies the relative strength of indirect flows in an ecosystem model. The understanding of indirect effects is essential to the study of ecosystem behavior [13, 14], and provides a holistic perspective of the complex interactions among compartments. The algebraic formulation of I/D is based on the flow matrix F, which contains the values in the flow vector f, placed in matrix form, where F_{ij} represents the direct flow rate from compartment j to compartment i. By definition F is a sparse matrix. The flow intensity matrix G is defined by normalizing the flow matrix F by compartmental throughflow, that is, $G_{ij} = F_{ij}/T_j$. By definition, entries of G are always between zero and one. G is used to define the integral throughflow matrix $N = I + G + G^2 + \cdots = (I - G)^{-1}$. N_{ij} represents the amount of throughflow generated at compartment i per unit input at compartment j. For an ecosystem with n compartments, the computation of indirect to direct effect ratio (I/D) is obtained by

$$I/D = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} (N_{ij} - I_{ij} - G_{ij})}{\sum_{i=1}^{n}\sum_{j=1}^{n} G_{ij}}$$

By definition, I/D can take any value between zero and infinity. When I/D takes values larger than one, it means that the indirect flows are greater than direct flows in that system; otherwise, direct effects are dominant. However, when the ratio I/D is arbitrarily large, it is hard to make comparisons with other indices like FCI, which vary between zero and one [18]. As a solution, the indirect effects index (*IEI*) is defined as the ratio of direct effects to the sum of all effects, direct and indirect:

$$IEI = \frac{I}{I+D} = \frac{I/D}{1+I/D} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} (N_{ij} - I_{ij} - G_{ij})}{\sum_{i=1}^{n}\sum_{j=1}^{n} (N_{ij} - I_{ij})}$$

The range of IEI is between zero and one; and reflects the proportion of the indirect effects. In this study, we use IEI to investigate the changes of indirect effects in the ecosystems in response to the elimination of fluxes. In addition to IEI[2], we also compute $\mathrm{IEI}_{\mathrm{rev}}$[18] and $\mathrm{IEI}_{\mathrm{realized}}$[2] for further investigation of the sensitivity of indirect effects to model perturbations. These two measures are defined as improvements over IEI, and are defined as

$$IEI_{\mathrm{rev}} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} (N_{ij} - I_{ij} - G_{ij})T_j}{\sum_{i=1}^{n}\sum_{j=1}^{n} (N_{ij} - I_{ij})T_j}, \quad IEI_{\mathrm{realized}} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} (N_{ij} - I_{ij} - G_{ij})z_j}{\sum_{i=1}^{n}\sum_{j=1}^{n} (N_{ij} - I_{ij})z_j}.$$

Figure 3.3 shows the changes in IEI, $\mathrm{IEI}_{\mathrm{rev}}$ and $\mathrm{IEI}_{\mathrm{realized}}$ with respect to the percent flux loss in three ecosystems.

As shown in Figure 3.3 in Georgia salt marsh model and the intertidal oyster reef model, the values of all three indirect effects indices are over 0.5, which means that in these two ecosystems the amount of indirect flows are greater than direct flows, in other words, indirect

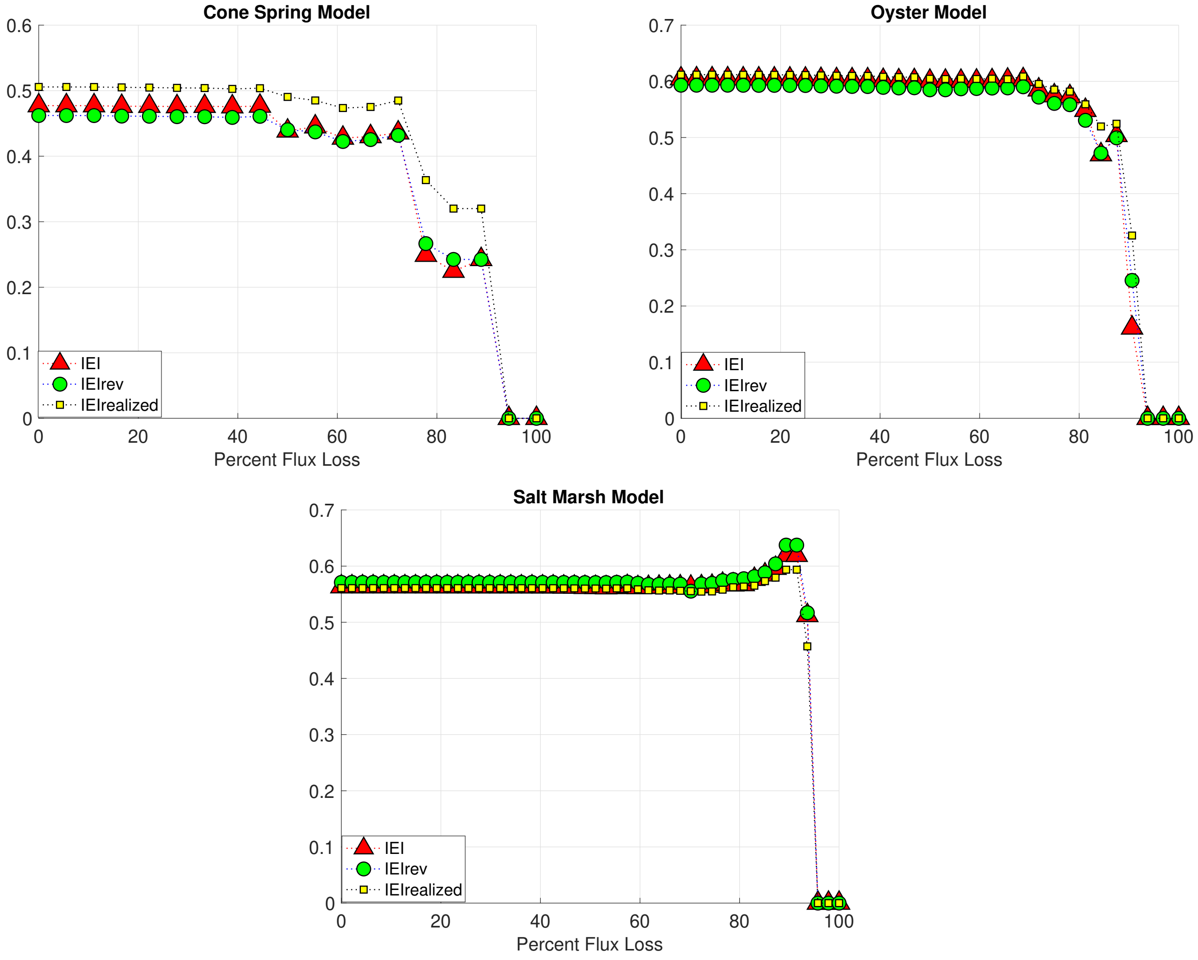


Figure 3.3: The changes of the three indirect effects indices IEI, IEI_{rev} and $\text{IEI}_{\text{realized}}$ associated with the elimination of fluxes (according to the procedure described in Section 2.5) in three ecosystem models.

effects are dominant. In the Cone Spring model, IEI values are less than 0.5, but still above 0.45, indicating that direct flows are slightly stronger than indirect flows. Furthermore, all three IEI indices are not only similar in value, but also similar in their responses to flux loss, meaning that any one of the three could be used as a representative of the others for the purpose of this study.

In all three models, all three IEI measures tend to stay relatively constant up until at least 50% of the fluxes are eliminated. In Georgia salt marsh model however, IEI values tend to stay steady up until 80 percent of the fluxes are removed. This percentage appears to be correlated with model size, in that Georgia salt marsh model has more compartments, flows and fluxes compared to the other two models. Oyster reef model lies in between the other two models.

Unlike TST, IEI values do not steadily decrease as fluxes are removed. In all three models, there are instances where all IEI values increase after a particular flux is eliminated. However, the general trend is that IEI values slightly decrease towards the end, until a sudden drop, which is due to the loss of the last few chains and cycles that support indirect effects. Interestingly, in the case of the Georgia salt marsh model, IEI values tend to increase towards the end, before a sudden drop. While this observation requires further investigation, we believe that it might be related to the fact that this model has the smallest proportion of cycle fluxes (11%, Table 2.1) compared to the other two models (28% and 31%). This result supports Higashi and Patten's finding[10] that the indirect effects ratio does not only depend on the network size, but also on other factors such as connectance, FCI, and the structure of interactions among compartments.

3.4 Changes in synergism and mutualism associated with flux elimination

Utility analysis [21], a part of Network Environ Analysis (NEA), measures the qualitative and quantitative relationships between each pair of compartments in an ecosystem model. The direct utility matrix (D) represents the direct relations between all pairs of compartments in the system: $D_{ij} = \frac{F_{ij} - F_{ji}}{T_i}$. The integral utility matrix (U) represents the overall relationships between compartments in an ecosystem, which can be computed as the sum of all powers of the direct utility matrix *(D)* :

$$U = I + D + D^2 + D^3 + ... + D^n + ... = (I - D)^{-1}$$

On the basis of the integral utility matrix (U), mutualism [21] was established as

$$\text{Mutualism } = \frac{\sum \text{sign}U^{+}}{|\sum \text{sign}U^{-}|}$$

to reflect the proportions of positive and negative entries in the U matrix. By definition, the system-wide mutualism occurs when this ratio is greater than one. Similarly, by calculating the ratio of the sum of positive utilities over negative utilities in the integral utility matrix (U), another system-wide measure called synergism [21] is defined as

$$\text{Synergism } = \frac{\sum U^{+}}{|\sum U^{-}|}$$

where U^{+} and U^{-} represent the positive and negative partition matrices of the utility matrix U.

By definition, the system-wide synergism is said to occur when this value is greater than one. In this study, we investigate the sensitivity and robustness of mutualism and synergism associated with the elimination of fluxes in the same three ecosystems. Figure 3.4 represents the variations of mutualism and synergism along with the elimination of fluxes in these ecosystems.

From Figure 3.4, we observe that the numerical values of both mutualism and synergism are greater than one in all three ecosystems, and stay that way until the very last few fluxes are removed. This reveals that the elimination of fluxes does not change the prevalence of system-wide mutualism and synergism in these models. Similar to previous observations, changes in values of both measures remain negligible up until at least 40% to 60% percent of flux loss. Similar to indirect effects measures, we do not observe a monotone change in mutualism and synergism values as fluxes are eliminated. Unlike indirect effect measures, however, a general trend of increasing synergism values in all three models exist, until the final collapse. This result is somewhat consistent with Fath's finding [4] that synergism is higher in smaller networks. This work further generalizes this statement, that synergism appears

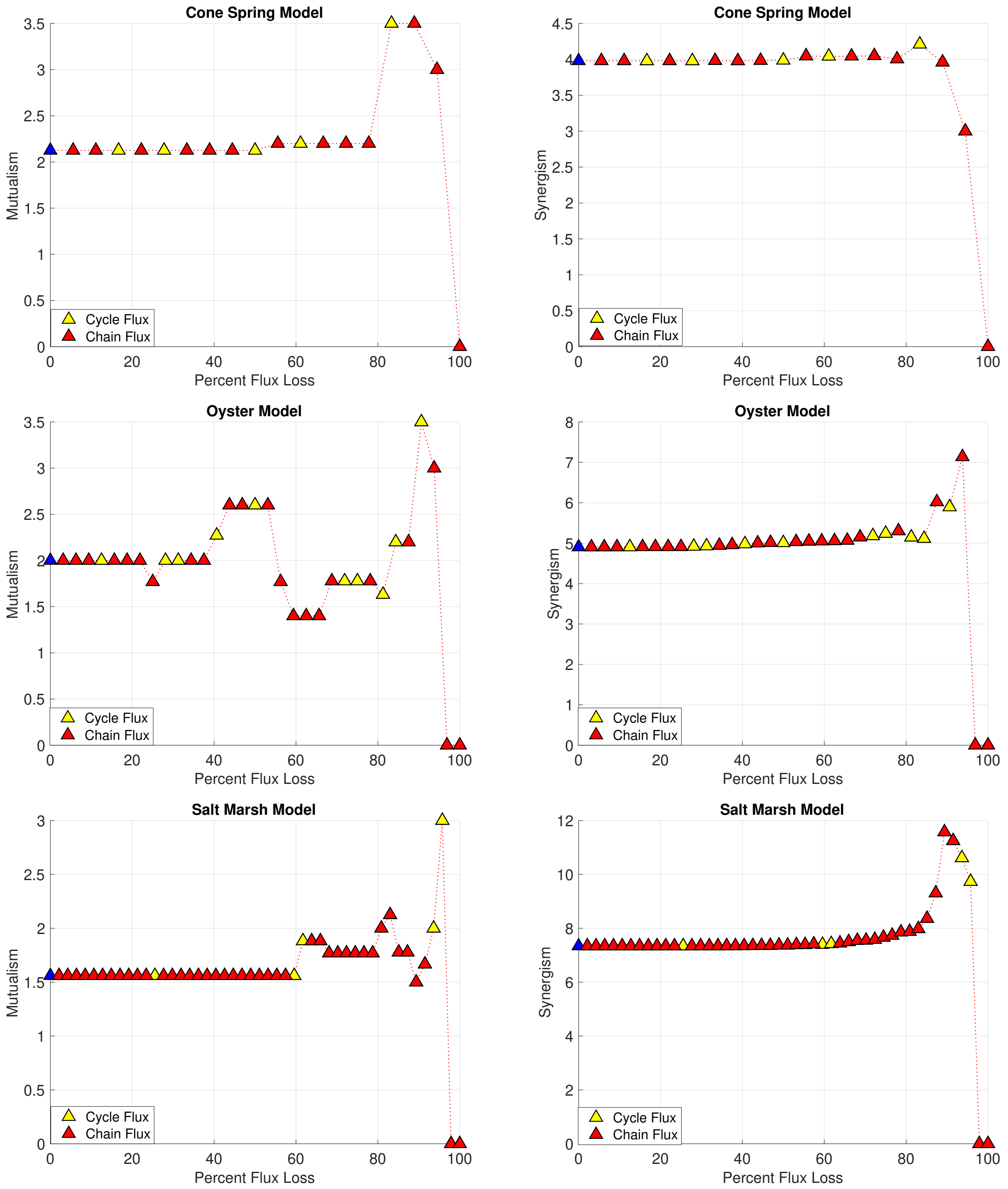


Figure 3.4: The changes of mutualism and synergism associated with the elimination of fluxes (according to the procedure described in Section 2.5) in three ecosystem models. Figures on the right are changes of mutualism; figures on the right are changes of synergism. Red and yellow markers indicate the type of flux removed. Blue marker indicates the original full model, before any fluxes are removed.

to increase not only with decreasing network size, but also with weakened connections and decreased flows rates as well. However, other researchers [22] suggest that decreasing flow rates and compartment numbers should lead to a decrease in synergism as well. Therefore this behavior needs further investigation, perhaps by including more and larger models, with 40 to 50 compartments for instance.

3.5 Changes in FCI associated with flux elimination

Finn's cycling index (FCI) [8] is based on economic input-output analysis [16]. It has been widely used to measure the amount of cycling from the perspective of throughflows. FCI calculates the proportion of total system throughflow (TST) that is generated by cycling (TST_c):

$$FCI = \frac{TST_c}{TST} = \sum_{i=1}^{n} \frac{T_i}{TST} \frac{N_{ii} - 1}{N_{ii}}$$

The diagonal value N_{ii} represents the amount of throughflow generated at compartment i per unit input into itself. By definition, $N_{ii} - 1$ represents the throughflow generated at compartment i entirely due to cycling. In this study, we do not only investigate the change of FCI associated with the elimination of fluxes, but also pay special attention to the types of fluxes eliminated at each step.

Figure 3.5 shows FCI vs. percent flux loss in three ecosystems. Different colors denote the types of fluxes eliminated. Values of FCI in all three ecosystems remain steady until over 70% of the fluxes are removed from the system. Similar to earlier measures, the change in FCI is not monotone, but it is clear that the loss of cycle fluxes (yellow triangles) cause a decrease, whereas the loss of a chain fluxes (red triangle) cause an increase in FCI. This observation is not without exceptions, however, as there are a few cases where the loss of a chain flux actually causes a decrease in FCI, which is rather unexpected. This issue is investigated in the next section.

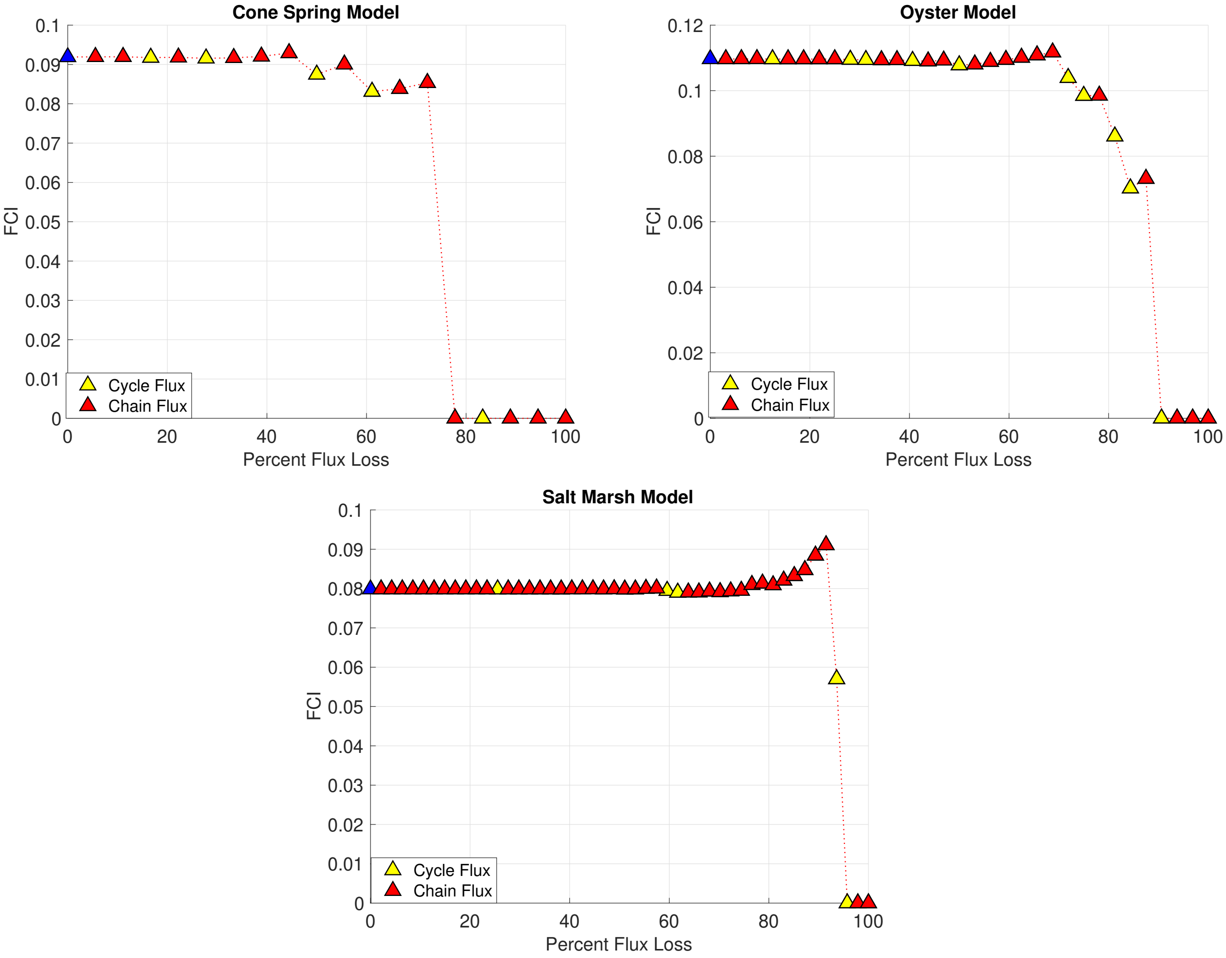


Figure 3.5: The changes of FCI associated with the elimination of fluxes (according to the procedure described in Section 2.5) in three ecosystems. Red and yellow markers indicate the type of flux removed. Blue marker indicates the original full model, before any fluxes are removed.

Among the three ecosystems, the Georgia salt marsh ecosystem model has the lowest proportion of cycle fluxes. This causes an upward trend of FCI values towards the end, as the chain fluxes with higher rates are removed from the system.

3.6 A deeper look into the changes in FCI associated with chain flux elimination

Throughout this work we observed some unexpected results which were difficult to interpret. Even though we tried providing answers to some, it was not feasible to tackle them all. In this section, we present one such example, that conveys the unexpected and rather complicated change of a system-wide measure, in response to the seemingly simple operation of adding or subtracting a flux.

As discussed in the previous section, FCI computes the proportion of cycling throughflow

$$FCI = \frac{TST_c}{TST} = \frac{TST_c}{TST_n + TST_c} = \frac{1}{1 + \frac{TST_n}{TST_c}}$$

where TST_c and TST_n represent the cycling and non-cycling portions of the total system throughflow. Flux decomposition is especially suitable to study cycling, as fluxes are either 100% cycles or 100% chains. Then considering the equation above, we expect that removing a cycle flux would cause a decrease in FCI, and similarly, removing a chain flux would cause an increase in FCI.

To better illustrate this point, a simple balanced three compartment model is shown in Figure 3.6. For this model, the flow matrix (F) and the throughflow vector (T) are:

$$F = \begin{bmatrix} 0 & v+z & 0 \\ 0 & 0 & v \\ u+v & 0 & 0 \end{bmatrix}, \quad T = \begin{bmatrix} u+v+w+z \\ v+z \\ u+v \end{bmatrix}$$

Based on these values, the integral throughflow matrix can be computed as $N = (I - G)^{-1}$ where $G = F(\text{diag}(T))^{-1}$. Interestingly, the diagonal of N contains the same values for all compartments:

$$\frac{N_{11} - 1}{N_{11}} = \frac{N_{22} - 1}{N_{22}} = \frac{N_{33} - 1}{N_{33}} = \frac{v}{u+v+w+z}$$

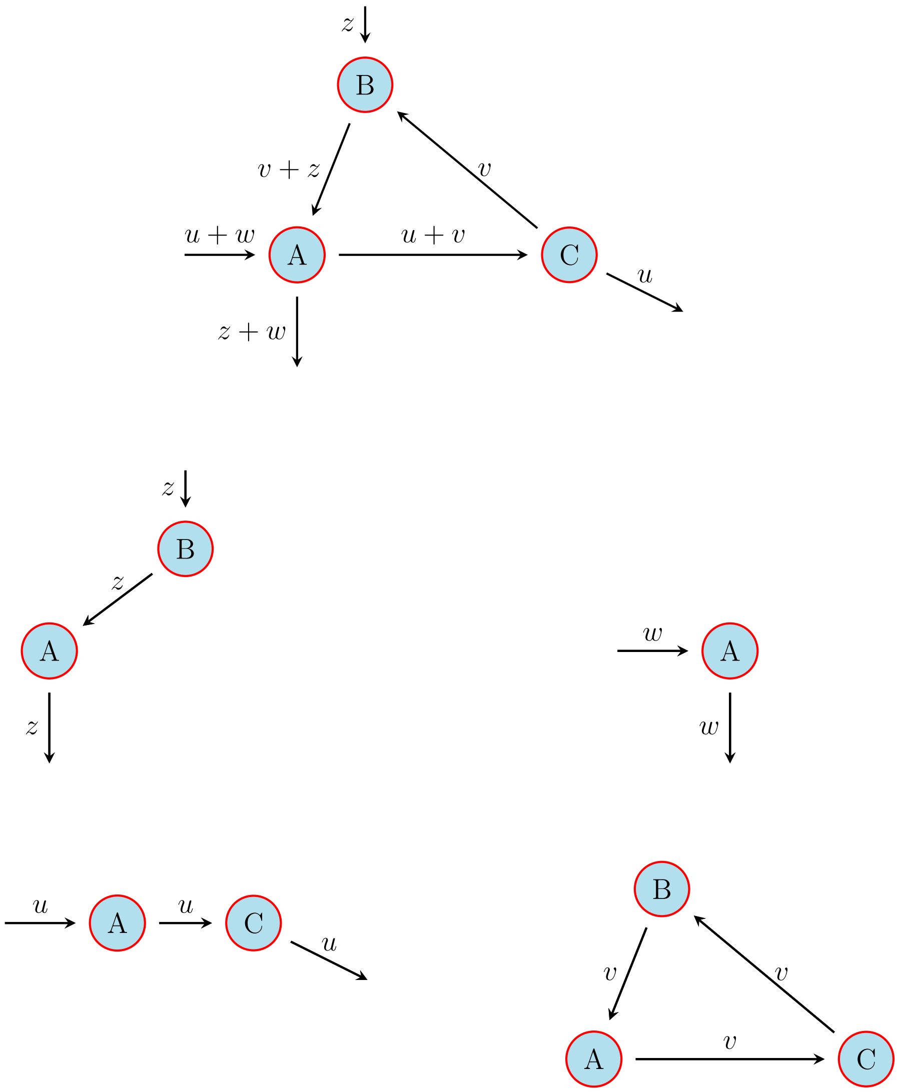


Figure 3.6: A three compartment model and four of its fluxes ($\mathcal{X}_1, \mathcal{X}_2, \mathcal{X}_3, \mathcal{X}_4$) are shown. The algebraic expressions on the edges represent the flow rates. The model is at steady state by construction. The variables u, v, w, z correspond to the rates of the four fluxes. The model can be expressed as a linear combination of the fluxes as follows $z\mathcal{X}_1 + w\mathcal{X}_2 + u\mathcal{X}_3 + v\mathcal{X}_4$, where $\mathcal{X}_4$ represents the cycle flux.

in which case,

$$FCI = \sum_{i=1}^{3} \frac{T_i}{TST}\frac{N_{ii}-1}{N_{ii}} = \frac{v}{u+v+w+z} \underbrace{\sum_{i=1}^{3} \frac{T_i}{TST}}_{=1} = \frac{v}{u+v+w+z}.$$

Considering that the model is made of three chain fluxes with rates u, w, z and one cycle flux with rate v, this result makes perfect sense as the entire cycled throughflow is due to the single cycle flux. As expected, removing any of the chain fluxes, or even decreasing their rate, causes an increase in the value of FCI. However, this is not what we observed.

Figure 3.7 shows the corresponding changes in FCI when a chain or a cycle flux is eliminated from the model. For all three models, when a cycle flux is removed, the value of FCI always decreases. On the other hand, when a chain flux is eliminated, the value of FCI can both increase or decrease, which is rather unexpected. To further investigate this issue, we analyze the changes in each component of FCI:

$$FCI = \sum_i FCI_i, \qquad FCI_i = \underbrace{\frac{T_i}{TST}}_{(I)} \underbrace{\frac{N_{ii}-1}{N_{ii}}}_{(II)} \tag{3.1}$$

Equation 3.1 clearly shows that Finn's cycling index is actually a compartmental measure. Therefore to understand the changes in cycling, we focus on the cycling at each compartment. Furthermore, each compartmental cycling has two components:

(I) Proportion of throughflow at compartment i.

(II) Proportion of cycling per unit throughflow at compartment i.

In order to understand the changes in cycling, we need to analyze the changes in these two components, at each compartment. First, we focus on the first component. Assuming the

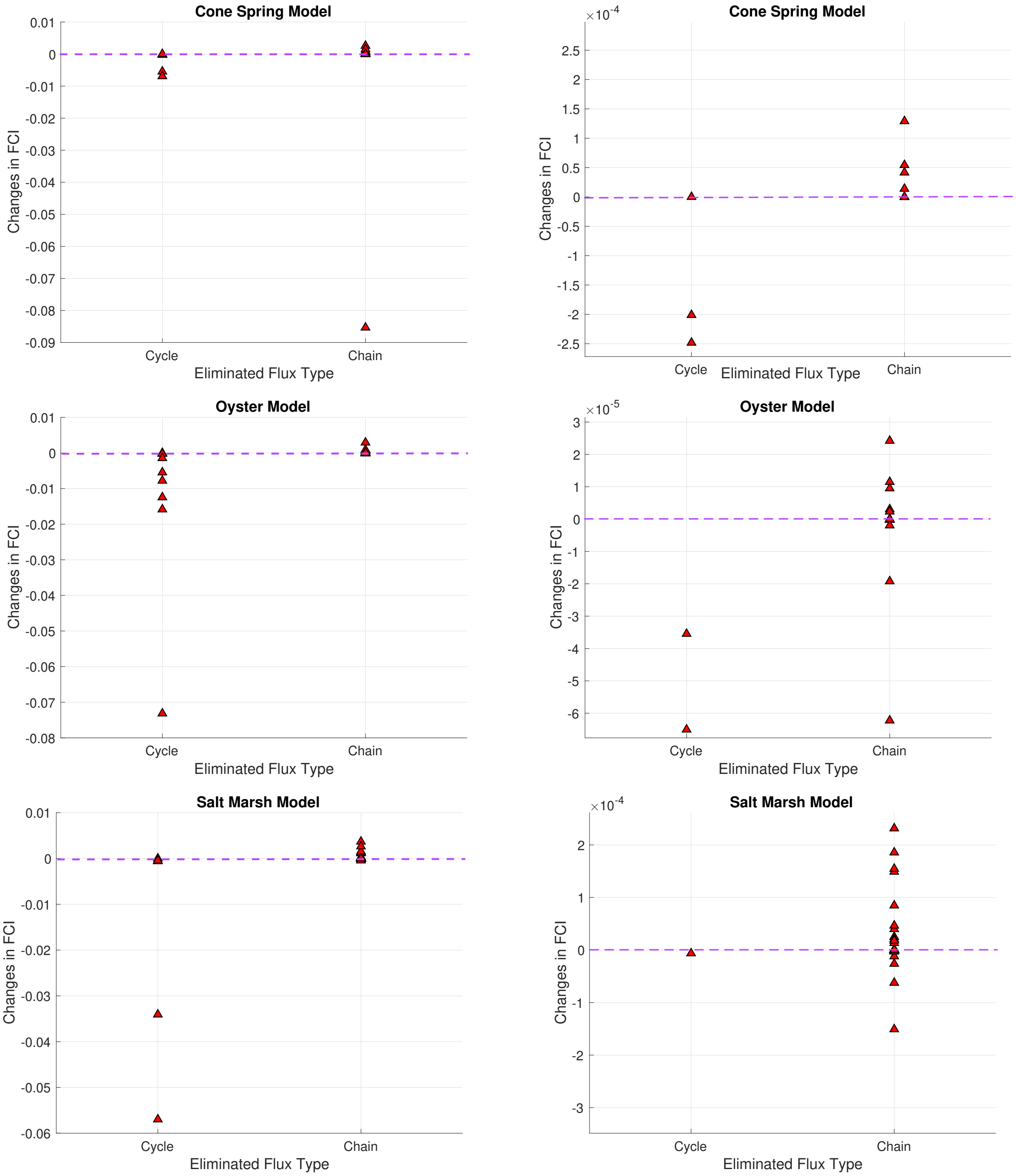


Figure 3.7: The changes in FCI after a flux of a certain type is eliminated from the ecosystem model. Each row of the figure describes a different model. Figures on the right are zoomed versions of the same figure on the left.

removal of a flux with rate r and s flows, the change in the first component is

$$\Delta\left(\frac{T_i}{TST}\right) = \frac{T_i}{TST - rs} - \frac{T_i}{TST}$$

Assuming that compartment i is not part of that flux, the numerator T_i remains unchanged after the flux removal. In this case, the change is always positive. On the other hand, if the removed flux includes compartment i, then the change in the first component is

$$\begin{aligned}\Delta\left(\frac{T_i}{TST}\right) &= \frac{T_i - r}{TST - rs} - \frac{T_i}{TST} \\ &= \frac{r(sT_i - TST)}{TST(TST - rs)}.\end{aligned}$$

In this case, the change can be either positive or negative, depending on the sign of the expression $sT_i - TST$. For instance, if T_i were high, or if the removed flux involves a lot of compartments (high s), then the change can be positive. If that is not the case, the change can be negative.

The change in component (I) is independent of the type of flux removed. Then it might explain the decrease in FCI when a chain flux is removed. However, in order to be conclusive, we need to consider the product of both component (I) and component (II), as even though T_i/TST decreases, $(N_{ii} - 1)/N_{ii}$ might increase enough to force their product (FCI_i) to increase (equation 3.1). This is exactly what happens for the simple model shown in Figure 3.6. For instance, assume that $u = 1\,, v = 2,\ w = 2, z = 0$. In this case,

$$\frac{T_3}{TST} = 0.3, \qquad \frac{N_{33} - 1}{N_{33}} = 0.4, \qquad FCI_3 = 0.3 \times 0.4 = 0.12$$

Removing the chain flux $\mathcal{X}_3$ with the lowest rate of $u = 1$, we get $u = 0\,, v = 2,\ w = 2, z = 0,$

Compartment	$\Delta(T_i/TST)$	ΔN_{ii}	ΔFCI_i
Filter feeders	0.000160	0	0
Deposited detritus	3.565E-05	0.000127	2.750E-05
Microbiota	-5.523E-05	-0.000256	-2.568E-05
Meiofauna	-5.321E-05	0.000130	-4.327E-06
Deposit Feeders	1.585E-05	-4.824E-06	1.69701E-06
Predators	-0.000103	-6.302E-05	-1.047E-06

Table 3.1: Change in $\frac{T_i}{TST}$, N_{ii} and FCI_i at each compartment after the chain flux →1→6→2→3→4→ (Figure 2.2, Table 2.3) is removed from the oyster reef model [3].

in which case

$$\frac{T_3}{TST} = 0.25, \quad \frac{N_{33}-1}{N_{33}} = 0.5, \quad FCI_3 = 0.25 \times 0.5 = 0.125.$$

Even though component (I) decreases from 0.3 to 0.25, that change gets offset by the increase in component (II), causing an overall increase in the compartmental cycling index FCI_i from 0.12 to 0.125.

While this simple three compartment model is useful to investigate the relationship between cycling and fluxes, perhaps it is too simple to explain the decrease in FCI when a chain flux is removed, as shown in Figure 3.7. Therefore we shift our focus to the oyster reef model, to investigate this issue further. Table 3.1 shows the changes in each component of the compartmental cycling index after the removal of the chain flux →1→6→2→3→4→ (Figure 2.2, Table 2.3), where there is a decrease of 1.9518E-06 in FCI. Even though FCI decreases system-wide, removal of this flux affects the cycling at different compartments differently, causing some to increase (e.g. Deposited detritus), some to stay constant (e.g. Filter feeders), and some to decrease (e.g. Microbiota). Furthermore, there is a decrease in component (II) in three compartments (Microbiota, Deposit Feeders, and Predators), which is impossible for the three compartment model (see Figure 3.6).

Even though the removed chain flux does not pass through the compartment Deposit Feeders (compartment 5), its elimination causes a decrease in the value of N_{55}, and hence, in $(N_{55}-1)/N_{55}$ as well. These changes are rather small in value, so in order to confirm this

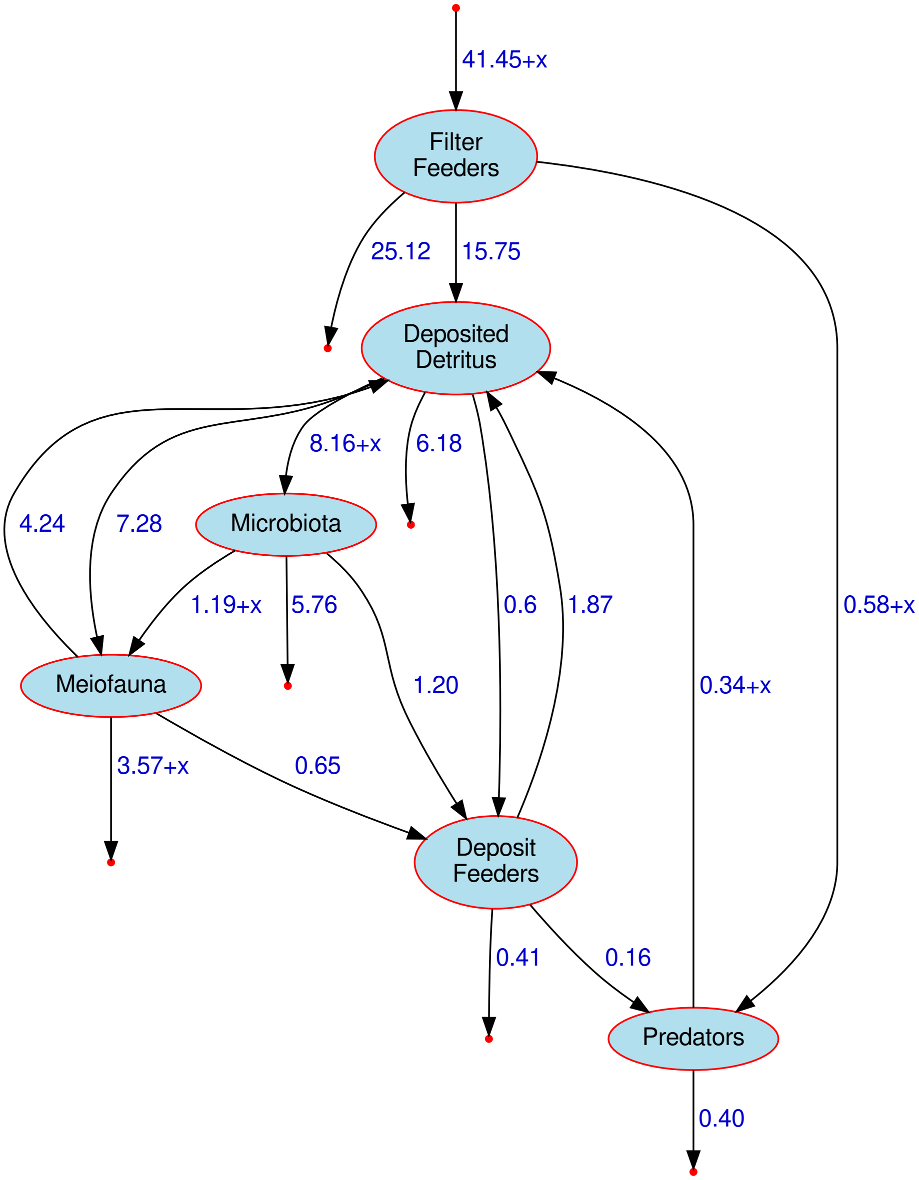


Figure 3.8: Oyster reef ecosystem model, with the chain flux →1→6→2→3→4→ (Figure 2.2) added at a variable rate of x. The numbers from one to six represent the compartments: Filter Feeders (1), Deposited Detritus (2), Microbiota (3), Meiofauna (4), Deposit Feeders (5), and Predators (6). The flows containing the term "$+x$" are part of the added chain flux. The model is always at steady-state, regardless of the value of x.

observation, we decided to add back this chain gradually, and record the changes in N_{55}. In order to do so, we created a continuously variable model as shown in Figure 3.8, with the following flow matrix and throughflow vector:

$$F = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 15.75 & 0 & 0 & 4.24 & 1.87 & 0.34+x \\ 0 & 8.16+x & 0 & 0 & 0 & 0 \\ 0 & 7.28 & 1.19+x & 0 & 0 & 0 \\ 0 & 0.60 & 1.20 & 0.65 & 0 & 0 \\ 0.58+x & 0 & 0 & 0 & 0.16 & 0 \end{bmatrix}, \quad T = \begin{bmatrix} 41.45+x \\ 22.21+x \\ 8.16+x \\ 8.47+x \\ 2.45 \\ 0.74+x \end{bmatrix} \tag{3.2}$$

The matrices above represent the model before and after the removal of the chain flux →1→6→2→3→4→ for $x = 0.009$ and $x = 0$, respectively (Table 2.3). The values above are rounded to two decimal places for practical reasons, in actual calculation we traced up to 15 decimal places for accuracy. The integral throughflow matrix N can be computed using F and T for any value of x. Figure 3.9 shows the changes in N_{55}, which indicates the changes in $(N_{55}-1)/N_{55}$, component (II) of compartmental cycling at Deposit Feeders, with respect to x. Figure 3.9 confirms the data in Table 3.1, that removal of the chain flux →1→6→2→3→4→ indeed decreases N_{55}, which indicates the cycling at Deposit Feeders compartment per unit throughflow. This case is particularly interesting for four reasons. First, cycling decreases after the removal of a chain flux, not a cycle flux. Second, the decrease in cycling is not due to a change in the throughflow value of the compartment (T_i). Third, the removed flux does not even pass through the compartment where the decrease in cycling occurs. Last but not least, as we increase x beyond $x = 0.009$, the value of N_{55} stops increasing and starts decreasing. In other words, the response of cycling, and perhaps many other system-wide measures, to the addition or removal of a flux is not simple and linear.

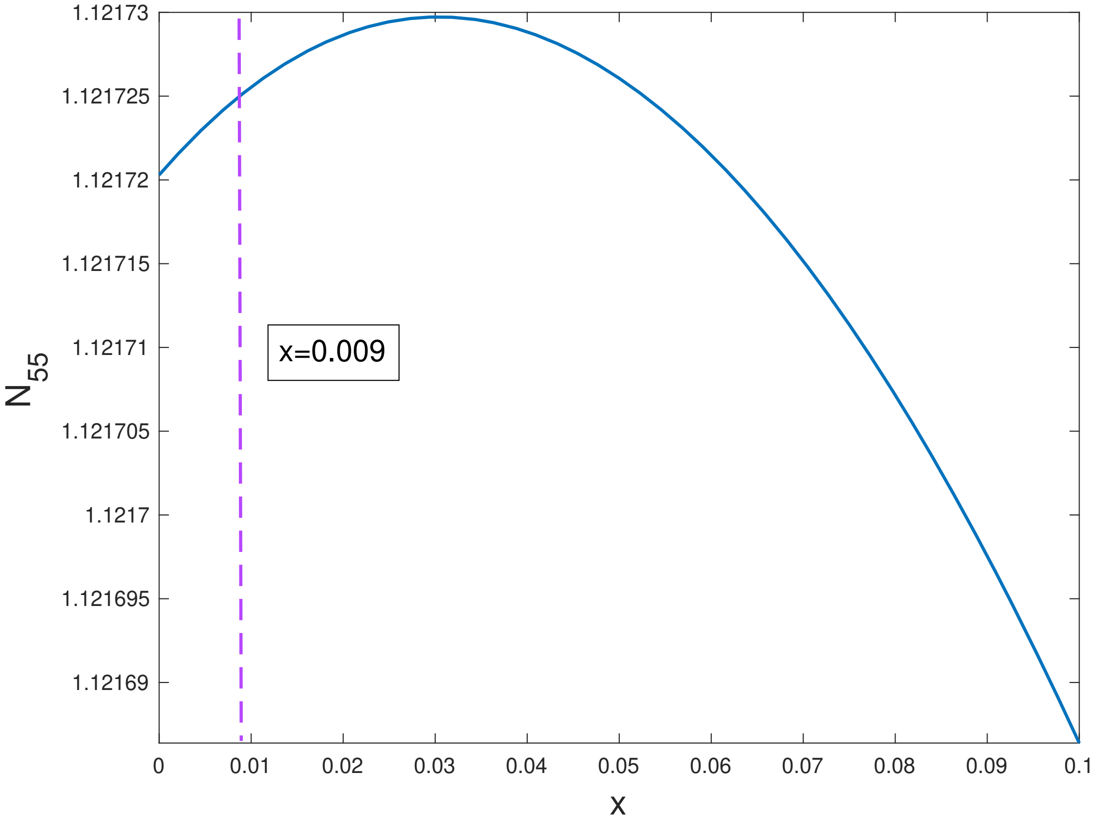


Figure 3.9: The value of N_{55} (corresponding to Deposit Feeders) for the oyster reef model with variable flow rates that depend on x, shown in Figure **??** and Equation 3.2. $x = 0.009$ and $x = 0$ represent the models before and after the removal of the chain flux →1→6→2→3→4→, respectively (Table 2.3).

Chapter 4

Discussion

Through this investigation of the sensitivity and robustness of the flow-based system-wide measures (such as TST, FCI, IEI, synergism, mutualism) to the elimination of fluxes, we observe that most system-wide measures remain relatively unchanged until the removal of at least 60 percent of the fluxes in the system. This percentage increases with system size. For the larger Georgia salt marsh ecosystem model [24], all system wide measures (except mutualism) are within 5% of their original value up until more than 80% of the fluxes are removed. Based on the limited number of models and perturbation types used in this study, all system-wide measures we tested appear to be resilient to moderate changes in the model data.

We observe that 90% of the total system throughflow in the three models with 8, 19 and 25 flows, are handled by 5 out of the 18, 7 out of 32, and 6 out of 47 of the fluxes, respectively. These observations indicate that a relatively low number of fluxes carry the majority of the throughflow burden in these models. In addition, the larger the model, the better the representation of the model with fewer fluxes. This is a promising finding from an experimental data gathering point of view, especially considering the often higher than 10% error rate of most experimental methods. Smaller amount of empirical data may be enough to predict system-wide measures with reasonable accuracy. Exploiting this fact may enable building more accurate models using less data.

Most system-wide measures respond to the removal of fluxes by decreasing slowly, before a total collapse at the very end. Two exceptions are the synergism and mutualism measures. The elimination of fluxes from the ecosystem does not appear to influence the occurrence of synergism and mutualism. Interestingly, there's a significant increase in both synergism and mutualism values towards the end of the flux elimination procedure. For instance, mutualism values are maximized when 3 out of 18, 2 out of 32, and 5 out of 47 fluxes are left, for each model. In this regard, model simplicity appears to be correlated with synergism and mutualism.

Effects of flux elimination on system-wide measures can be quite complicated. Investigating the relationship between the change in FCI and the type of flux (cycle or chain) eliminated reveals this complexity. Furthermore, the addition (or removal) of the same flux to a model can cause opposite effects on a system-wide measure, depending on the rate of the flux added (or removed), as demonstrated by Figure 3.9, where adding a chain flux to a model increases its cycling, if and only if the rate of the added flux is low. While this study answers some questions, it poses new questions as well, most of which lie outside the scope of this study. Future work focusing on these questions may improve our understanding of the system-wide measures themselves.

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