RESILIENCE ENHANCEMENT OF MUTUALISTIC NETWORKS

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ABSTRACT

Pollination networks are in decline and not operating as effectively as they used to due to factors such as pesticides, diseases, and the advent of climate change[1]. Ensuring that these networks are resilient is vital for the health of numerous ecosystems, so improving the resilience of these networks is of paramount importance. We can define network resilience as the ability of a network to retain its basic functionality when errors, failures, and environmental changes occur[2]. To improve the resilience of these networks, ecological research has repeatedly shown the benefits of biodiversity[3]. While increasing the biodiversity of a network will improve resilience, there is no literature on how just adding one new species to a network will improve resilience. Network scientists usually study the structure of mutualistic networks[4] and how over time these networks change[5]. The novel part of this research is using network science to understand how adding just one species will affect an ecosystem. To do this, we compiled data from 143 different pollination networks around the world and created a worldwide pollination network to find species that could be added to different locations. Then, we calculated the resilience of the corresponding flower and pollinator projection networks. There are two methods we tried to improve the resilience of these networks, either adding one or deleting one species from the network. We found that when trying to improve network resilience there is always a cost and benefit to species addition and deletion. Both methods can be used to improve resilience, but resilience usually decreases or does not change if a species added. If a species is deleted there is a high probability that the location's resilience will decrease as well. We were able to derive equations to predict how resilience would change due to species deletion or addition as well as predict in some cases what the optimal species to add would be. We were also able to predict for all cases what the optimal species to delete would be in a network.

CHAPTER 1
Introduction

1.1 Pollination and Mutualism

Without pollination the effects on the world would be staggering[6,7,8]. A world without pollination effectively means a world without food since pollination is the method by which flowers germinate, which is a term for seed creation. While some flowers can self-germinate, most flowers require a male or female flowers pollen to germinate and this occurs when one flower's pollen is spread from itself to another flower. There are many different ways that a flowers pollen can be spread. One way a flowers pollen can be spread is via wind. However, the most common way that pollen is spread is through animals or insects. Animals and insects visit flowers to gather or eat the nectar from them. When this happens, a random amount of pollen grain is attached since the grains are placed near the nectar. Then when the animal visits another flower, a random amount of pollen might fall in and germinate it. Pollination occurs randomly then, and, is based on which types of animals visit certain kinds of flowers. The animals and insects that spread pollen are called pollinators. In an ecosystem, we can refer to the network of pollinators and the flowers they pollinate as a pollination network.

Pollination networks are a type of mutualistic network since both pollinators and flowers mutually benefit from their interactions[5]. The pollinators benefit since they get to collect nectar from the flower and the flower benefits since the rate of reproduction would be lessened without the pollinators. Some other examples of mutualistic networks are seed dispersal networks and symbiotic ant-plant networks[9]. In all cases, both species in the network benefit from interacting with one another. These networks are vital to ecosystems around the world due to how connected the networks are to other ecological systems. Virtually all plants around the world depend on seed dispersal or pollination to reproduce. There is much existing literature about mutualistic networks from the network science and ecological communities due to their importance.

1.2 Structure of mutualistic networks

The structure and operations of mutualistic networks are well understood[4,10,11,12]. One important structural characteristic about mutualistic networks is that they are nested networks. According to Bascompte, "Nestedness entails a nonrandom pattern of structure beyond the topological pattern of connectedness frequently assessed in networks of ecological interactions"[4].Most ecological networks have very well-defined structures[13], and mutualistic networks are no exception. Due to their nested structure mutualistic networks are recognizable from their structure. A nested structure is one in which specialist and generalist species emerge through the interactions[4]. A specialist can be thought of as a species that only interacts with a few other species, while a generalist is one that interacts with many others species[14]. Specialists only interact with a subset of species that generalists interact with. Effectively, few species interact with other species in the networks and a few species interact with the majority of species in the network. The nestedness of a network can be quantified[4],and, other studies have found that species abundance and nestedness are correlated. Robustness and nestedness are connected, since, if some specialist species die out, the network can still function. However, if generalists began dying out, then the network is in real trouble since these species are very important to the network.[11]. While the robustness of a network is connected with nestedness[5], there is no such connection between resilience and nestedness. This might be because of all the different definitions of resilience, so there is no one ground truth to compare against.

1.3 Details of ecological research

Ecologists have extensively studied different types of mutualistic networks, since mutualistic interactions are one of the most fundamental ecological interaction types[15].Numerous studies[16] have detailed how different types of species interact with one another in a mutualistic way. When ecologists study mutualistic networks, there is a focus on interactions between two very specific species in a small location[17]. Many studies with a purely ecological bent focus on these very granular interactions to glean some truth that can be extrapolated in very general ways. The main conclusion from these studies is that biodiversity is a known way to improve these network's resilience . However, there is no granular method to understand what the effect of one species will be on a network. While studies have been conducted of effects of individual species on certain ecosystems, studying this using a large worldwide

data source to understand global pollinator interactions is the novel part of our research.

1.4 Ecosystem Restoration

Ecological restoration is the process by which ecologists attempt to improve a collapsed or poorly performing ecosystem by adding a new species or eliminating problematic ones[18,19,3] .Other than species addition or deletion, there are other ways that an ecosystem can be improved. One of the most common ways to improve an ecosystem is to actually change an ecosystem's physical terrain, like diverting water flow or keeping ecosystems in mind when building levees or other man-made structures. However, modeling the effects of these changes would require changing more than the network topology, so, for the sake of this research we will be focusing on species additions and deletion. Since a species' behavior can be well-defined within its own ecosystem, deletion is a sure way to ensure that a network's resilience will improve. What's also intriguing is that deletion sometimes has no effect on a network's resilience[20] Species addition is problematic because it is hard to predict how an added species will acclimate in its new environment. When a new species is added there is also the issue that it could potentially out-perform the other species in the network and become the prototypical "invasive" species[21 ,22] . An invasive species is a non-native species that is introduced to a network and ends up hurting the ecosystem it is introduced in[23]. What's interesting though is that this trend rarely occurs, and, in fact when non-native species are introduced into a network, it is highly unlikely that the newly added species will dominate the network. Instead, the majority of non-native species have a negligible effect on the network and do not meaningfully affect the networks they are added to[24]. However, since we cannot predict all the possible effects of a non-native species addition due to all the complexities seen in nature, this research would be best used in conjunction with an ecosystem restoration effort. If species were already identified to not negatively affect an ecosystem, our research could be used to predict which species would be the best to add to maximally improve resilience.

1.5 Thesis Organization

The organization of this thesis is as follows. In Chapter 2, an overview of how we collected data and analyzed data will be discussed as well as what the formal definition and quantification of resilience is. The second chapter we will also include how we modeling

adding and deleting species to a network. Chapter 3 is titled "Numerical Simulation" and details the results of species deletion and addition on the resilience of a network. All the simulation results using real species are summarized and the initial findings are analyzed. In the next chapter, "Theoretical Framework" we derived equations to predict how the resilience would change due to species addition or deletion. From these equations, we were then able to predict - for certain projection networks and added species - what the optimal species to add were. The final chapter, chapter 5, is the conclusion and we give a summary of results and recommendations for topics of future work and study.

CHAPTER 2
Research Methods & Data

2.1 Initial Data Information

Figure 2.1: Network data from locations all around the world. Each red dot represents a unique dataset. Some locations have multiple unique ecosystems, which is why some spots on the map have so many dots.

143 different plant-pollinator networks were downloaded from the Web of Life dataset (www.web-of-life.es) which aggregated ecological interaction data from numerous studies. The locations from where the data was collected from can be seen in Figure 2.1. Each individual network contained multiple different plant-pollinator interactions, these interactions were represented as weighted values in an adjacency matrix. The larger a value, the more

Table 2.1: Amount of different species in network. Number of unique species refers to the total number of unique species in a network. The cumulative amount column refers to the total number of added species in all networks.

Species Type	Number of Unique Species	Cumulative Amount
Pollinator	5922	8100
Flower	2567	3612
Total Species	8489	11712

times a plant is visited by a pollinator. Since we only wanted to understand if it was possible to improve resilience via species addition, we decided to simplify the data to only contain unweighted data. If an interaction count was greater than 0, that interaction value was scaled down to 1 and interactions that had a value of 0 were kept at 0.

These networks are from all around the world and are of differing sizes and species types. There are some species that are shared between all networks. Totally, there are 8100 pollinators and 3612 flowers in all 143 networks. Only counting for unique pollinators and flowers, there are 2565 unique flowers and 5922 unique pollinators. Since these networks share species, we created an overall network detailing all the interactions between all species. Using this network, we could identify all existing species in a specific network and decide which unique species could be added to that network from different locations. Using this overall network we can add species to a new location. To add a new species to a network, all the species in the network are identified. Then, using the overall network, we find the potential new species that could be introduced into the network. Any potential species that are to be added could not be repeats of any species in the network since we wanted to observe the effect of a completely new species being added to the network that was not a part of the ecosystem. After adding this new species the change in resilience was recorded.

2.2 Measuring Resilience

There exist a multitude of different definitions for resilience[25]. Depending on the academic field and context, the world 'resilient' can mean something different. Understanding how long it can take for a network to recover from resilience is called "engineering" re-

silience[26]. When an engineer is studying a network or system they are concerned with how long it might take for that system to recover from some disaster or big change. We are more concerned with a concept known as system resilience. System resilience is how long it takes before a system reaches its breaking point and operates at a lower state. Given our context of studying mutualistic network resilience, resilience can be defined using J.Gao's definition where resilience is "a system's ability to adjust its activity to retain its basic functionality when errors, failures and environmental changes occur"[2],[27]. A pollination network can be considered resilient then if it is able to recover from any sort of perturbation. Much of the theoretical basis for resilience is detailed in J.Gao's "Universal resilience patterns in complex networks". We will be using the β_{eff} metric to quantify resilience and understand how resilience changes.

Before discussing how exactly resilience is measured, we first must mention how state is measured. In our research, the state of a species i corresponds to the abundance value x_i. Abundance is defined as the number of individuals per species. The abundance value of a species fluctuates over time due to a number of ecological factors. The ecologists have modeled how abundance changes using a differential equations, which models a variety of ecological factors. The general form of how x changes is shown in the equation below. Note how this equation can be applied to any mutualistic network if the individual dynamics F, mutualistic projection network A, and the interaction dynamics G are known.

$$\frac{dx_i}{dt} = F(x_i) + \sum_{j=1}^{N} A_{ij} G(x_i, x_j) \tag{2.1}$$

After calculating the abundance of each individual species, the overall state of the network can be calculated. This value is known as x_{eff} and is calculated in the following way, where x is a vector of abundance values corresponding to flower or pollinator species and s is a vector of the column-sum of the matching projection network:

$$x_{eff} = \frac{< xs >}{< s >} \tag{2.2}$$

x_{eff} will either be in a high or low state. If x_{eff} is in a high state, this means the abundance of all species is high, while if x_{eff} is low the abundance of all species is low. Predicting how will change is difficult, due to the multi-dimensionality of the differential equation.

When adding or deleting a species it becomes impossible to predict exactly how the state of the system will change, since a new species addition affects both projection networks and modifies their weights. Due to this complexity, x_{eff} is not a good predictor for resilience. If a species is added to or deleted from the network x_{eff} can change quite drastically. Since species can interact in wildly different ways, it is hard to predict if x_{eff} will go down to the low state without completely re-calculating all values using the differential equation above and remaking the projection networks. If a location has numerous species and interactions, re-running all calculations can take a long time. Another issue with the x_{eff} metric is that the point at which the state decreases from x_H to x_L varies wildly between different networks. Using x_{eff} there is no universal critical x_{eff} value which will tell when the state will move from a high state to a low state. Without a universal critical value there is no method to actually compare different networks, since each network has a different critical x_{eff} value. x_{eff} cannot be used to measure resilience then, since to measure resilience there needs to a be a universal way to measure how close a network is to moving to the low state.

Because x_{eff} can only be used to measure state, another metric had to be used to measure resilience. The β_{eff} approach to resilience is preferred since it is derived exclusively from the network interactions of the adjacency matrix's projection network. The equation for β_{eff} is as follow, where s represents the column sum of the flower or pollinator projection networks:

$$\beta_{eff} = \frac{< s^2 >}{< s >}$$

Using this framework, the dynamics of the network are not important. Now, we have a more general method to describe the state of a network. From this general method, we can simplify the state equation above to the following equation using x_{eff} and β_{eff}:

$$\frac{dx_{eff}}{dt} = F(x_{eff}) + \beta_{eff} G(x_{eff}, x_{eff}) \tag{2.3}$$

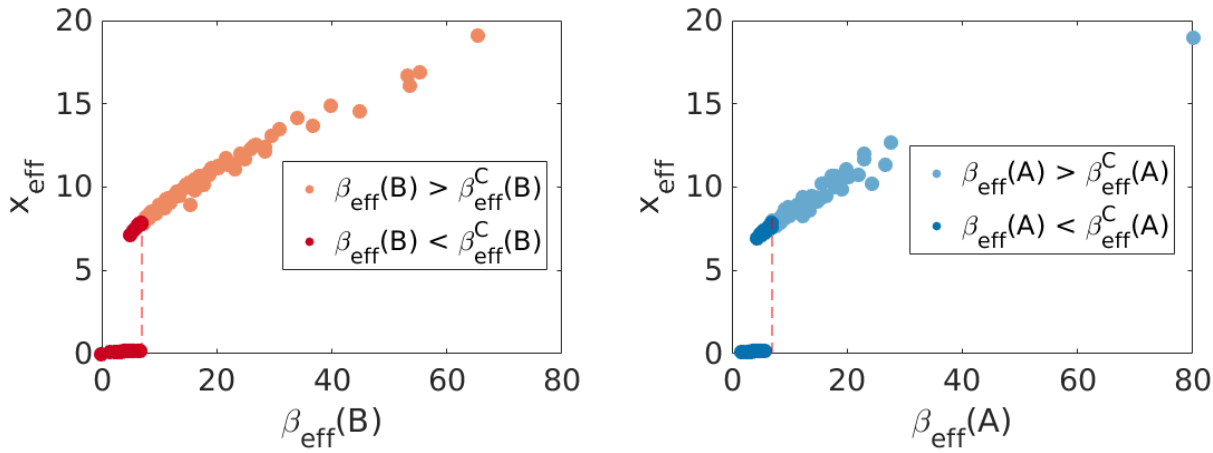
A network can either be considered resilient or non-resilient. Since we are specifically studying pollination networks, F and G are replaced with the individual and interaction dynamics of pollination networks, which is shown in equation 2.4. The below equation details how the

abundance of a species i changes over time.

$$\frac{dx_i}{dt} = B_i + x_i\left(1 - \frac{x_i}{K_i}\right)\left(\frac{x_i}{C_i} - 1\right) + \sum_{j=1}^{N} A_{ij}\frac{x_i x_j}{D_i + E_i x_i + H_j x_j} \tag{2.4}$$

The dynamics in the equation 2.4 are derived from ecological phenomena, and the different parameters represent different ecological phenomena[2]. The first term, B_i describes the migration rate of species i from neighbouring ecosystems. The migration rate is added with with the multiplied product of the logistic growth equation and with a fraction relating to the Allee effect, which models negative growth if $C_i > x_i$. The K_i parameter describes the carrying capacity for a location and limits the growth of species. The last right-most term captures the effect that species i has on species j, by multiplying the projection network's value with x_i and x_j. This value is divided by D_i, E_i, and H_j which represent the saturation rate of the response function[2]. This equation is also used to determine what the critical resilience value. β_{eff}^{C} of the system is. The critical value determines when a system is considered "resilient" versus when its considered "non-resilient".According to the dynamics, resilient systems have a β_{eff} greater than 6.97, while non-resilient network's have a β_{eff} less than 6.97. 6.97 can be considered the critical resilience value, β_{eff}^{C}. Resilience is tied to the overall state of the network, x_{eff}. A resilient network is a network that is in the high state x_H. All networks that have a β_{eff} greater than 6.97 will not have a low x_{eff}, x_L. However, a network can be non-resilient and either have a high or low x_{eff} value, as seen in Figure 2.2. Networks with a low x_{eff} are expected to be non-resilient, but networks that have a high x_{eff} and are non-resilient are the networks that are very fragile. These networks might be operating at a high state, but there is a high chance that if a single species is taken out, these networks will move to the low state. Describing a network as resilient effectively means that if a species is taken out or added, there is a small chance that the network's x_{eff} will radically change. However, if a network is non-resilient, this means that the network is either in the low state or can very easily change and move to the low state.

β_{eff} cannot be found for the initial network of unweighted flower-pollinator interactions. That network contains no information on how strong the mutualism is between species. Instead, the β_{eff} metric is calculated from the projection networks of these bipartite graphs. There are two β_{eff} values then for each given location, there is a resilience value for the flower projection network and one for the pollinator projection network. From the given M



(a) Comparing $x_{eff}(B)$ against initial $\beta_{eff}(B)$

(b) Comparing $x_{eff}(A)$ against initial $\beta_{eff}(A)$

Figure 2.2: We compare x_{eff} with β_{eff}, notice how networks that have a $\beta_{eff} > \beta^C_{eff}$ are always in the high state, while networks that have a $\beta_{eff} < \beta^C_{eff}$ are either in a low-state or high-state.

plant-pollinator adjacency matrix the two projection networks can be created, the pollinator projection network A and the flower projection network B. The projection networks are wired from the M network, but these networks are weighted networks unlike the M network. The weights represent the mutualism between species - the larger the weights, the more powerful the mutualism is between species. We can represent the resilience of these networks as $\beta_{eff}(A)$ and $\beta_{eff}(B)$ which correspond to pollinator resilience and flower resilience respectively.

2.3 Analyzing Initial Data

Before adding any new species, we first graphed the initial β_{eff} distribution for both the A and B network as shown below:

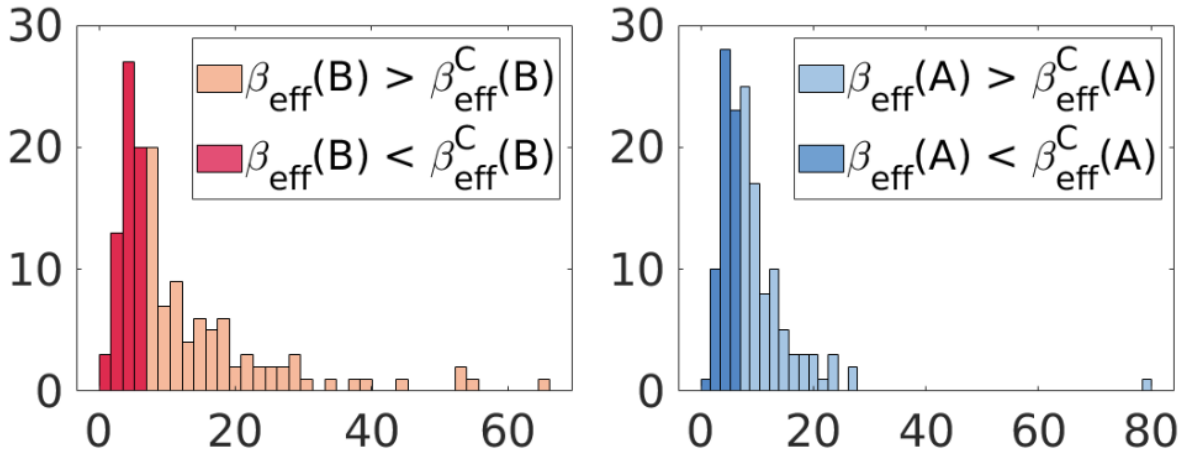


Figure 2.3: Histogram detailing initial resilience values for flower and pollinator projection networks. The x-axis refers to a range of β_{eff} values, while the y-axis refers to the number of locations that match a given range of values. These graphs show the number of locations that are non-resilient versus resilient.

Half of that networks that we have collected are non-resilient while the other half are resilient. The resilience of a location can be calculated from a network's density and heterogeneity. Density is defined as $< s >$ while the heterogeneity of a network is defined as the variance of the network's degree. Together, the two values make up β_{eff}.

$$\beta_{eff} = H + D \tag{2.5}$$

β_{eff} can be represented as a sum of its' networks heterogeneity and density. When a new species is added the network's heterogeneity and density will change. All network's initial heterogeneity and density distribution is shown below in Figure 2.4. Note that the green shaded portion represents a β_{eff} greater than 6.97 while the green shaded portion represents a β_{eff} less than 6.97.

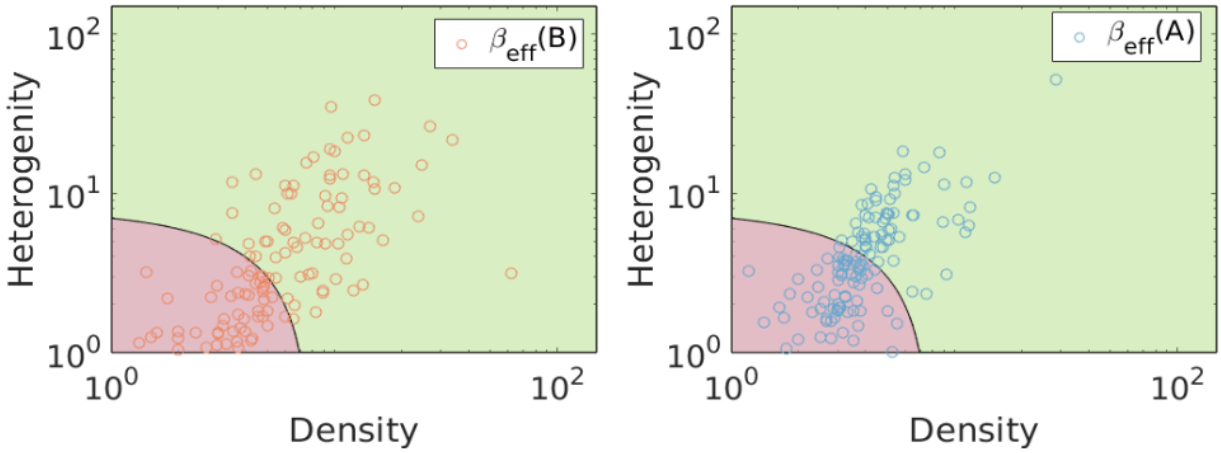
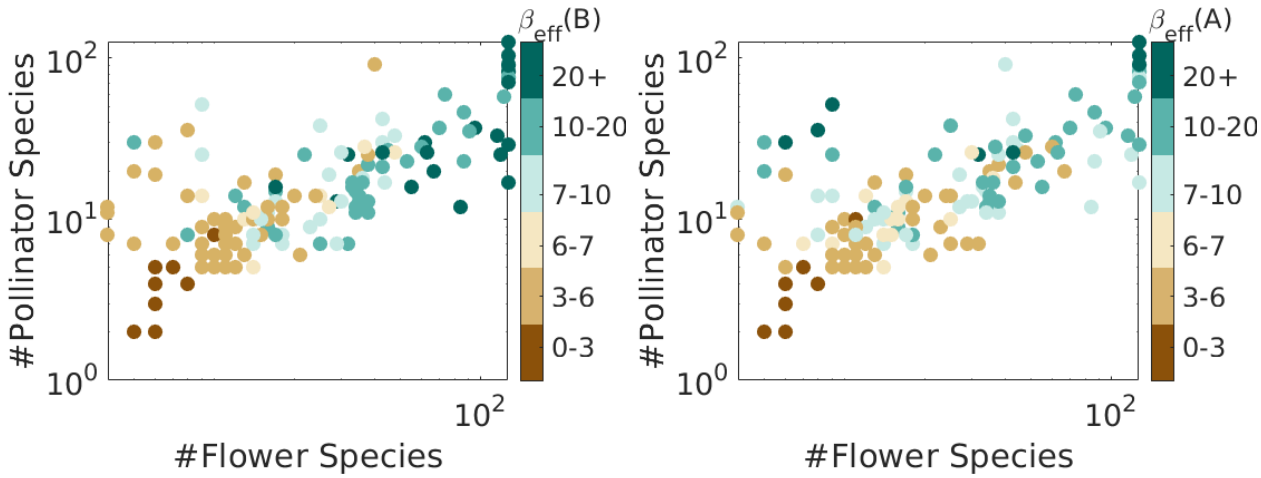


Figure 2.4: Initial heterogeneity and density values. Dots in the green represent resilient locations, while dots in the red are non-resilient locations.

From Figure 2.2, we can see that there a multitude of different network configurations that can lead to resilience. Two networks can have similar density values but wildly different heterogeneity values. Though density and heterogeneity can be used to break up the β_{eff} value and give a high level overview of how a network is structure, they are derived from the A and B projection networks. Thus, they cannot be used to predict what a network's resilience will be. While these attributes cannot be used to predict how resilient a network will be, the total number of species that are in a network is usually a good indicator of how resilient a network will be. The more species that are part of a location the chance that the location is more dense and heterogeneous.



(a) Effect of species on $\beta_{eff}(B)$ **(b) Effect of species on $\beta_{eff}(A)$**

Figure 2.5: Effects of species addition on small locations. Species that have a large species count tend to be more resilient.

This theory is supported in Figure 2.3, where the larger locations are generally resilient while locations with a smaller species count are non-resilient. While there are some exceptions to this rule, locations with a large species count are usually resilient. This matches the ecological research, which states that the more bio-diverse an ecosystem is the more resilient the location will be[28].

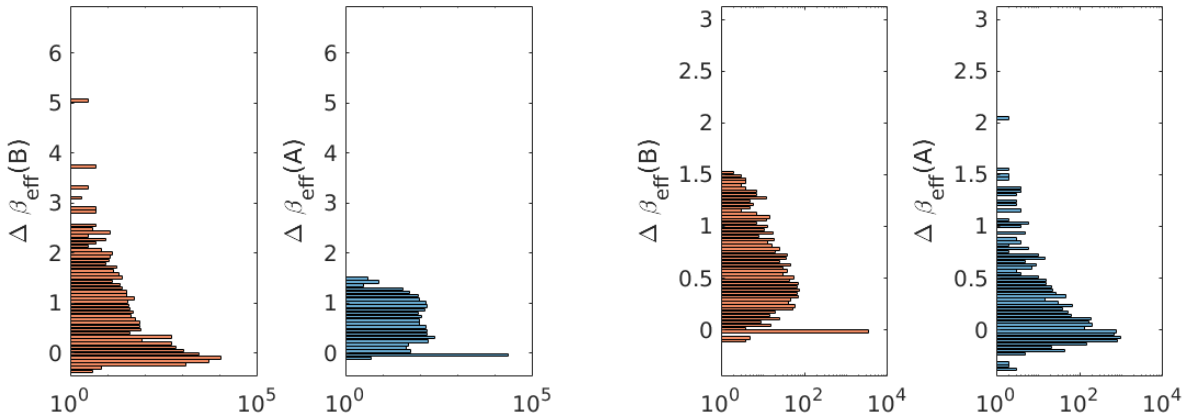
In the coming chapters we will analyze the effects of species addition and deletion on the 143 different pollination networks.

CHAPTER 3
Numerical Simulation

To test if the resilience of mutualistic networks can be improved, we simulated adding one new species to a network and deleting one species from a network.

3.1 Species Addition

When adding a species to the network we tested the effects of adding new pollinator or flower to a network. After adding one new species to the network, we measured the change in resilience due to addition. If a flower is added to the network, we measured the changes in the A and B projection network as $\Delta\beta^F_{eff}(A)$ and $\Delta\beta^F_{eff}(B)$ respectively. Similarly, the effects of pollinator addition can be recorded as $\Delta\beta^P_{eff}(A)$ and $\Delta\beta^P_{eff}(B)$. From Figure 2.5 we hypothesized that locations with different species counts would be affected differently by species addition. Instead of graphing individual locations and observing the effects of species addition, we binned networks by their species counts. Networks that had less than or equal to 30 species were considered to be "Small", networks between 30 and 60 species were considered to be "Medium", and networks that contained greater than 60 total species were considered to be "Large". Then, we simulated the effects of adding one pollinator or one flower to these networks and measured the resilience change. We will now compare the effects of species addition between large and small locations to understand if species size does affect resilience change in any way.

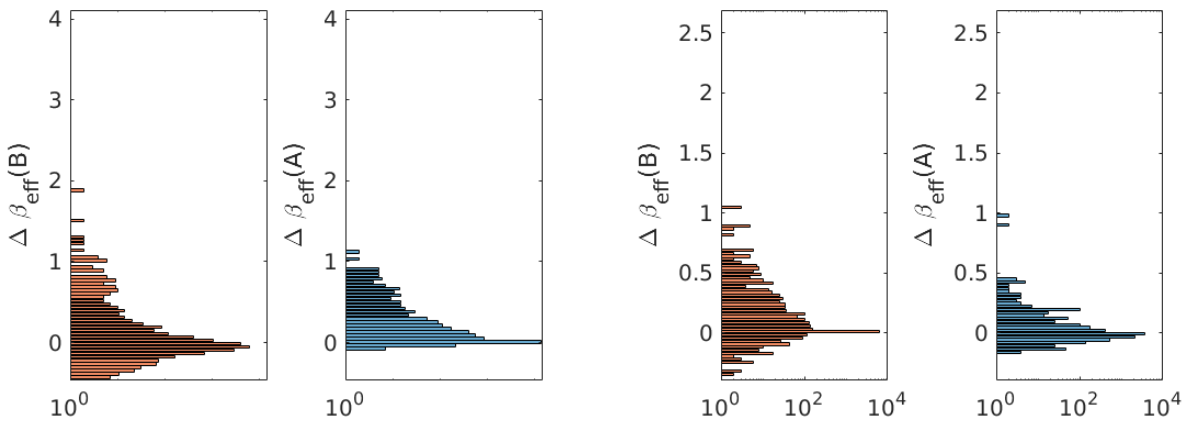


(a) Effects of flower addition on small locations

(b) Effects of pollinator addition on small locations

Figure 3.1: Histogram showing effects of species addition on small locations, the orange bars represent resilience change in flower networks and the blue bars represent resilience change in pollinator networks. The x-axis refers to the total number of added species, while the y-axis represents the change in resilience. The graph shows the frequency at which certain ranges of $\Delta\beta_{eff}$ values will be occurring.

From Figure 3.1, it is clear that adding a species can either benefit a network or harm it. When adding a flower, the maximum $\Delta\beta_{eff}$ is larger in the B network than the A network. The same effect can be seen when one pollinator is added to the network. The larger change in resilience is observed in the projection network of the same species type as the added species; it is possible for the A projection network to benefit more than the B network depending on the added species. However, in both 3.1a and 3.1b the projection networks that were of the same type as the added species contained the majority of $\Delta\beta_{eff}$ values that were negative. It seems that adding a species can benefit both projection networks. Further, there is a large chance that the newly added species has the potential to greatly benefit the projection network of the same species type. At the same time, the networks of the same type also have a high probability of decreasing their resilience value after a species is added. The projection network of the opposite type only benefits from a species addition of the opposite species type, and, in only a small number of cases does the resilience of these networks decrease. The next figure will examine large networks and we will see if these networks exhibit different traits than small networks.



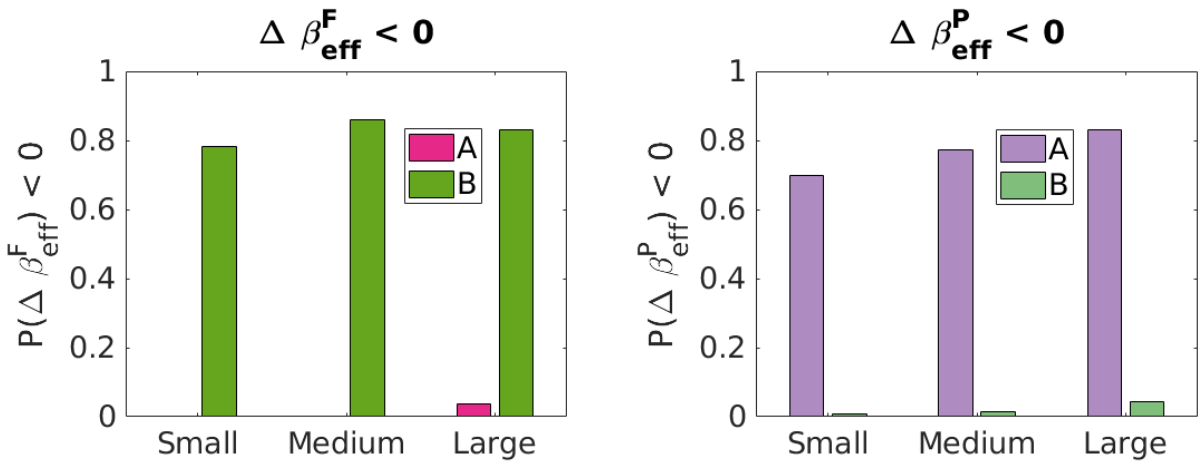
(a) Effects of flower addition on large locations

(b) Effects of pollinator addition on large locations

Figure 3.2: Histogram detailing effects of species addition on large locations. The x-axis represents the number of added species and the y-axis represents the change in resilience. The graph shows the frequency at which certain ranges of $\Delta\beta_{eff}$ values will be occurring.

What we can see from Figure 3.2 is that overall the resilience changes from adding a flower or pollinator is just not as large as the resilience change in small networks. Similar to small networks, the resilience change in the projection networks of the same type as the added species both contain the largest resilience change and also have a larger amount of potential negative values. The difference between Figure 3.1 and 3.2 lies in the fact that for larger locations the maximum resilience change is not as large as the resilience change in smaller locations. This is occurring because the density and heterogeneity values are larger in large locations, so these values are not as affected by a new species addition. Since heterogeneity and density determine a location's resilience, the resilience of large locations do not change as drastically as the resilience of small locations.

From Figures 3.1 and 3.2 it is clear that species addition can benefit ecosystems. However, the majority of added species appeared to have a detrimental effect on resilience. We measured how often a newly added species would negatively affect the resilience of a network as compared with how often it would cause a positive change in resilience in Figure 3.3. We found that there is a large probability that new species that are added to the M network will negatively affect the projection network that matches the type of the added species.Conversely, this extremely likely that a newly added species will only have a positive effect on the projection network of the opposite type.

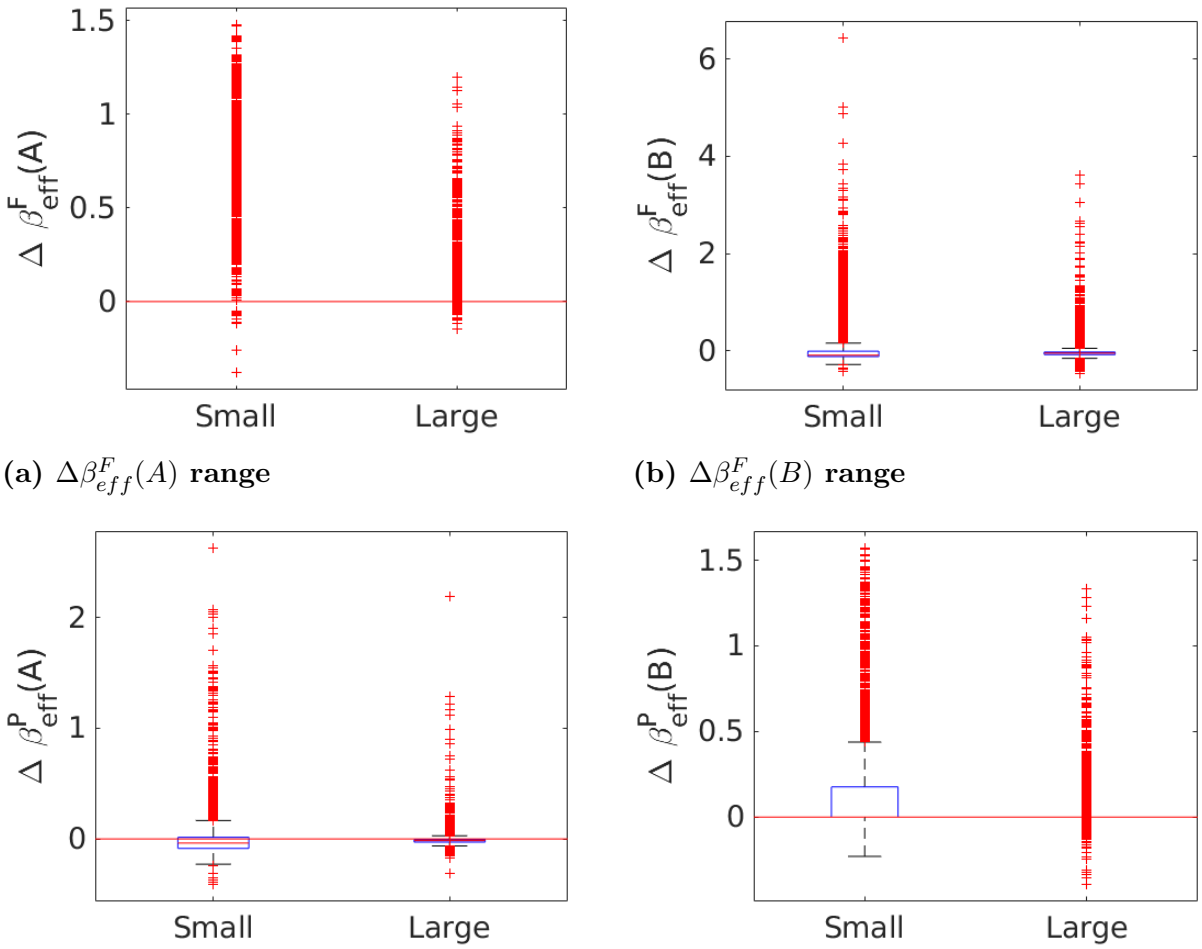


(a) Probability of Resilience Decrease due to Flower Addition

(b) Probability of Resilience Decrease due to Pollinator Addition

Figure 3.3: Probability of resilience decrease due to species addition. Adding a flower will benefit the pollinator projection network and usually hurt the flower projection network. Adding a pollinator will benefit the flower projection network and usually hurt the pollinator projection network

More specifically, a newly added flower has a large probability of affecting the A network in a positive way. There is also a large chance this same flower will decrease the resilience of the B network. No matter the added species type, this effect persists. In Figure 3.3a note that regardless of location size, there is always at least a 80% that adding a flower will negatively affect the resilience of the B network while, except in large locations, there is no chance that adding a flower will negatively affect the A network. The extent to which a new species will affect resilience does not vary that much though as seen in Figure 3.4, where the average added species will only negligibly affect its added network. Species that affect β_{eff} greater than 1 are generally outliers. These boxplots confirm that species addition generally does not hurt or greatly benefit a network. Note also how adding a species to a small location will help that location more than a species addition to a large location will. Since small locations are not as heterogeneous or dense, one new species has a greater effect on these locations than one large locations. Adding a flower seems to have a greater effect on resilience than adding a pollinator, which might be occurring since the number of possible flowers to add is less than the number of potential pollinators.



(a) $\Delta\beta^F_{eff}(A)$ **range**

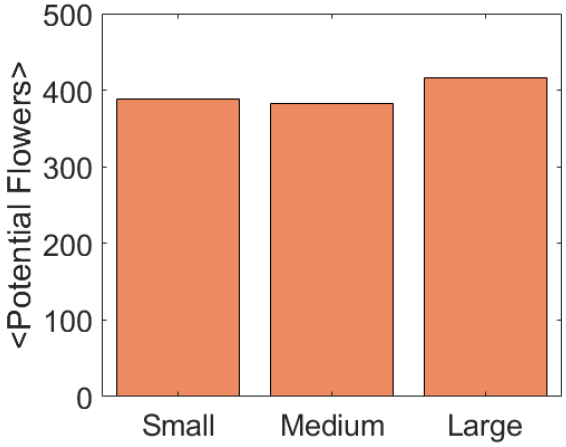
(b) $\Delta\beta^F_{eff}(B)$ **range**

(c) $\Delta\beta^P_{eff}(A)$ **range**

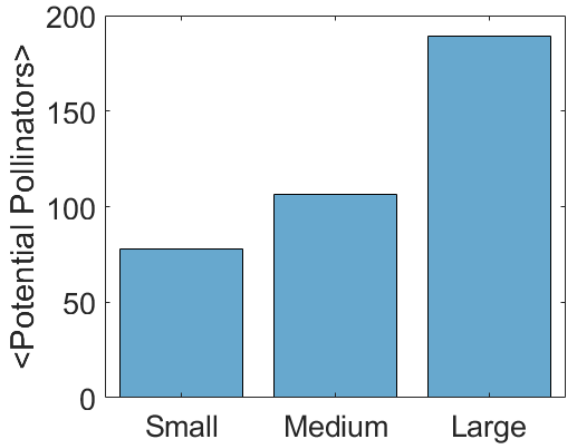
(d) $\Delta\beta^P_{eff}(B)$ **range**

Figure 3.4: Boxplots showing range of $\Delta\beta_{eff}$ values. Adding a species generally has a negligible effect on an ecosystem, excluding the outliers.

This generally occurs because there is a larger amount of flowers that can be added to the network as compared to pollinators. Figure 3.5 displays how among locations of all types, the average number of unique flowers that can be added is around 400 while the average number of unique pollinators increases based on species size. Even among large locations, the number of pollinators that can be added is around 180. Since there are not as many pollinators that be added to a location, $\Delta\beta^P_{eff}(A)$ and $\Delta\beta^P_{eff}(B)$ will not be as large as $\Delta\beta^F_{eff}(A)$ and $\Delta\beta^F_{eff}(B)$ because the number of different possible pollinator species configurations pales compared to the number of potential flower species configurations. The number of added pollinators is less because the number of total flowers is much less than the number of total pollinators.



(a) **Average number of potential flowers**



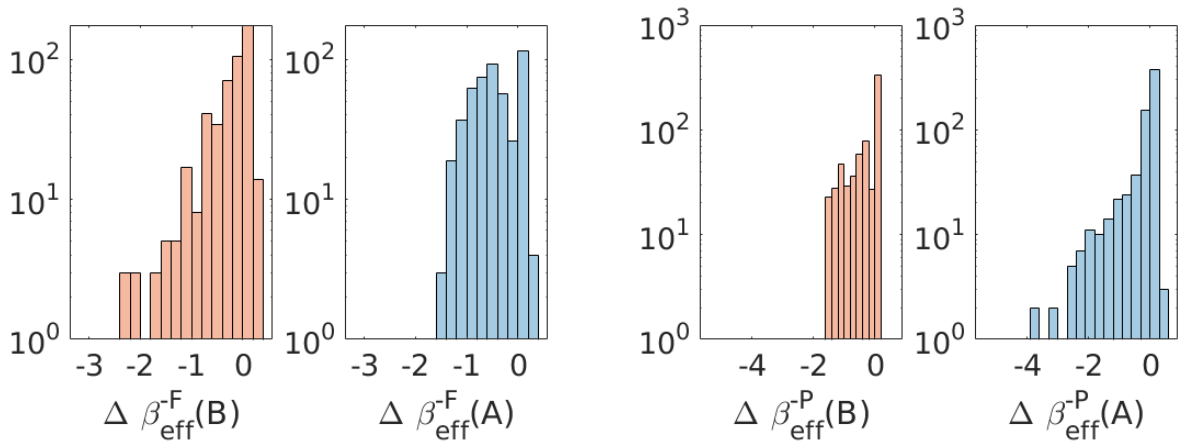
(b) **Average number of potential pollinators**

Figure 3.5: Average number of species to be added to a network. The average number of flower that can be added to a network is consistently large, regardless of location size, while the average number of pollinators that can be added to a network varies heavily depending on location size.

While there are some outlier species that can have a large,positive impact on a location an added species will generally not have a large impact on either projection network. Randomly adding a new species to the network will not be effective to improve resilient, instead targeted addition of species species for specific location configurations will be helpful. We will now examine if the opposite of species addition will help improve resilient - species deletion.

3.2 Species Deletion

The deletion of a species is a much more defined operation than species addition. When adding a species, there is a degree of uncertainty as to how a new species will interact with the species in the network. For species deletion all the interactions of the delete species are well-defined within the context of that network. To delete a species we simply remove a row or column from the M network and then measure the change in resilience: $\Delta\beta_{eff}^{-F}$ for flower deletion and $\Delta\beta_{eff}^{-P}$.

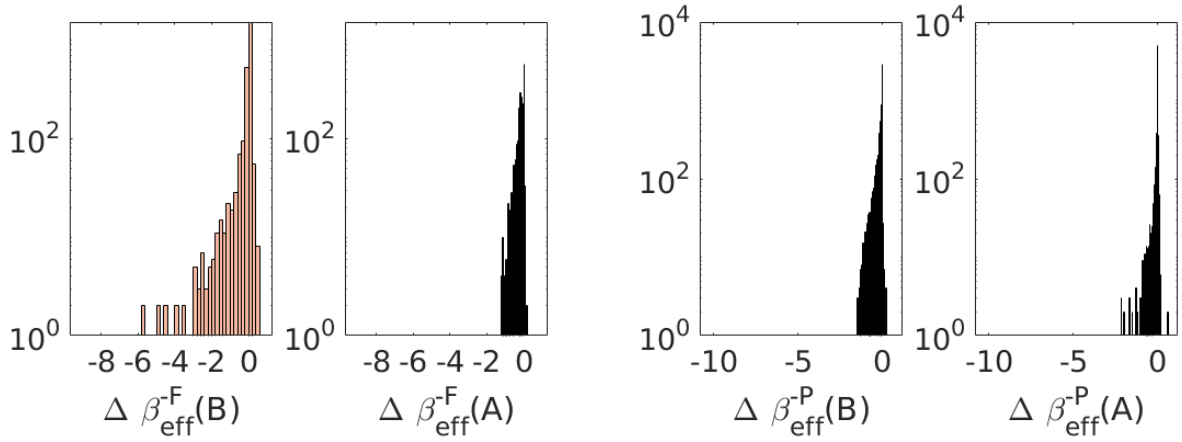


(a) Deleting flower from small networks

(b) Deleting pollinator from small networks

Figure 3.6: Histogram detailing effects of species deletion on small locations.

Similar to section 3.1, we will compare the effects of deletion on small and large networks. The above Figure 3.6 showcases how species deletion is a mostly negative operation that hurts the resilience of a location. The simulation results are understandable, since in a small location every species counts, and the mutualism between species decreases radically if a species is deleted.



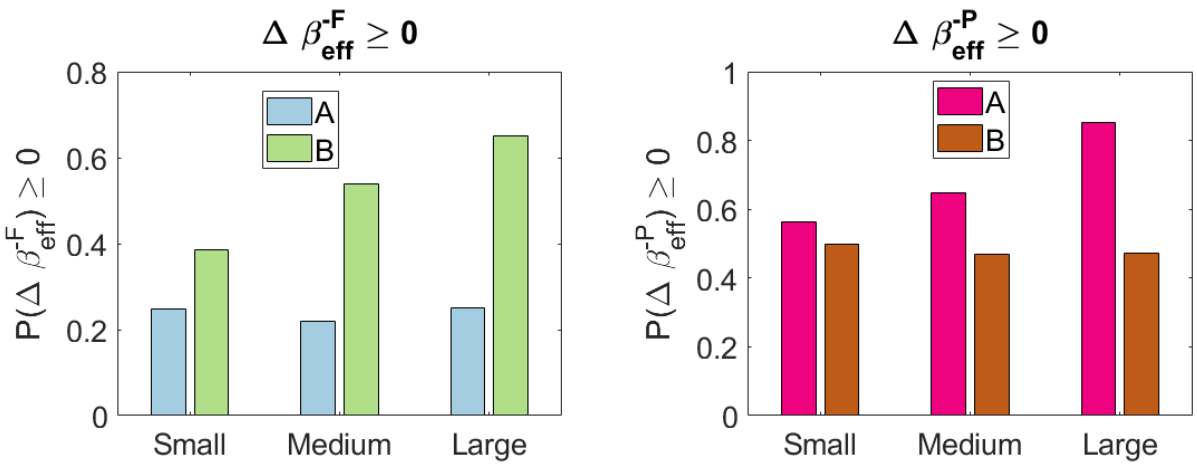
(a) Deleting flower from large networks

(b) Deleting pollinator from large networks

Figure 3.7: Histogram detailing effects of species deletion on large locations.

In Figure 3.7 we see the conclusion from Figure 3.6 challenged, since species addition appears to positively increase resilience in many instances. Large locations would benefit

more from species deletion, since deleting a species would increase the mutualistic effects between species, and, since there is a large amount of species, the loss of a species would not have a large negative effect on the density or heterogeneity of the ecosystem. We analyze of effects of species deletion in Figure 3.8 and 3.9. Figure 3.8 details the probability of a resilience increase due to species deletion. Deleting a flower has a high chance of increasing the resilience of flower projection networks, while there is a small chance that flower deletion will improve pollinator projection networks. A similar phenomena can be seen when deleting a pollinator where there is a higher chance of the projection network of the same type, the pollinator one in this case, benefiting instead of the flower projection network. This matches with species addition, where there is a higher chance of increase for the projection network of the same type.



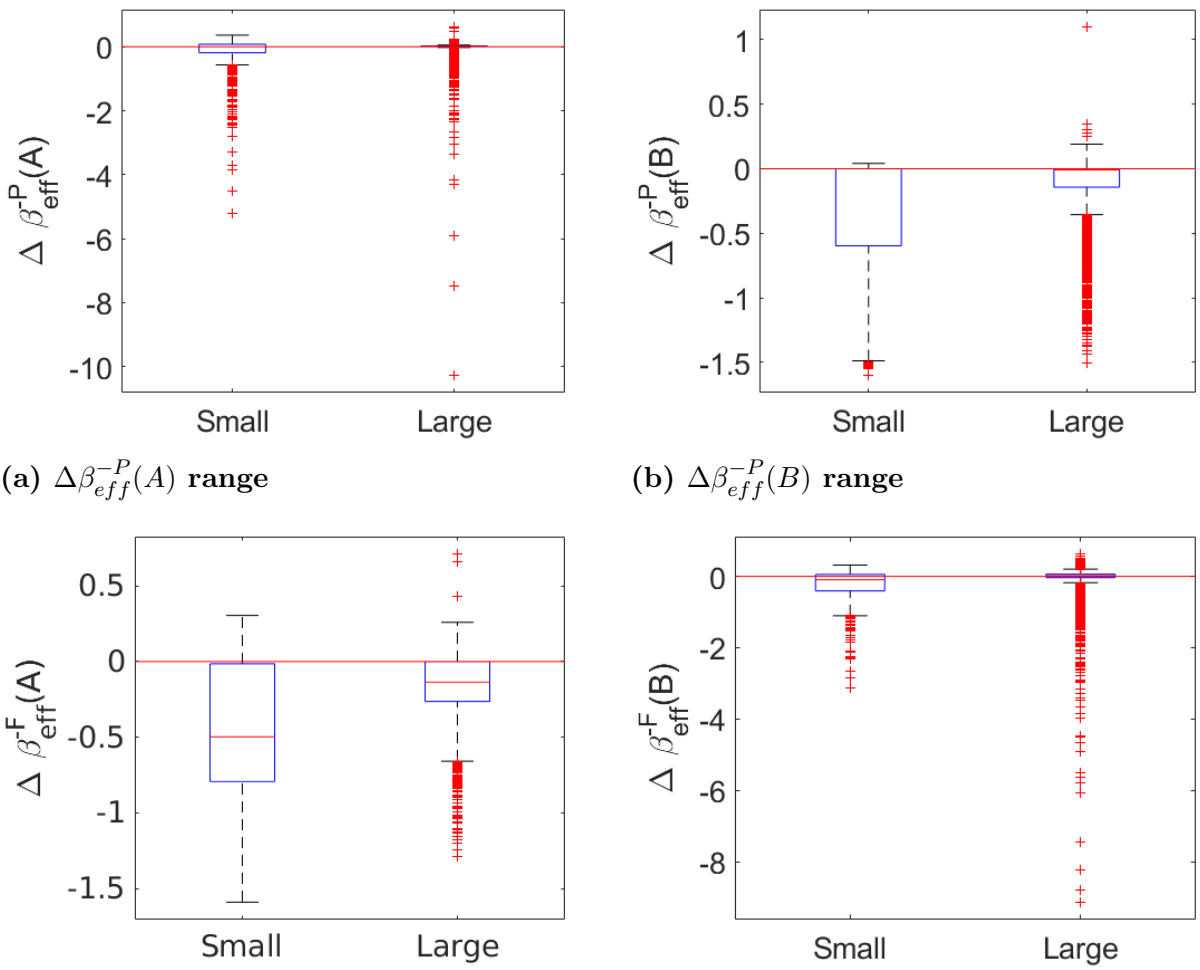
(a) Probability of flower deletion positively increasing resilience

(b) Probability of pollinator deletion positively increasing resilience

Figure 3.8: Probability of resilience increase due to species deletion. Deleting a flower has a large probability of negatively effecting the A network in locations irregardless of size, though the B network always benefits no matter the location size. If a pollinator is deleted, there is a large chance that the A network will benefit while the B network nearly consistently has a 50% of increasing its resilience value.

However, even though there is a large probability of increasing the network through deletion, the possible gains through deletion are minimal. In Figure 3.9, we can see how there is a small positive range of $\Delta\beta_{eff}$ values but a large range for negative $\Delta\beta_{eff}$ values. From these simulations, we can see that removing a random species is not a good way to

improve a network's resilience. Targeted species deletion would work to improve a network's resilience, however, the maximum resilience change due to species deletion is not as large as the possible gains through species addition.



(a) $\Delta\beta_{eff}^{-P}(A)$ **range**

(b) $\Delta\beta_{eff}^{-P}(B)$ **range**

(c) $\Delta\beta_{eff}^{-F}(A)$ **range**

(d) $\Delta\beta_{eff}^{-F}(A)$ **range**

Figure 3.9: Boxplots showing range of $\Delta\beta_{eff}^{-F}$ and $\Delta\beta_{eff}^{-P}$ values. Deleting a species has even less of an impact on a network than species addition. On average, the resilience of a network will not change if a species is deleted from it. Some outliers have a positive effect greater than 0, but this is rare.

3.3 Simulation Analysis

After simulating random species addition and deletion we have found that species addition is the better way to improve resilience. When a new species is added to the network there is a greater range of possible values than species deletion. In both cases, we found

that randomly adding or deleting a species does not provide the greatest benefit to resilience as seen in Figures 3.3 and Figure 3.8. Instead, finding the optimal species to delete or add is more important to improve resilience, since outlier species provide the best benefit to resilience, as shown in Figures 3.4 and 3.9. In the next chapter we discuss how to predict resilience change due to species addition and deletion. Using new theory we can then predict the optimal species to add or delete from the network.

CHAPTER 4
Theoretical Framework

In Chapter 3 we showed that species addition and deletion can benefit the resilience of a network. Adding a new species to a network randomly does not have a high probability of improving the network's resilience in a meaningful way. Deleting a random species from a network will usually have no effect on resilience or a negative effect on resilience , but, there is the occasional harmful species that could be deleted which actually improves a network's resilience. Targeted species addition and deletion is necessary then to improve the resilience of these networks. To understand which species to add or delete from the network understanding how a network's resilience changes when a species is added or deleted is necessary. In this chapter we will show how we derived equations to predict resilience change. Using these equations we were then able to determine how to predict the optimal species, both for species deletion and species addition, though we could not predict the optimal added species for projection networks of the same species type as the added species.

4.1 Predicting Resilience Change due to Species Addition

4.1.1 Projection Network Basics

When adding a new species α to the M matrix the species type determines if a new column or new row is added to a network. Originally, the M network is of size $[m, n]$ with m flowers and n pollinators. If a flower is added to M, a new row is added while if a pollinator is added a new column is added to the network. When a new flower is added to the network, the dimensions of the A projection network will not change but the B projection network will gain a new row and column. The dimensions of the A projection network increase by one when a new pollinator is added to the M network. The projection networks of the same species type as the added species acquire a new row and column because the projection networks track the mutualism between species of the same type. The A projection network tracks the mutualism between pollinators and the B projection network tracks the mutualism between the flowers. Each row and column of the projection networks represents a species, and, the elements in the projection networks are weighed based on the mutualism between two species.

Each element in the projection networks represent the mutualism between two species. A_{ij} represents the mutualism between the i-th and j-th species of the pollinator projection network while B_{ij} represents the mutualism between the i-th and j-th species of the flower projection network. The A and B projection networks are calculated in similar ways, except the A projection network is calculated using columns, where two columns in the M matrix, $\mathbf{m}_i$ and $\mathbf{m}_j$ are multiplied with one another and with a vector representing the sum of each column in M, K.

$$K_i = \sum_{r=1}^{m} M_{ri} \tag{4.1}$$

$$A_{ij} = \mathbf{m}_i * \mathbf{m}_j * \frac{2}{K} \tag{4.2}$$

Calculating the B network is similar to calculating the A network, except we use rows instead of columns when calculating the B network. So, $\mathbf{m}_i$ and $\mathbf{m}_j$ represent two rows in the M network, and K is a vector representing the sum of each row in M.

$$K_i = \sum_{c=1}^{n} M_{ic} \tag{4.3}$$

$$B_{ij} = \mathbf{m}_i * \mathbf{m}_j * \frac{2}{K} \tag{4.4}$$

We will also commonly be referring to the s vector, which is a vector of size $[1, n]$ or $[1, m]$ depending on its use.

$$s_i = \sum_{r=1}^{n} A_{ri} \quad OR \quad \sum_{r=1}^{m} B_{ri} \tag{4.5}$$

Each element in the the projection network represents the strength of the mutualistic interaction between species i and j. The vector product of $\mathbf{m}_i$ and $\mathbf{m}_j$ generates all the interactions that are shared between species i and j, and, this value is multiplied with the degree vector K to produce a weight. After defining these values in more depth, we can now expand on these equations to understand how resilience changes. Since β_{eff} is effectively a measure of s understanding Δs will allow us to understand $\Delta\beta_{eff}$.

Before predicting resilience change, we first have to understand Δs. Δs changes depending on what projection network we are calculating Δs for. If a pollinator is added to the network, $\Delta\beta^{P}_{eff}(A)$ and $\Delta\beta^{P}_{eff}(B)$ will have different values since adding a new pollinator will

change the dimensions *and* weights of the A network. The B network's dimensions will not change but some of the weights in the network might change. When a flower is added to the network, the opposite occurs where only the A network's weights might be modified while the B network's dimensions will increase by one and the weights will be different as well. We will first examine the effects of adding a flower on the A and B projection networks.

4.1.2 Predicting $\Delta\beta^F_{eff}(A)$ & $\Delta\beta^P_{eff}(B)$

The Δs equation differs for the A and B projection networks. When a flower is added, the A network's dimensions do not change since the A network records the mutualism only seen between pollinators, not flowers. When a new species α is added to M, the values in the A network changes since a new flower means that there is a new possible species to interact with. Thus, adding a new flower will usually only positively benefit $\beta_{eff}(A)$. The associated s vector will change based on the number of interactions that α contains, which we will denote as ζ. Each element in the s vector will increase the same depending on ζ as seen in equation 4.6,

$$\Delta s_i = \frac{2(\zeta - 1)}{\zeta} \tag{4.6}$$

since Δs will be added to the original s value s_0. To calculate $\beta^F_{eff}(A)$ we added Δs with the initial s value before species addition, s_0. After finding how to predict the new resilience

$$\beta^F_{eff}(A) = \frac{< (s_0 + \Delta s)^2 >}{(s_0 + \Delta s} \tag{4.7}$$

value, deriving how resilience changes meant subtracting the new resilience value from the old resilience value as shown in equation 4.8:

$$\Delta\beta^F_{eff}(A) = \frac{< (s_0 + \Delta s)^2 >}{< s_0 + \Delta s >} - \frac{< s_0^2 >}{< s_0 >} \tag{4.8}$$

After simplifying the above equation, the change in resilience can be properly quantified. The simplification for this equation can be found in the appendix.

$$\gamma = \frac{4\alpha s_0(\zeta - 1)}{n\zeta} \tag{4.9}$$

$$\Delta\beta^{F}_{eff}(A) = \frac{< s_0 > \gamma + < \Delta s > (\Delta s_i < s_0 > - < \Delta s >)}{< s_0 > (< s_0 > + < \Delta s >)} \tag{4.10}$$

When adding a new species to the network, ζ will differ since each species might interact with a different number of species. Species might have the same ζ but interact with different species from one another, so, γ will be different as well. In equation 4.9, α is being multiplied with s_0 and $\zeta - 1$ which shows that the configuration of α matters. The only way that the resilience of the A network could decrease if a flower is added would be if $< \Delta s >$ is larger than $< s_0 > \gamma + < \Delta s > \Delta s_i < s_0 >$, which has a small likelihood of occurring due to how much larger γ is than $< \Delta s >$. After finding how the A network will change, we then examined how the B network would change after a flower is introduced. Unlike the A network, the B network's dimensions would change, resulting in a $[m+1, m+1]$ sized matrix, where$m$ is the number of flower in the M network. The weights in the B change in a different way from the A network when a flower is added. Unlike the A network, the values in the B network will decrease somewhat due to species addition. This is offset though by the benefit the added species brings to the B projection because the individual mutualism between each species decreases since the new species is effectively competing with species of its own type. We can define a vector of values to be the benefit of the added new species N to s and a vector of values to be the cost of addition, C.

$$\Delta \mathbf{s}_i = -\mathbf{C}_i + \mathbf{N}_i \tag{4.11}$$

Since a new species added to the network there is a new set of mutualistic interactions that is added to the network. If the weighted degree sum of the new set of interactions is greater than the cost, the resilience change is positive. Most of the time this does not happen, since the new species usually does not interact with enough species or the right types of species for the benefit to be greater than the cost. Something else to note is that the C and N vectors are of different sizes. When a new species is added, the weights of all the existing species decrease which is represented through the C vector being only of size $[1, m]$. Each element of the C vector is calculated using equation 4.14. To calculate C_i, a special matrix Z_i had to be used where all the elements of the row i in the initial M matrix $M0$ are 0. When a species is added to the network the existing species' mutualism will decrease, which

is represented by the fraction $(\frac{2}{s_0(s_0+1)})^T$.

$$\mathbf{Z} = \mathbf{M0} \quad where \quad \mathbf{m}_i[1..n] = 0 \tag{4.12}$$

$$\begin{aligned} s_j &= \sum_{i=1}^{n} \mathbf{M0}_{ij} \\ \mathbf{S} &= [s_1, s_2 ... s_i ... s_n] \end{aligned} \tag{4.13}$$

$$\mathbf{C}_i = \mathbf{1}^{m*1} * \mathbf{m}(i) * \alpha * \mathbf{Z} * \left(\frac{2}{(s_0(s_0+1))} \right)^T \tag{4.14}$$

We know from equation 4.11 that finding the cost is only half of the Δs equation. We will now calculate the values for N, which signifies the benefit of adding a new species. The N vector is of size $[1, m+1]$. The largest added benefit comes from the $m+1$-st element of the vector, which represents the column-sum of the $m+1$-st column in the B matrix. Similar to the C vector, a vector summing up all columns in the M matrix is needed. Note in equation 4.15 how M is used instead of $M0$. M refers to the M matrix after species addition while $M0$ refers to the initial interactions of the plant-pollinator matrix.

$$\begin{aligned} k_j &= \sum_{i=1}^{n} \mathbf{M}_{ij} \\ \mathbf{K} &= [k_1, k_2 ... k_i ... k_n] \end{aligned} \tag{4.15}$$

Using the defined K vector, we can then calculate $m+1$ elements of the N vector. When calculating the benefit vector, we simply used M matrix and multiplied each row against the K matrix, which is a recalculated s_0 vector.

$$\mathbf{N}_i = \left(\alpha * \mathbf{m}(i) * \frac{2}{\mathbf{K}} \right)^T * \mathbf{1} \tag{4.16}$$

Using equations 4.11,4,14, and 4.16 we can find how the degree of the B network will change. After finding this value, we can derive $\beta^F_{eff}(B)$ by the inputting the values for C and N into equation 4.11. We define the sum of equation 4.11 using D which is defined below in equation 4.18

$$D = \sum_{i=1}^{m} \mathbf{s}_i^0 - \mathbf{C}_i + \mathbf{N}_i \tag{4.17}$$

Since C is of size $[1, m]$ and N is of size $[1, m+1]$, D is keeping track of the modified weights for the original m species. To actually measure the new resilience value we must add D with N_{m+1}, which is the last element of the benefit vector. Adding this new value with D is necessary, since N_{m+1} is the cumulative benefit that the new species brings to the network, divorced of any cost.

$$\beta^F_{eff}(B) = \frac{< (D + N_{m+1})^2 >}{< (D + N_{m+1}) >} \tag{4.18}$$

Unfortunately, we could not find a simple form for $\Delta\beta^F_{eff}(B)$ as compared to $\Delta\beta eff^F(A)$ (as seen in equation 4.10, which clearly showed what is causing the change in resilience. This is because C and N can only be calculated by taking the account the effect that the added species has on the entire network. In the future, this could be a new area of research. Since we could not find the simplification, the equation for $\Delta\beta^F_{eff}(B)$is fairly simply, where we take the difference between equation 4.18 and $\frac{<s_0^2>}{<s_0>}$.

In the above equations we focused on adding a flower, but the equations for adding a pollinator are similar since the equations are symmetric. When adding a pollinator, there is a cost and benefit to $\Delta\beta^P_{eff}(A)$ and only a benefit for $\Delta\beta^P_{eff}(B)$. When adding a pollinator, the A network's dimensions will increase by 1 to become $[n+1, n+1]$ and both the A and B network's weights will change.

What we have shown is that it is possible to predict resilience change just given a new species α and M. After finding the equations for species addition, we now look at species deletion and see if it is possible to predict the change in resilience due to species deletion.

4.2 Predicting Resilience Change due to Species Deletion

Similar to species addition, species deletion affects the weights of the projection network. Like addition, the equations for predicting species deletion fall into two types. The first equation type describes what occurs to the projection network of the same species type as the removed spices, while the second equation describes what occurs what happens when a species is removed that is of a different type as the calculated projection network. When a species is removed, if it is of the same type as the calculated projection network, there is both a cost and benefit to doing so. However, if a species is removed and it is of the same type as the calculated projection network there is only a cost value that is subtracted from the initial value.

We use much of the same terminology as used in section 4.1.1 when describing species deletion. When a species κ is removed, a row or column is removed from the M network. If a flower is removed, the A network's dimensions do not change and stay $[n, n]$ but the weights in the network change since a flower that all the pollinators were interacting with was removed, causing a decrease in resilience. This can be seen in equations

$$\Delta s_i = \kappa_i * \frac{2(\zeta - 1)}{\zeta} \tag{4.19}$$

$$s = s_0 - \Delta s \tag{4.20}$$

4.19 and 4.20, where the ζ value of κ is needed to predict how the degree value s will change. This equation is similar to equation 4.6, except when deleting a species, this same value is subtracted from s_0. When a flower is deleted, the B network's dimensions decrease and become $[m - 1, m - 1]$, however, the majority of weights in the B network will increase marginally since one less flower in the M network increases the importance of their own mutualistic interactions. The B network weights will decrease somewhat as well since it is losing the mutualistic interactions of κ. In the below equations, z refers to the row to be deleted, E refers to a vector where each element represents the column sum of a column in M, and M_{ix} refers to the vector of row interactions in row i of the M network. The purpose of the below equations is to fill each element with Δs_i with a value representing the effects of deleting a row on the i-th column of the M network.

$$E_i = \sum_{k=1}^{m} M_{ki}, i \in [1, n] \tag{4.21}$$

$$G = E * M_{ix} * M_{zx} \tag{4.22}$$

The G vector tells us the effect that deleting M_{zx} will have on the i-th row of M. When M_{ix} and M_{zx} are multiplied together, the result conveys the shared interactions between the i-th and z-th indexed species. The result of that is multiplied with the vector E where each element represents the total number of plant-pollinator interactions.

$$D = G * (G - 1) \tag{4.23}$$

$$I = D \bigoplus \mathbf{1}^{1*m} \tag{4.24}$$

Using the G vector we calculate the D and I vectors. The D vector describes the denominator value that will occur when one subtracts the old projection network value and the new projection network value. The I vector uses the D vector to understand which elements in D are 0. The elements that are 0 become 1, and, any non-zero element becomes 1 due to the *xor* operation.

$$D = D + I \tag{4.25}$$

$$D = \frac{2}{D} - 2 * I \tag{4.26}$$

Since the I vector is a measure of whether an element in D is 0 or not, we add it to 1 so that there are no values in D that are 0. This is important, since each element in D is used as a denominator where 2 is the numerator value. If the I vector wasn't added to D, some values in D could be zero so dividing it with 2 would result in an undefined value. Since some elements in D have a value of 1, we must subtract each divided value with $2 * I$ so that the denominator value can become zero.

$$V = D * (G - 2) \tag{4.27}$$

$$\Delta s_i = -B_{zi} + (V * \mathbf{1}^{m*1}) \tag{4.28}$$

The D vector represents how values will change if a species deleted. The G vector represents the total number of species that interact with one another. Subtracting G by 2 gives the total number of other species that interacted with the species about to removed. These flowers will benefit when a flower is deleted. The V vector measure the benefit from species deletion. This vector is multiplied by $\mathbf{1}$ to convert the vector into a scalar value. The true effect of deletion comes from subtracting the positive effects of deletion with the negative effects of losing a species.

We apply the result of equation 4.26 to equation 4.19, and take its difference with the original s_0. The equations written for deleting a flower are symmetric to those derived for pollinator addition, similar to species addition. Using the formulas derived in sections 4.1 and 4.2 we can now predict the optimal species to add or delete to maximize resilience change.

4.3 Optimal Species Prediction

Since we have now derived how the projection networks will change due to species addition or deletion, we can predict how resilience will change. Before using these equations to predict optimal species addition, we verified that these equations were accurate by graphing the effects of theoretically adding a species against the actual effects of adding the same species.

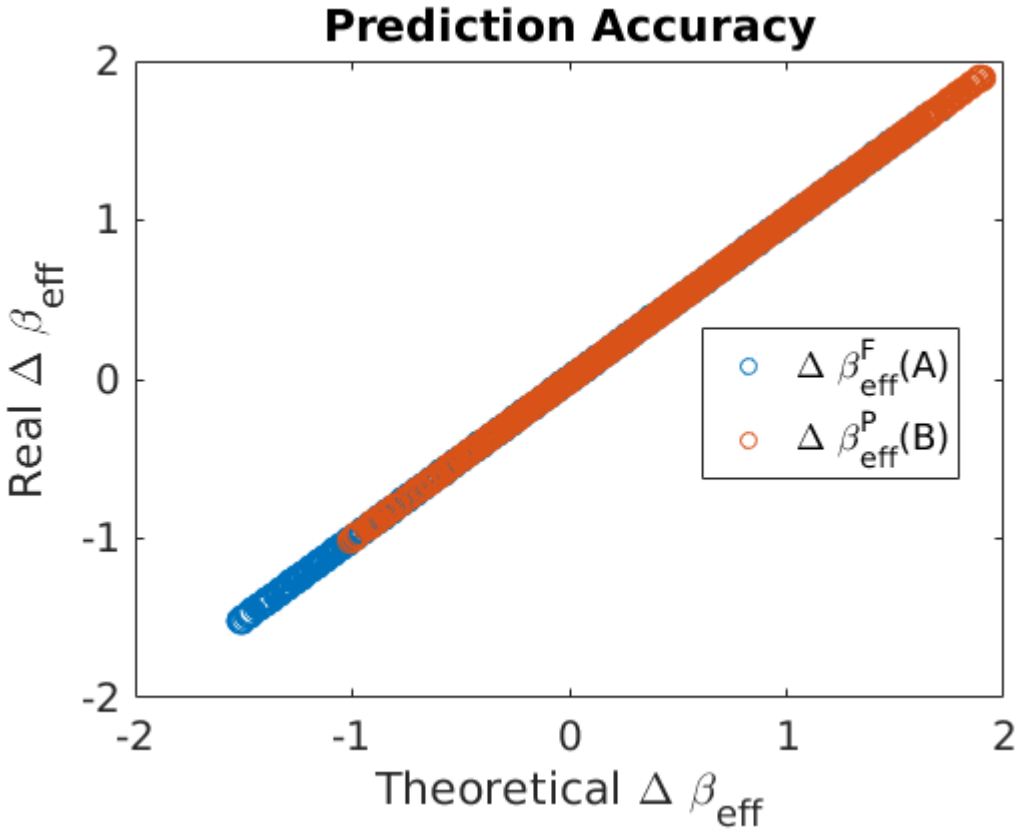
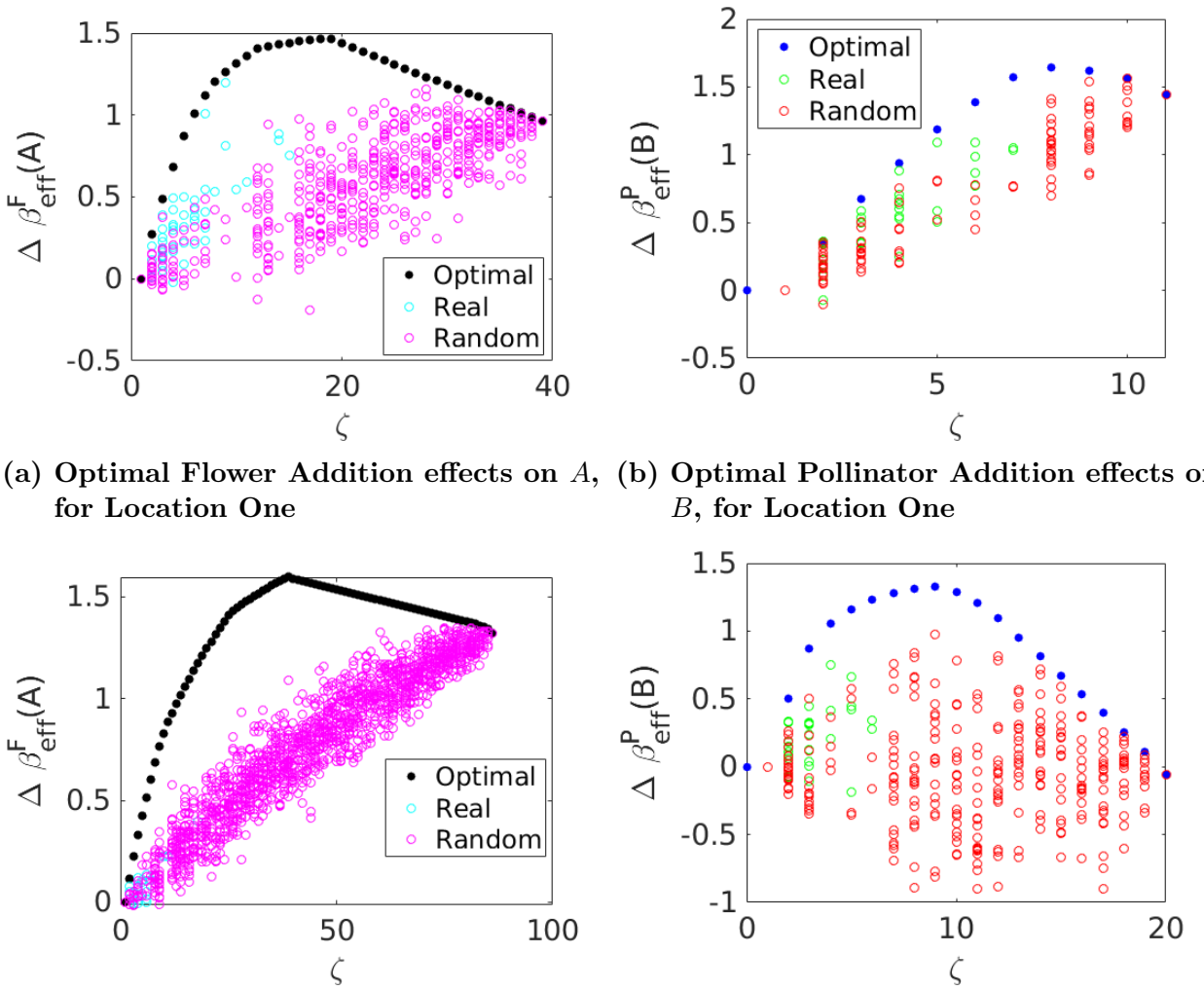


Figure 4.1: Accuracy of species addition.

When adding a species as well, we assume that the newly added species will be a part of the giant component of the network, ensuring the accuracy of the calculations. Optimal species prediction is useful, because the potential number of α that can be added to a network is 2^n, where n is the number of columns in the M network. Even for small locations, the 2^n calculation is not trivial - for large locations it would be impossible to guess the optimal alpha. Equations must be derived to find the optimal α to add to M, since guessing the optimal species would take too long.

4.3.1 Predicting Optimal Species Addition

From Section 4.2 we were able to predict $\Delta\beta^F_{eff}(A)$ and $\Delta\beta^P_{eff}(B)$ using equation 4.8. Since the equation is simple, we were able to understand what the leading term of the equation was, $\alpha * s_0$. In the equation, γ is the largest value that is changing. As part of γ, $\alpha * s_0$ is the truly dynamic part of the equation since it determines which of the original s_0 values will be increased. Thus, we guessed that $max(\alpha * (s_0))$ would cause the largest $\Delta\beta^F_{eff}(A)$ and $\Delta\beta^P_{eff}(B)$.



(a) **Optimal Flower Addition effects on A, for Location One**

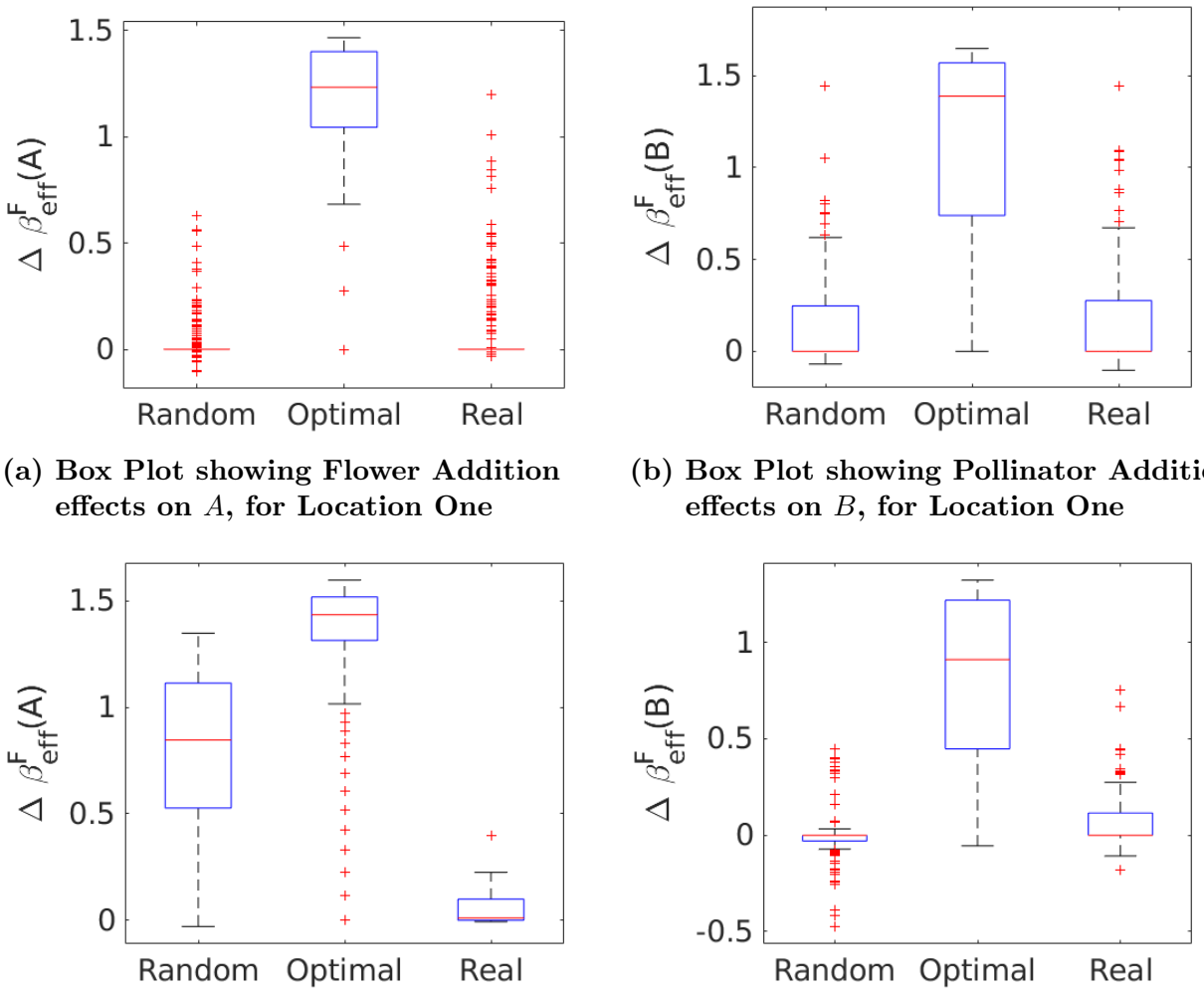
(b) **Optimal Pollinator Addition effects on B, for Location One**

(c) **Optimal Flower Addition effects on A, for Location Two**

(d) **Optimal Pollinator Addition effects on B, for Location Two**

Figure 4.2: Effects of optimal species addition on two locations, location one and location two. We find that the optimal species to add is often not the species with the largest ζ value.

In the above figures, we compared the optimal, theoretical species with the real added species and randomly generated species. What we found was that oftentimes the species with the largest ζ were **not** the species that would have the largest effect on resilience. We also show that the optimal added species will consistently have a larger effect on resilience than the real added species or any real species. Since we are maximizing $*s_0$, the factor to consider most would actually be the nearest neighbor coefficient instead of the average degree of a network. When maximizing $\alpha * s_0$, we are really trying to find the nearest neighbor value, because we are trying to find the largest s_0 - not ζ.



(a) Box Plot showing Flower Addition effects on A, for Location One

(b) Box Plot showing Pollinator Addition effects on B, for Location One

(c) Box Plot showing Flower Addition effects on A, for Location Two

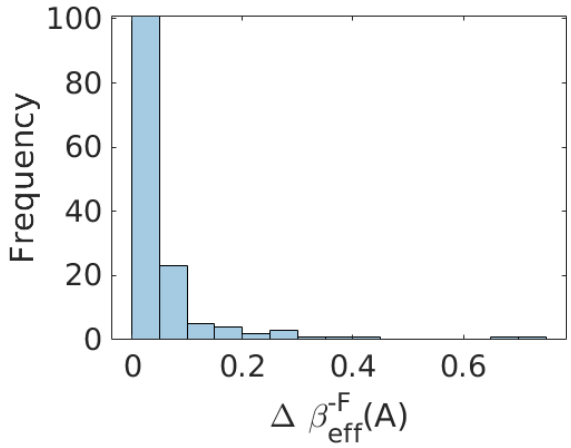
(d) Box Plot showing Pollinator Addition effects on B, for Location Two

Figure 4.3: Boxplots containing range of optimal additions for locations one and two. The average optimal species is larger in all cases than randomly generated species or real species.

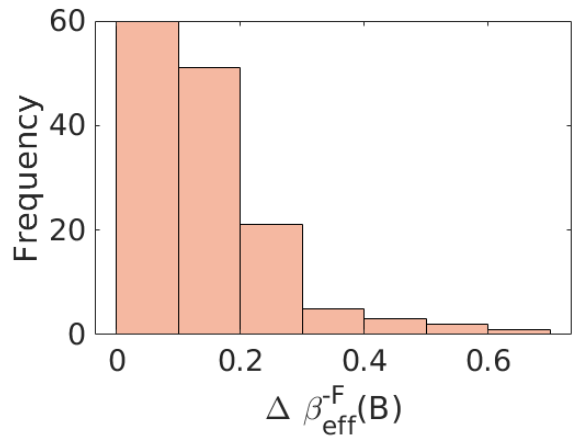
The above boxplots show the power of predicting the optimal species to add, since in all cases, since the average added optimal species is much larger than the average random or real species that is added to the network, even when the number of optimal species is smaller than the number of added or randomly generated species. Next, we will show the effects of optimal species deletion, and how it compares to optimal species addition.

4.3.2 Predicting Optimal Species Deletion

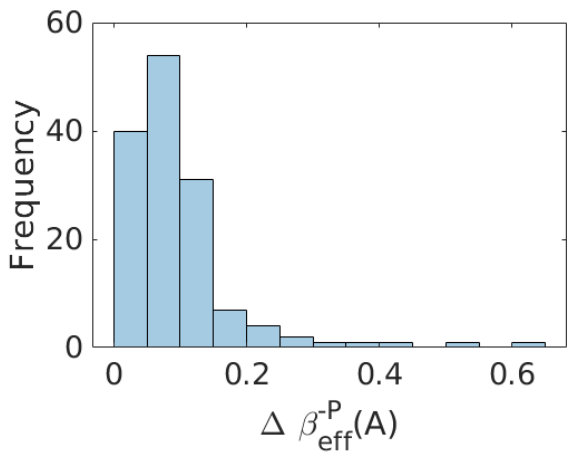
Using the equations derived from section 4.2, we can predict how deleting a species from M will effect the A or B network. Unlike species addition, the κ vectors for deletion are already known since the M network's interactions are already known, unlike α which requires the overall interaction network to calculate. To calculate the optimal species to add, we took the κ value from each row and column in M and then predicted how κ would affect the A and B network's resilience. Then, we graphed the largest predicted $\Delta\beta_{eff}$ values.



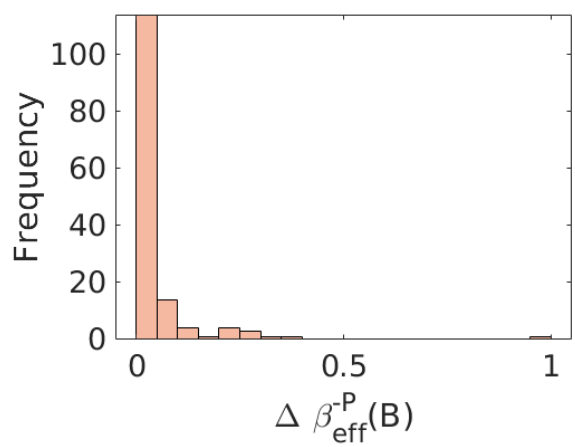
(a) **Effects of optimal flower deletion on A network**



(b) **Effects of optimal flower deletion on B network**



(c) **Effects of optimal pollinator deletion on A network**



(d) **Effects of optimal pollinator deletion on B network**

Figure 4.4: Histograms showing effects of optimal species deletion on projection networks. Optimal species deleltion is not as effective a method as optimal speices addition to improve resilience

From Figure 4.4, we can conclude that optimal species deletion is not as effective as optimal addition. Note the change in β_{eff} rivaled the change found when adding a species. Sometimes it might be more effective to delete a species than it would be to add one.

4.4 Concluding Remarks

We can predict resilience change due to species addition or deletion. One of the most significant conclusions we found is that when adding a new species nearest neighbor degree matters most. Having a species that can connect to the biggest mutualistic contributors is

more important than having a species become a hub. When it comes to species deletion we were not able to find distinguishing characteristics to identify which species would be the best to delete. Instead, using equations 4.19 and 4.28, one can identify potential species to delete by seeing how much s changes when that species is gone. Using those equation it is simple to recalculate β_{eff} and identify if deleting that species causes a positive increase in resilience.

CHAPTER 5
Conclusion

From this research we have clearly shown the benefits and trends of species addition and deletion. Like in many real world studies, we found that deleting or adding a species will generally have a negligible effect on an ecosystem. The majority of real species that were added to a network or deleted from a network did not effect resilience in a significant way. However, there were a small number of real species that provided a positive resilience change when added or deleted. The most reliable way to increase resilience is through targeted species addition or deletion. We were able to derive equations to predict how resilience will change if a new species is added to or deleted from a network. Using these equations, we were able to predict the optimal pollinator to add that maximally benefits the B network and also able to predict the optimal flower to add that maximally benefits the A network. Species with the largest nearest-neighbor degree values were found to be the ones most optimal to add to improve resilience. For species deletion, we were able to find the optimal species by finding Δs after deleting each row and column in a location's M network and then recalculating β_{eff} and comparing the new resilience value to the old value. The optimal species to delete in this case would create the largest positive difference between the two. We hope that our research can help ecologists better understand how non-native species addition can effect ecosystems and how species deletion can effect an ecosystem.

5.1 Future Work

Having theoretical equations to predict resilience is important, however, being able to understand how these equations relate to individual species is more important still. A new avenue research would be to shed more light on optimal species characteristics. The current equation for predicting species deletion of a type similar to a projection network (deleting a flower and predicting its change on the flower network) is not simple enough. It is difficult to predict which one value in the equation plays the largest part in determining resilience change. The similar problem can also be found in adding a species and predicting the effects on the projection network of a similar type (adding a new flower and predicting the resilience change of the B network), since the equation for prediction is complex. There is no one term

to maximize to predict a optimal resilience change in this instance.

In this thesis we focused on understanding if it was possible to increase the resilience of a network through species addition or deletion. Since we have proven that this is the case, future research could approach this problem from an optimization standpoint. Instead of adding just one species and finding the optimal one new species to add, one could predict which species should be added to or deleted from the network to have the largest possible resilience change. Another area for future work would be simulating the effects of species addition based on the percentage of species that are added to the network instead of simply adding just one new species. Since we only added one new species to a networks and observed the resilience change the changes to small networks were larger than the additions found in small networks. To observe the change properly, species should be added based on a percentage of the existing species count instead of just adding one species. One other potential avenue of research is making the differential model more complex to more properly be attuned for the changes in the climate. The current model takes that into account using the K variable, but, this could be made more complex since global warming is a complex phenomena.

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APPENDIX A
Simplifying $\Delta\beta^F_{eff}(A)$ and $\Delta\beta^P_{eff}(B)$

To simplify $\Delta\beta^F_{eff}(A)$, start by defining some terms

$$M = [m, n] \tag{A.1}$$

$$A = [n, n] \tag{A.2}$$

$$B = [m, m] \tag{A.3}$$

$$\alpha = [1, n] \tag{A.4}$$

$$\tag{A.5}$$

After flower addition via α

$$M^* = [m+1, n]B^* = [m+1, m+1] \tag{A.6}$$

Note that the dimensions of A do not change, since A represents the pollinator projection network. The values inside A are different though, sine the mutualisms change.

$$\Delta s = [1, n] \tag{A.7}$$

Now, let's further define how s changes.

$$\Delta s_i = \alpha(i) \sum_{j=1, j\neq i}^{n} \alpha(j) * \left(\frac{2}{\sum_{k=1}^{n} \alpha(k)} \right) \tag{A.8}$$

$$\sum_{i=1}^{n} \Delta s_i = 2 * \sum_{i=1}^{n} \alpha(i) \tag{A.9}$$

$$\Delta s = 2 * \left(\left(\sum_{i=1}^{n} \alpha(i) \right) - 1 \right) \tag{A.10}$$

In vector form we define Δs as follows:

$$\Delta s = \alpha * [\Delta s_1, \Delta s_2 ... \Delta s_n] \tag{A.11}$$

We will use these equations to now predict $\beta_{eff}(A)$ and calculate $\Delta\beta^F_{eff}(A)$. We will refer to the original s value as s_0 to differentiate between the new s and the old s. Thus, $\beta_{eff}(A) = \frac{<{s_0}^2>}{<s_0>}$ while $\beta_{eff}(A^*) = \frac{<(s_0+\Delta s)^2>}{<(s_0)>}$

$$\Delta\beta^F_{eff}(A) = \beta_{eff}(A^*) - \beta_{eff}(A) \tag{A.12}$$

$$\Delta\beta^F_{eff}(A) = \frac{<(s_0+\Delta s)^2>}{<s_0+\Delta s>} - \frac{<s_0^2>}{<s_0>} \tag{A.13}$$

Now, we expand Δs

$$\Delta\beta^F_{eff}(A) = \frac{<s_0^2> +2<s_0\Delta s> + <\Delta s^2>}{<s_0+\Delta s>} - \frac{<s_0^2>}{<s_0>} \tag{A.14}$$

$$\Delta\beta^F_{eff}(A) = \frac{<s_0>(<s_0^2> +2<s_0\Delta s> + <\Delta s^2>) - <s_0^2>(<s_0+\Delta s>)}{<s_0>(<s_0> + <\Delta s_0>)} \tag{A.15}$$

$$\Delta\beta^F_{eff}(A) = \frac{2<s_0\Delta s><s_0> + <\Delta s^2><s_0> - <s_0^2><\Delta s>}{<s_0><s_0> + <s_0><\Delta s>} \tag{A.16}$$

To simplify, expand $<\Delta s>$

$$<\Delta s> = \frac{2\left(\sum_{i=1}^{n}\alpha(i)\right) - 2}{n} \tag{A.17}$$

The $\sum_{i=1}^{n}(\alpha_i)$ is equivalent to the number of non-zero values in α, which we will define as ζ. The following defined terms will be used to simplify equation A.16.

$$\Delta s_i = \frac{2(\zeta-1)}{\zeta} \tag{A.18}$$

$$<\Delta s> = \frac{2(\zeta-1)}{n} \tag{A.19}$$

$$<\Delta s^2> = \frac{4(\zeta-1)^2}{\zeta n} \tag{A.20}$$

$$<s_0\Delta s> = \frac{s_0\Delta s}{n} \tag{A.21}$$

$$<s_0\Delta s> = \left(s_0 * \alpha * \frac{2(\zeta-1)}{\zeta}\right) * \frac{1}{n} \tag{A.22}$$

Now, introduce these values into $\Delta\beta_{eff}(A)$

$$\Delta\beta^F_{eff}(A) = \frac{2\alpha s_0 \frac{2(\zeta-1)}{n\zeta} < s_0 > + \frac{4(\zeta-1)^2}{\zeta n} < s_0 > - < s_0^2 > \frac{2(\zeta-1)}{n}}{< s_0 > (< s_0 > + \frac{2(\zeta-1)}{n})} \tag{A.23}$$

$$\Delta\beta^F_{eff}(A) = \frac{\frac{4\alpha s_0(\zeta-1)}{n\zeta} < s_0 > + \frac{4(\zeta-1)^2}{\zeta n} < s_0 > - < s_0^2 > \frac{2(\zeta-1)}{n}}{< s_0 > (< s_0 > + \frac{2(\zeta-1)}{n})} \tag{A.24}$$

$$\Delta\beta^F_{eff}(A) = \frac{\frac{4\alpha s_0(\zeta-1)}{n\zeta} < s_0 > + \frac{2(\zeta-1)}{n}(\frac{2(\zeta-1)}{\zeta} < s_0 > - < s_0^2 >)}{< s_0 > (< s_0 > + \frac{2(\zeta-1)}{n})} \tag{A.25}$$

Can simplify the left-most term as the following:

$$\gamma = \frac{4\alpha s_0(\zeta - 1)}{n\zeta} \tag{A.26}$$

The final equation for $\Delta\beta^F_{eff}(A)$ then becomes the following after using γ and swapping some terms out.

$$\Delta\beta^F_{eff}(A) = \frac{\gamma < s_0 > + \Delta s(\Delta s_i < s_0 > - < s_0^2 >)}{< s_0 > (< s_0 > + < \Delta s >)} \tag{A.27}$$

The equation for $\Delta\beta^P_{eff}(B)$ is the same, except for the dimensions of s now referring to m and instead of n, and, ζ is can now only maximally be ζ since a new column is being added instead of a row.