The Predictability of Qualitative Food Web Dynamics in Response to Extinction and Invasion

by
David J. Rockow

A THESIS

submitted to

Oregon State University

Honors College

in partial fulfillment of
the requirements for the
degree of

Honors Baccalaureate of Science in Biology
(Honors Scholar)

Presented May 21, 2021
Commencement June 2021

AN ABSTRACT OF THE THESIS OF

David Rockow for the degree of Honors Baccalaureate of Science in Biology presented on May 21, 2021.
Title:
The Predictability of Qualitative Food Web Dynamics in Response to Extinction and Invasion.

Abstract approved:____

Mark Novak

Food webs are extraordinarily complex, containing myriad direct interactions and indirect effects. Determining how this network of interactions and effects influences a food web's qualitative dynamics is a challenging task, especially because data on food web structure and individual interaction strengths is unknown in virtually all real-world ecosystems. The goal of this project was to determine how extinctions and invasions impacted the probability of correctly predicting species dynamics in computationally generated food webs, when these webs were subjected to press perturbations under progressively higher levels of interaction strength uncertainty.

It was expected that extinctions, by reducing the number of direct interactions and indirect effects, would generally make responses easier to predict. Since introductions would have the opposite impact, it was predicted adding species would generally make responses harder to predict.

Overall, removing species had varied results, but generally made responses easier to predict. There was a strongly supported negative relationship between the number of direct interactions had by a species, and the median percent of mispredicted press perturbation responses of remaining species interactions, after that species was removed. Adding species generally made responses easier to predict. It is possible that network instability caused this pattern to occur.

Key Words: Interaction, network, perturbation, food web, prediction

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I understand that my project will become part of the permanent collection of Oregon State University, Honors College. My signature below authorizes release of my project to any reader upon request.

David Rockow, Author

Introduction

Predicting how species will react to perturbations is fundamental to numerous applications of real-world ecology, where network-based approaches and ecosystem-based management are increasingly advocated (Proulx et al., 2005). Ecological communities contain myriad species connected through a network of interactions. Due to the interconnectivity of these networks, species do not have to directly interact to affect each other's populations. Indirect effects make the task of predicting community effects to environmental disturbances difficult, and sensitive to uncertainty regarding the strengths of each species' interactions (Yodzis, 1988). For example, even in the simple three species system in Figure 1, reducing the abundance of Sp. 2 can have either a positive or negative effect on Sp. 3; the web's qualitative responses depend on the relative strengths of the direct interactions and indirect effects.

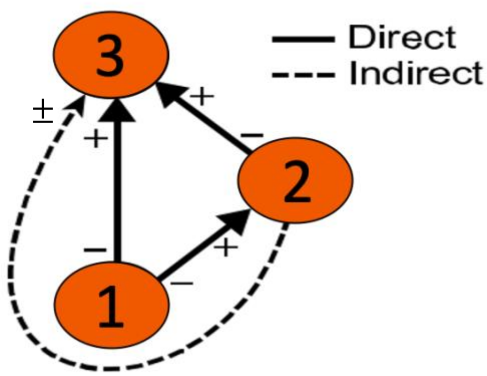


Figure 1. If the direct interaction between Sp. 3 and 2 is stronger than the direct interaction between Sp. 3 and 1, then reducing the abundance of Sp. 2 will have a negative effect on Sp. 3. If the interaction between Sp. 3 and Sp. 1 is stronger, reducing the abundance of Sp. 2 will have a positive effect on Sp. 3. In this specific example, the indirect effect is known as a trophic cascade, a phenomenon in which changing the abundance of a predator species alters the abundance of associated predator and prey species in opposing ways. (Figure adapted from Novak et al., 2011)

Ecological communities can be drastically altered through the addition or subtraction of species. Through anthropogenic climate change and increased human encroachment on ecosystems, species extinctions and introductions are becoming increasingly common (Davies et al. 2006; Hulme, 2016). Understanding how ecological networks may react to such disturbances, and other perturbations, is therefore fundamental to the contemporary and future management of real-world ecological systems (Ives & Carpenter, 2007).

There are two main types of perturbations on ecological systems: pulse perturbations and press perturbations. Pulse perturbations are short-term, acute disturbances, while press perturbations are long-term and chronic, having lasting effects (Novak et al., 2016). The effect of both perturbation types on ecological networks can be represented mathematically using the "community matrix", a Jacobian matrix whose elements quantify the instantaneous change in each species' population growth rate due to a small change in the abundance of a given species. The response of networks to pulse perturbations is characterized by the eigenvalues of this Jacobian, where the dominant eigenvalue reflects the network's components exhibiting the slowest rate of return to the pre-perturbation state. Jacobian matrices whose eigenvalues are all negative reflect networks that are asymptotically stable and resilient to pulse perturbations. In contrast, how a network's species abundances respond to press perturbations is characterized by the negative inverse of the Jacobian matrix. Conditional on the asymptotic stability of the Jacobian matrix, the net effects matrix that results from taking the negative inverse of the Jacobian reflects the sum total of all direct and indirect chain of effects that ripple through the network as species respond to press perturbations (Novak et al., 2016) This study will focus on press perturbations.

Within food webs, pairwise interactions among species can be broken down into three major types. The first are intraspecific self-effects. In the Jacobian matrix, these interactions are represented in the diagonal elements, and reflect how a given species population growth rate responds to small changes in its own abundance. The second interaction type are top-down interactions, which are the effect of a predator on its prey. In the Jacobian matrix these interactions are conventionally represented by the upper triangle elements. Lastly, bottom-up interactions are the effect of prey on its predator. In the Jacobian matrix these interactions are conventionally represented by the lower triangle elements. Hereafter, interactions will be referred to by their matrix location. Non-trophic competition among basal species, though commonly used in similar analyses, is not considered in this study; thus within-species competition is assumed to occur for implicit resources. The three by three matrix in Figure 2 of the network from Figure 1 summarizes the matrix location names, with each species having its own column and row.

$$
\begin{array}{c c}
 & \begin{array}{ccc} 1 & 2 & 3 \end{array} \\
\begin{array}{c} 1 \\ 2 \\ 3 \end{array} &
\begin{bmatrix}
\text{Diagonal} & \text{Upper Triangle} & \text{Upper Triangle} \\
\text{Lower Triangle} & \text{Diagonal} & \text{Upper Triangle} \\
\text{Lower Triangle} & \text{Lower Triangle} & \text{Diagonal}
\end{bmatrix}
\end{array}
$$

Figure 2. Each number corresponds to the numbered species from Figure 1. It is important that the order of species in the columns and rows be the same. The column species affects the row species. So, the lower triangle interaction at [3,2] ([row, column]) can be read as the effect of Sp. 2 on Sp. 3. Because Sp. 3 is the predator and Sp. 2 is its prey, this interaction is a lower triangle interaction.

In undertaking this thesis I hoped to gain insight into the impact of adding and removing species on the ability to predict the qualitative responses of biological networks to press perturbations. I hypothesized that removing species (extinction) would make interaction responses easier to predict, because, by decreasing the species richness, the number of direct interactions and indirect effects should similarly decrease (Menge, 1995). The fewer links the less complex the web, and presumably, the easier to make accurate predictions about. Similarly, I hypothesized that adding species (invasion) would have the opposite effect, making press perturbation responses harder to predict. Increasing species richness would increase the number of direct interactions and indirect effects, thus complicating the web.

Methods

First, a network was created computationally using the niche model (Williams & Martinez, 2000; Novak et al. 2011). A richness of ten was selected, despite the fact that real-world food webs are often much more speciose than just ten species. Ten was selected to more easily observe the effects of adding or removing species from the web, while still being sufficiently large enough to represent a real-world system. In a larger web the effects of these additions and removals may not be as noticeable. A connectance (number of direct links divided by richness squared) of 0.14 was selected. Connectance in real-world food webs is generally smaller than 0.14 (Dunne et al., 2002). However, using a network with a larger connectance allowed for every species in the original web to be unique in how many direct interactions it had and allowed for some species to interact with species from differing trophic levels. The network ultimately created is shown in Figure 3.

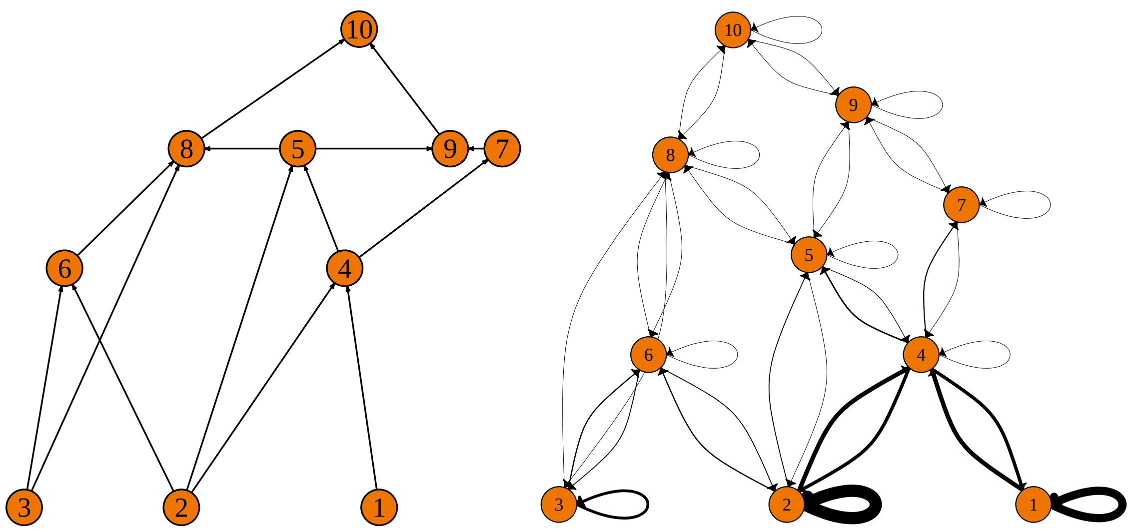


Figure 3. On the left is the network constructed with the niche model, henceforth referred to as the "original web". Arrows travel in the direction of the energy flow. The network on the right shows the magnitude of each direct interaction, with added intraspecific links. The darkness of each link is weighted by the magnitude of that interaction.

Next, each species was assigned an approximate trophic level. Species that did not feed on any other species were designated as basal species. Species that fed only on basal species were designated as primary consumers. Species that fed on at least one non-basal species were designated as secondary consumers. Any secondary consumer that was not consumed by any other species was designated as an apex predator. In the original web, Sp. 1-3 are basal; Sp. 4 and 6 are primary consumers; Sp. 5 and 7-9 are secondary consumers; and Sp. 10 is an apex predator. Each species was assigned a body size based on its trophic level. A one unit increase in a trophic level is accompanied by a 42-fold increase in body mass, on average (Brose et al., 2006). Thus, $^{1}/_{42}$ of a gram was selected as the basal body mass, for ease of analysis. Using the assigned body masses, additional species parameters were calculated as shown in Table 1.

Table 1. The parameters that the Fluxweb R package used to calculate the Jacobian matrices.

Parameter	Figure	Citation
Body Mass (g)	$^{1}/_{42}$ if Basal 1 if a Primary Consumer 42 if a Secondary Consumer 1,764 if an Apex Predator	Brose et al., 2006
Density ($\frac{g}{m^2}$)	$e^{-14.29}$ ● (Body Mass)$^{-0.77}$	Brown et al., 2004
Biomass ($\frac{g^2}{m^2}$)	Body Mass ● Density	Brown et al., 2004
Metabolic Losses ($\frac{Joules}{Year}$)	Basal: 0 Primary: 17.17 ● (Body Mass)$^{-0.29}$ Secondary: 18.18 ● (Body Mass)$^{-0.29}$ Apex: 19.50 ● (Body Mass)$^{-0.29}$	Gauzens et al., 2018
Growth Rate ($\frac{Joules}{Year}$)	0.71 ● (Body Mass)$^{-0.25}$ (If Basal, Zero for Non-Basals)	Gauzens et al., 2018
Feeding Efficiency (Unitless)	0.545 if Basal 0.906 if Non-Basal	Gauzens et al., 2018

Using these values and the *fluxing* function in the fluxweb R package, (Gauzens, 2018), the Jacobian matrix was produced for the original web. The *fluxing* function computes food web fluxes, assuming that all species are at equilibrium, and thus incoming and outgoing fluxes are equal for each species. The elements of the Jacobian matrix are the calculated fluxes between species. The Jacobian matrix, in an ecological sense, is a matrix that entails a small change in the abundance of each species on each species' population growth rates, including its own. These elements will be subsequently referred to as "interaction strengths". Jacobian matrices are commonly used in ecology to determine how food webs respond to disturbances. The negative of the inverse Jacobian summarizes how species are expected to react to the change in abundance of other species caused by press perturbations, as the direct, pairwise effects cascade throughout the entire network of indirect effects (Yodzis, 1988; Novak et al., 2016).

Asymptotic stability of the Jacobian matrix was achieved by assigning each species an intraspecific link, and making the magnitude of these intraspecific effects increasingly negative (de Ruiter et al., 1995). Stability is the ability of a biological network to return to pre-perturbation equilibrium values. If a network is unstable it cannot return to pre-equilibrium values, and the calculated percentages of mispredicted responses will be systematically incorrect.

Using the PressPurt R package (Koslicki et al., 2020), the "true" Jacobian matrix was subjected to increasing levels of interaction strength uncertainty to analyze how the predictions of species responses would be altered. For each interaction, a truncated normal distribution of error was assumed with a mean of zero and the interaction strength uncertainty as the variance about the mean. Data were collected at the following levels of interaction strength uncertainty: 0.1, 1, 10, and 100 standard deviations, scaled to each original Jacobian element, for comparison to the "correct" response predictions made when the interaction strength uncertainty was zero.

The proportion of all possible mispredictions that were made when each individual direct interaction was misestimated was calculated. Net effects that underwent a sign switch were considered mispredictions. The sign of a net effect represents how the species was expected to react, with a positive sign representing an increase in abundance and a negative sign representing a decrease in abundance. All calculations and simulations were ran through R (version 4.0.3) and Python (version 3.8.5).

To determine how species extinctions changed the tolerance of press perturbation predictions to interaction strength uncertainty, ten additional webs were constructed, each where one of the original ten species were removed from the network. After each removal, species parameters and biomass fluxes were recalculated prior to construction of the Jacobian matrix. As a special case, when Sp. 4 was removed, Sp. 7 was also removed, as Sp. 7 fed only on Sp. 4 and was presumed to go extinct in the absence of Sp. 4.

Next, to determine how species invasions changed the tolerance of press perturbation predictions to interaction strength uncertainty, three more webs were created, each adding one species to the original web (henceforth referred to as Sp. 11). The added species were a basal, an intermediate consumer, and an apex predator. The added species were assigned three links to most closely retain the approximate connectance of 0.14, with the exception of the added apex predator, which was given two links to best replicate the apex predator in the original web. When adding a basal species, the species that fed on the basal species were selected using a random number generator. When the intermediate consumer (a non-basal species that is also not an apex predator) was added to the original web, it was first determined with a random number generator if the new intermediate consumer should consume two species and be consumed by one species, or consume one species and be consumed by two species. Then, the species it interacted with were similarly selected randomly. Lastly, an apex predator was added to the original web. The new apex predator was assigned to feed on Sp. 10, to retain the number of apex predators in the web at one, as well as one additional species selected randomly. The three networks with the added species are shown in Figure 4.

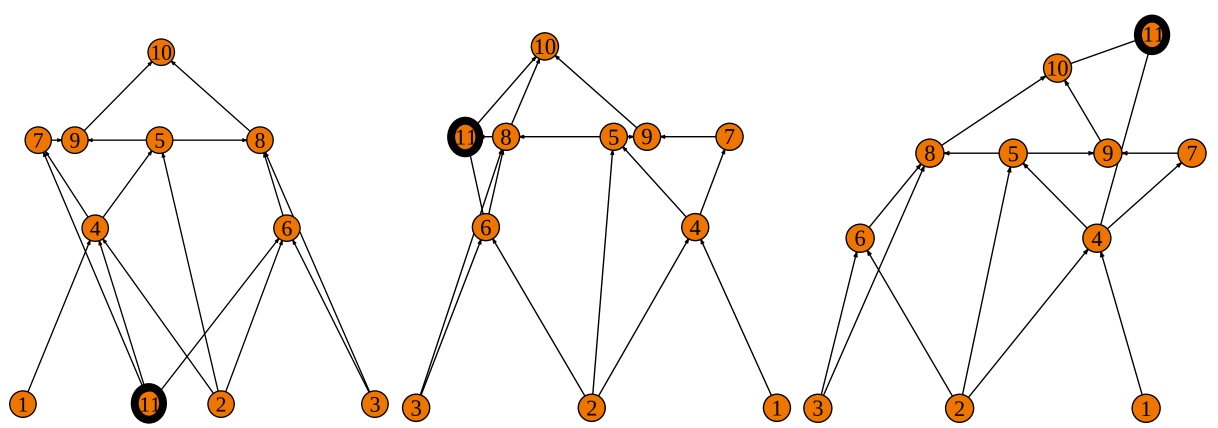


Figure 4. The three webs created after adding a species. The added species is referred to as Sp. 11, and is circled in black for easy visibility.

Each of the thirteen newly constructed webs were analyzed in the same fashion as the original web, using PressPurt to subject their fluxweb calculated Jacobian matrixes to increasingly higher interaction strength uncertainty and determine the proportion of qualitative mispredictions that resulted.

Results

Overall, both adding and removing species generally made it easier to predict species' press perturbation responses. Increasing the interaction strength uncertainty made species responses more difficult to predict up to an interaction strength uncertainty of approximately 10, at which point the probability of making mispredictions plateaued. Data are summarized in three following ways; heat maps, boxplots, and scatterplots comparing the number of links a species had, and the percent of mispredicted responses after it was removed. Gradated tables, an additional data visualization tool, are shown in the appendix.

Heat Maps (Fig. 5)
Overall, in the fourteen webs, and focusing on when the interaction strength was 100, the direct interaction that, when misestimated, resulted in the highest percent of mispredicted responses was an upper triangle interaction for nine webs (Sp. 1 removed, Sp. 3 removed, Sp. 6 removed, Sp. 7 removed, Sp. 8 removed, Sp. 9 removed, Sp. 10 removed, basal Sp. added, and intermediate Sp. added), lower triangle for two webs (original web and apex Sp. added), diagonal for two webs (Sp. 4 removed and Sp. 5 removed), and a tie between upper and lower triangle for one web (Sp. 2 removed). The most common interaction that, when misestimated, resulted in the highest percent of mispredicted responses was Sp. 9 on 5, which was the case for three webs (Sp. 2, 8, and 10 removed). Sp. 6 on 3 (Sp. 9 removed and apex Sp. added), Sp. 10 on 9 (Sp. 7 removed and intermediate Sp. added), and Sp. 5 on 2 (Sp. 1 removed and basal Sp. added) all resulted in the highest percent of mispredicted responses, when they were misestimated, for two webs apiece. At lower levels of interaction strength uncertainty, the interactions that, when misestimated, resulted in the highest percent of mispredictions were generally the same or similar than when the interaction strength uncertainty was 100. Analysis will mostly focus on the simulations done at higher levels of interaction strength uncertainty, as these more closely match how the results may look in a real-world system, where data on web topology and interaction magnitude is often severely limited, and thus conducted at high error.

Boxplots (Fig. 6)
Overall, diagonal interactions, when misestimated, resulted in the lowest percent of mispredicted responses. Upper and lower triangle interactions produced fairly similar values, on average. In some webs, such as the original web, removing Sp. 6, and removing Sp. 10, all had lower triangles interactions that, when misestimated, resulted in the highest percent of mispredicted responses, on average. The opposite was true for removing Sp. 1 and 7, where upper triangle responses, when misestimated, resulted in the highest percent of mispredicted responses. When the interaction strength uncertainty was 100, the original web had the highest median for diagonal and lower triangle interactions, while for upper triangle interactions removing Sp. 1 generated the highest median. Increasing the interaction strength uncertainty beyond 10 generated very little change in the data across all three interaction types.

Scatterplots (Fig. 7)
Overall, when the interaction strength uncertainty was 100, for all three interaction types there existed a strongly supported negative relationship between number of direct links had by a species, and the percent of mispredicted responses of remaining species interactions after that species was removed. Only for diagonal interactions did a strong relationship between number of links and percent of mispredicted responses exist at low levels of interaction strength uncertainty. At high levels of interaction strength uncertainty, the slope of the relationship between number of links and percent of mispredictions for all three interaction types was approximately -0.04, suggesting an approximate 4% decrease in the percent of mispredicted responses for every additional link a species had in the original food web. However, for many of the scatterplots the relationship that existed was better modelled (higher R^2 squared value) with an exponential decrease function, so the extent to which this 4% rule holds true decreases as the number of links increases.

Figure 5

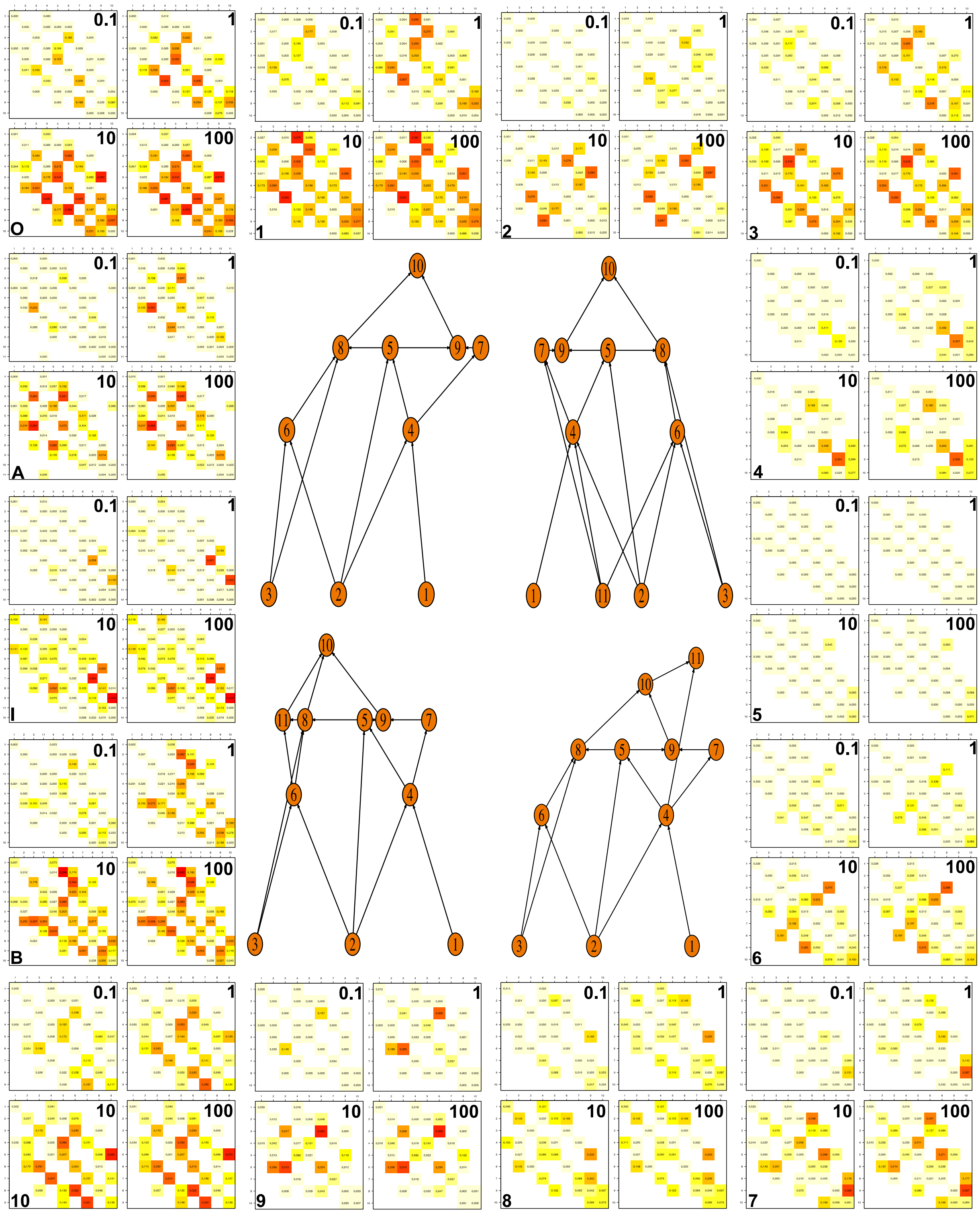


Figure 5. (Heat Maps). Each heat map was produced on the same scale, with a zero value producing a light beige color, and the highest overall value (0.402) producing a deep red color. The figures are the percent of mispredicted responses, when that interaction was misestimated. Each bundle of heat maps are from one web, with the bottom left corner labeled by which web the heat maps are from (O is the original web, each number correlates to the species that was removed from the original web, B is adding a basal species, I is adding an intermediate species, and A is adding an apex species). The interaction strength uncertainty is shown in the top right of each heat map.

Original Web- The interaction that, when misestimated, resulted in the highest percent of mispredicted responses was the effect of Sp. 4 on Sp. 7, at higher levels of interaction strength uncertainty. The original web had the largest difference in medians between the upper and lower triangle interactions, with the lower triangle interactions having a greater average median.
Species One Removed- Other than in the original web, removing Sp. 1 generally produced the highest values. At high levels of interaction strength uncertainty, the interaction that, when misestimated, resulted in the highest percent of mispredicted responses was the effect of Sp. 5 on 2.
Species Two Removed- Removing Sp. 2 produced a symmetric pattern, with interactions and their reciprocal interactions having approximately equal percents, with the exception of the effect of Sp. 8 on 3, which produced much higher values than the effect of Sp. 3 on 8. The diagonal interactions all produced relatively low values. At higher levels of interaction strength uncertainty, the effects of Sp. 9 on 5, and Sp. 5 on 9, when misestimated, resulted in the highest percent of mispredicted responses.
Species Three Removed- For all simulations, except at the lowest interaction strength uncertainty, the effect of Sp. 5 on 4, when misestimated, resulted in the highest percent of mispredicted responses.
Species Four Removed- When Sp. 4 was removed, Sp. 7 was also removed. In the original web, Sp. 7 fed only on Sp. 4, thus it was assumed removing Sp. 4 would cause Sp. 7 to also go extinct. For all simulations the intraspecific effect of Sp. 9, when misestimated, resulted in the highest percent of mispredicted responses.
Species Five Removed- Removing Sp. 5 produced the lowest values across all simulations. The intraspecific effect of Sp. 10, when misestimated, resulted in the highest percent of mispredicted responses.
Species Six Removed- The effect of Sp. 8 on 3, when misestimated, resulted in the highest percent of mispredicted responses, at high levels of interaction strength uncertainty.
Species Seven Removed- The effect of Sp. 10 on 9, when misestimated, resulted in the highest percent of mispredicted responses, at high levels of interaction strength uncertainty.
Species Eight Removed- The effect of Sp. 9 on 5, when misestimated, resulted in the highest percent of mispredicted responses, at high levels of interaction strength uncertainty.
Species Nine Removed- The effect of Sp. 6 on 3, when misestimated, resulted in the highest percent of mispredicted responses, at high levels of interaction strength uncertainty.
Species Ten Removed- The effect of Sp. 9 on 5, when misestimated, resulted in the highest percent of mispredicted responses, at high levels of interaction strength uncertainty.
Basal Species Added- The effect of Sp. 5 on 2, when misestimated, resulted in the highest percent of mispredicted responses, at high levels of interaction strength uncertainty.
Intermediate Consumer Added- The effect of Sp. 10 on 9, when misestimated, resulted in the highest percent of mispredicted responses, at high levels of interaction strength uncertainty. When an intermediate Sp. was added and the interaction strength uncertainty was 100, the effect of Sp. 10 on 9 was the interaction that produced the highest values out of all the webs constructed (0.402).
Apex Predator Added- The effect of Sp. 6 on 3, when misestimated, resulted in the highest percent of mispredicted responses, at high levels of interaction strength uncertainty.

Figure 6

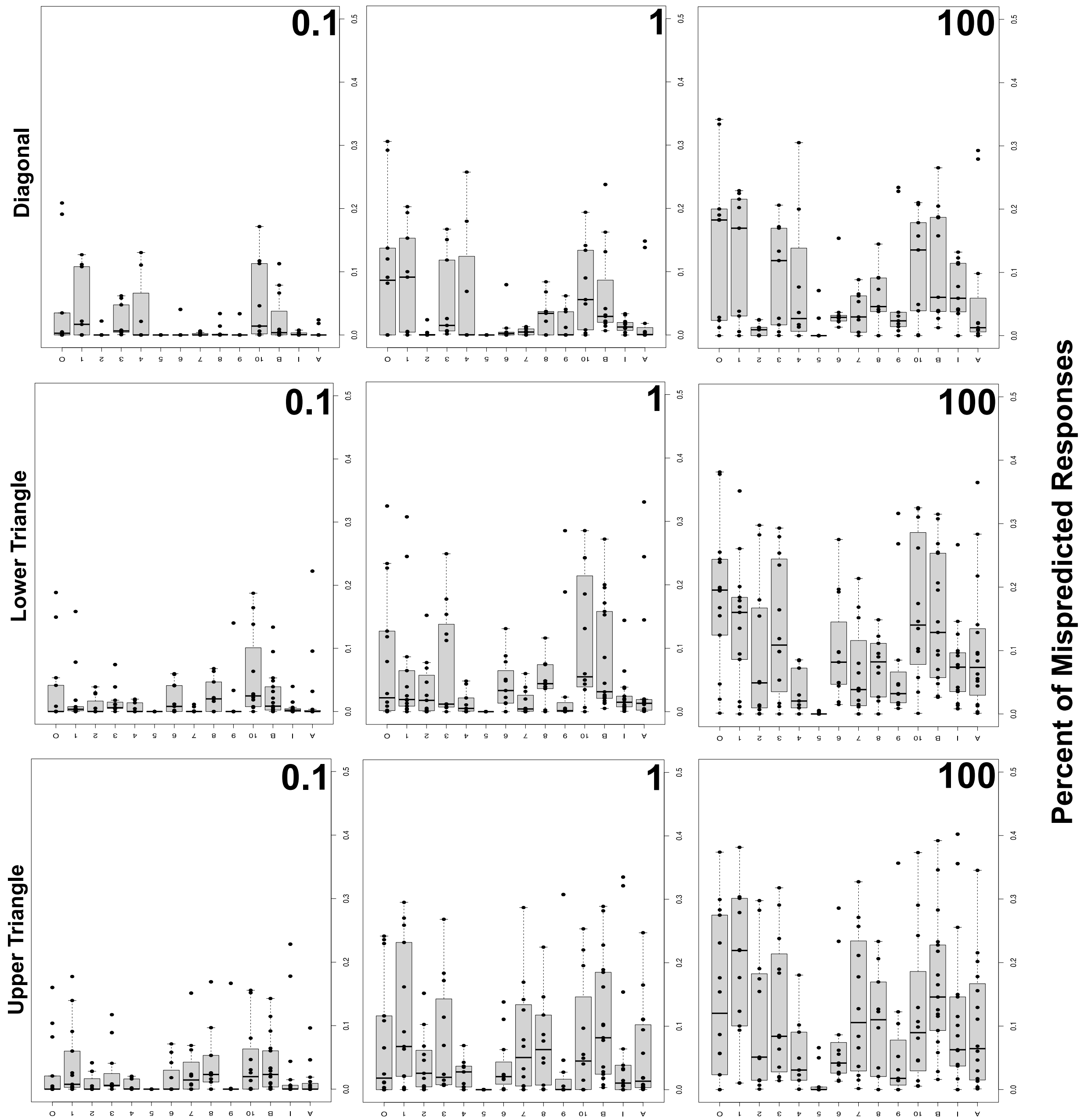

Diagonal
Lower Triangle
Upper Triangle
0.1
1
100
Percent of Mispredicted Responses

Figure 6. (Boxplots). In all boxplots, the x-axis corresponds to the fourteen different webs, with the "O" referring to the original web, each number referring to the species that was removed from the original web, the "B" referring to the added basal species, the "I" referring to the adding intermediate consumer, and the "A" referring to the added apex predator. The y-axis is the percent of mispredicted responses. Plotted are the five number summaries (minimum, first quartile, median, third quartile, maximum) for each web. The solid black line in each box is the median. Each point is percent of mispredicted responses when each direct interaction was misestimated in that web. Points to the right of the rightmost whisker are outliers. Data from when the interaction strength uncertainty was 10 is not included (though it is available in the appendix), as it was redundant when compared to when the interaction strength uncertainty was 100. The interaction strength uncertainty is located in the top right for each graph.

Diagonal (0.1)- The majority of median values are zero, or approximately zero, with the exception of removing Sp. 1 and 10.
Diagonal (1)- With the slight increase in interaction strength uncertainty, the medians mostly stayed at or around zero. The main exception being the original web, removing Sp. 1, and removing Sp. 10, all of which greatly increased the median.
Diagonal (100)- When the interaction strength uncertainty was increased to 100, all webs, with the exception of removing Sp. 5, have medians above zero. The original web and removing Sp. 1 still have the largest medians, followed by removing Sp. 10 and removing Sp. 3.
Lower Triangle (0.1)- At the lowest level of interaction strength uncertainty, the lower triangle interactions all had medians of zero, or approximately zero, with the exception of removing Sp. 6, 8, and 10.
Lower Triangle (1)- When the interaction strength uncertainty was increased to 1, the medians generally stayed fairly small. The largest median is when Sp. 10 is removed, followed closely by removing Sp. 8.
Lower Triangle (100)- Increasing the interaction strength uncertainty to 100 had a large effect on the webs. The original web has largest median. The only web that has not been significantly impacted is removing Sp. 5, which still has a median of approximately zero.
Upper Triangle (0.1)- In many of the webs, the medians were zero or approximately zero. Notable exceptions are removing Sp. 7, 8, and 10, as well as adding a basal species.
Upper Triangle (1)- When the interaction strength uncertainty was increased to 1, there is a drastic change in the percent of mispredicted responses for all webs but removing Sp. 5. Adding the basal species has the largest median, followed by removing Sp. 8 and 1.
Upper Triangle (100)- When the interaction strength uncertainty was increased to 100, the largest percent of mispredictions is caused by removing Sp. 1, with adding a basal species having the second largest value. The median for the original web has increased and has the third largest value among the webs.

Figure 7

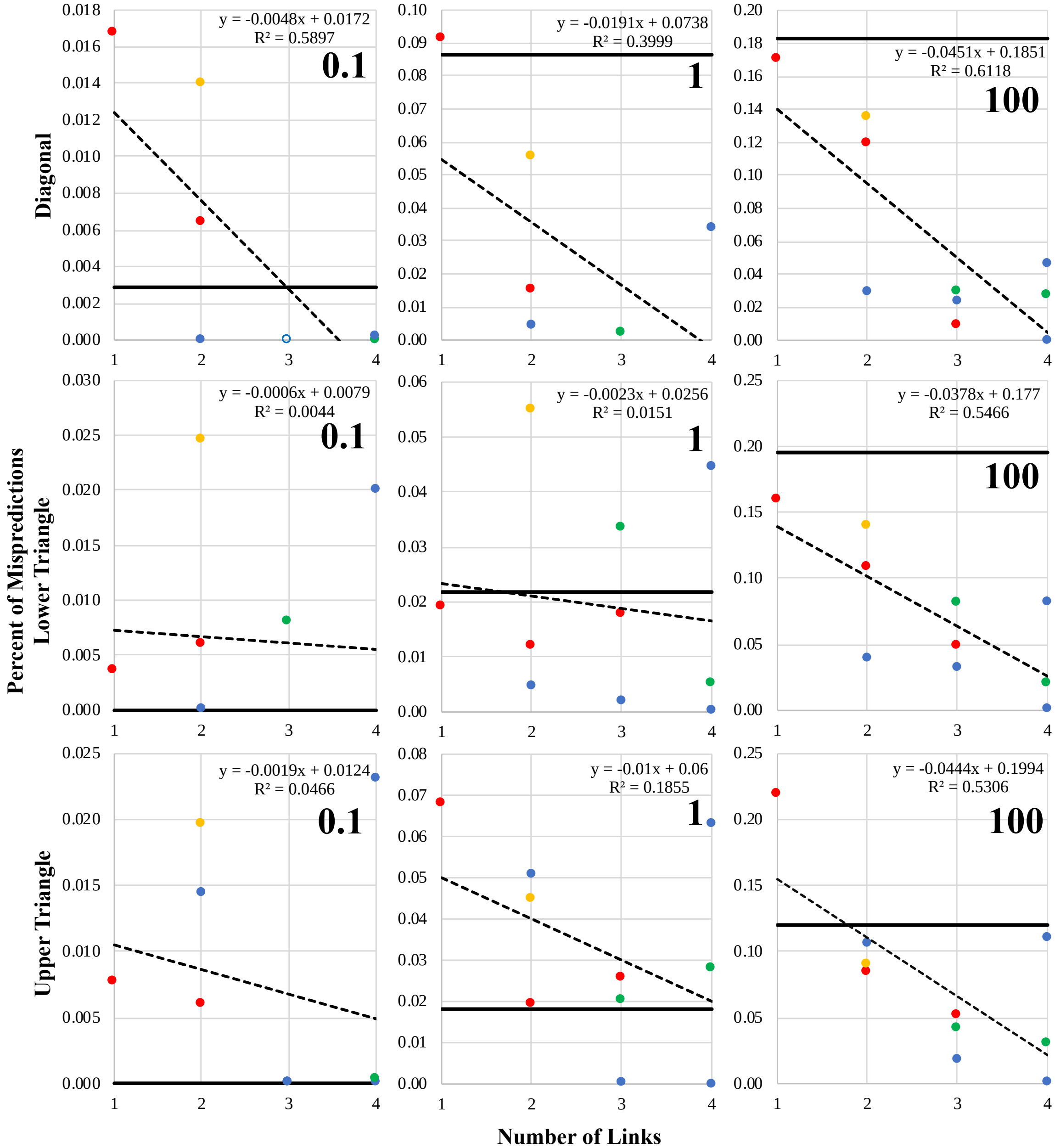

Diagonal
Percent of Mispredictions
Lower Triangle
Upper Triangle
Number of Links
y = -0.0048x + 0.0172
R² = 0.5897
0.1
y = -0.0191x + 0.0738
R² = 0.3999
1
y = -0.0451x + 0.1851
R² = 0.6118
100
y = -0.0006x + 0.0079
R² = 0.0044
0.1
y = -0.0023x + 0.0256
R² = 0.0151
1
y = -0.0378x + 0.177
R² = 0.5466
100
y = -0.0019x + 0.0124
R² = 0.0466
0.1
y = -0.01x + 0.06
R² = 0.1855
1
y = -0.0444x + 0.1994
R² = 0.5306
100

Figure 7 (Scatterplots). Each point in the following graphs is one of the ten webs constructed with a species removed. Basal species are represented by red dots, primary consumers with green, secondary consumers with blue, and the apex predator with yellow. The species represented by the dot is the species that was removed. The dashed black line is the linear line of best fit, and is modelled with the equation in top right. The R^2 value is also shown. The solid horizontal line is the median value from the original web. The x-axis is the number of direct interspecific species links the species had in the original web, prior to being removed. The y-axis is the median percent of mispredicted responses. Data from when the interaction strength uncertainty was 10 is not included (though it is available in the appendix), as it is redundant when compared to when the interaction strength uncertainty was 100. The interaction strength uncertainty is located in the top right for each graph.

Diagonal (0.1)- When the interaction strength uncertainty was very small, there was a strong negative correlation between percent of mispredictions and the number of links. All secondary consumers had percents of zero.
Diagonal (1)- As the interaction strength uncertainty increased, the correlation for diagonal interactions between percent of mispredictions and number of links becomes less strong, but is still somewhat strong. All points, except removing Sp. 1 are now below the original value.
Diagonal (100)- When the interaction strength uncertainty was increased to 100, the correlation between percent of mispredictions and number of links is strong again. All points are below the original value.
Lower Triangle (0.1)- When the interaction strength uncertainty was very small, there was no correlation between percent of mispredictions and the number of links for lower triangle interactions.
Lower Triangle (1)- When the interaction strength uncertainty was raised to 1, there was still no correlation between percent of mispredictions and number of links for lower triangle interactions.
Lower Triangle (100)- The correlation between percent of mispredictions and number of links is fairly strong and negative for lower triangle interactions when the interaction strength uncertainty was increased to 100. All points are below the original value.
Upper Triangle (0.1)- When the interaction strength uncertainty was very small, there was no correlation between percent of mispredictions and the number of links for upper triangle interactions.
Upper Triangle (1)- When the interaction strength uncertainty was raised to 1, there is a stronger, albeit still weak, correlation between percent of mispredictions and number of links for upper triangle interactions. Upper triangle interactions when the interaction strength uncertainty was 1 had the most data points above the original value.
Upper Triangle (100)- When the interaction strength uncertainty was raised to 100, the correlation between percent of mispredictions and number of links is fairly strong and negative for lower triangle interactions. Only removing Sp. 1 had a larger percent of mispredictions than the original web.

Discussion

Overall, both removing and adding species generally made the qualitative net effects of press perturbations easier to predict. For removing species, at high levels of interaction strength uncertainty, the extent to which species responses became easier to predict was strongly correlated with how many links the removed species had in the original web. At low levels of interaction strength uncertainty a strongly supported relationship was only true for diagonal (intraspecific) interactions.

The original web consisted of ten species with fourteen direct interactions. The webs where a species was removed decreased the richness by one (in one case two) and decreased the number of direct links by between one and six. Decreasing the species richness, should also decrease the number of direct interactions and indirect effects that form (Menge, 1995). Indirect effects play a large role in ecosystem dynamics due to their high frequency in ecosystems, despite the magnitude of indirect links generally being relatively small when compared to direct links (Shevtsov & Rael, 2015, but see also Menge, 1995). Thus, reducing the species richness likely made responses easier to predict due to the decrease in indirect effects.

Removing Sp. 1 resulted in one of two webs that produced a larger percent of mispredictions than the original web for one of the interaction types, in this case upper triangle interactions (the other such case being upper triangle interactions when a basal species was added). Why removing Sp. 1 had a contrasting effect when compared to most of the other webs other species is likely due to the topology of the original web. In the original web Sp. 1 was the least connected species, having just one direct interaction, and therefore fewer indirect links, than all other species. In the original web, the effects of Sp. 1 were the least sensitive to interaction strength uncertainty. Thus, removing Sp. 1 removed with it these easy to predict responses, increasing the median probability of correctly predicting the remaining responses in the process. Still, removing Sp. 1 produced smaller lower triangle (prey on predator) median values than the original web (0.160 versus 0.196, when the interaction strength uncertainty was 100), and higher upper triangle (predator on prey) median values than the original web (0.219 versus 0.121, when the interaction strength uncertainty was 100). In the original web, upper triangle interactions were harder to predict than lower triangle interactions, but the opposite was true when Sp. 1 was removed. Overall, in some of the webs, upper triangles produced larger probabilities of misprediction, while in others lower triangle interactions produced larger probabilities. Why this pattern occurred is not immediately clear.

Whether food webs are governed by top-down (predators control prey) or bottom-up (prey controls predators) control in natural ecosystems has been a hotly debated topic among ecologists. Simplified, top-down control occurs when interactions between predators and their prey control the food web, and reductions in predator abundances will result in significant changes in abundance for prey species (Power, 1992). A dominant form of bottom-up control is nutrient control, where the availability of nutrients dictates the abundance of basal species, in turn controlling the abundance of consumer species (Power, 1992). However, in this study there was no correlation between basal or predator species abundance and whether or not upper triangle or lower triangle interactions promoted a higher percent of mispredicted responses. Thus, more research should be conducted to determine what promotes top-down and bottom-up controls in computer generated and real-world food webs, and how this relates to whether upper or lower triangle interactions have greater effects on the overall predictability of the network.

If decreasing the number of indirect links resulted in species responses being easier to correctly predict, it would then be expected that increasing the number of indirect links would have the opposite effect. Yet, this pattern was not observed. Adding species generally made species responses easier to predict. Why this pattern occurred may be due to network stability, or in this case, instability. It has been shown that increasing species richness destabilizes networks (May, 1972). Additionally, it was found that the transition from stable to unstable can occur rapidly (May, 1972). It is possible that in this study, the original web was stable, but that adding just one species caused the web to become too complex and unstable. PressPurt, and the mathematical framework on which it operates, is predicated on having asymptotically stable Jacobian matrices. As the interaction strength uncertainty increases, networks could become increasingly unstable. If a network was more unstable to begin with, it will reach a state of instability faster and the full error distribution will not be factored into PressPurt's calculations. It is possible that the increased instability of adding a species pushed the original web into an unstable state that resulted in a smaller than expected percent of mispredictions when a species was added because the full interaction strength uncertainty could not be applied without destabilizing the web.

Conclusions

The two main takeaways from this thesis are as follows:

1. Of the three interaction types, diagonal interactions, when misestimated, resulted in the highest percent of mispredicted responses, and therefore can therefore be the least accurately estimated in real-world systems to most precisely predict the qualitative food web dynamics in response to press perturbations. In turn, upper and lower triangle interactions produced relatively similar values, and should be equally accurately estimated to precisely predict the qualitative food web dynamics in response to press perturbations.
2. Species extinctions generally promote responses being easier to predict with certainty. Species invasions similarly promote responses being easier to predict with certainty, but this pattern may be due to network instability associated with the increased richness. Thus, I conclude this thesis offers little insight into the impact of species invasions on biological networks until the extent to which network instability factored into the results can be ascertained.

General insights gained in this project about network stability, the effect of different general reaction types on overall network predictability, and the impact of adding and removing nodes on network predictability can all be applied to a wide range of fields, other than theoretical ecology, that also employ network theory. Further research in this subject area should focus on a wider variety of webs to determine the extent to which the results observed in this project are specific to the web(s) created or are instead representative of a general trend in the majority of food webs. Webs of varying richness and connectance should also be analyzed to better explore food web dynamics in a wide array of different systems. Specific to PressPurt, a way to explore web stability that can give the user a good idea about the stability of their web, and the extent to which their observed probabilities are reduced due to instability in the web, should be developed.

References

1. Brose, U., et al. (2006). Consumer-Resource Body-Size Relationships in Natural Food Webs, *Ecology, 87*, 2411-2417. doi: 10.1890/0012-9658
2. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., West, G. B. (2004). Toward a Metabolic Theory of Ecology, *Ecology, 85*(7), 1771-1789. doi:10.1890/03-9000.
3. Davies, R. G., Orme, C. D., Olson, V., Thomas, G. H., Ross, S. G., Ding, T., Rasmussen, P., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Owens, I.F., Gaston, K. J. (2006). Human impacts and the global distribution of extinction risk. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1598), 2127-2133. doi:10.1098/rspb.2006.3551
4. de Ruiter, P. C., Neutel, A., Moore, J. C. (1995). Interaction Strengths and Stability in Ecosystems. *Science*, *269*, 1257-1260.
5. Dunne, J. A., Williams, R. J., Martinez, N. D. (2002). Food-web structure and network theory: The role of connectance and size. *PNAS*, *99*, 12917-12922. doi: 10.1073/pnas.192407699
6. Gauzens, B. (2018). fluxweb: Estimate Energy Fluxes in Food Webs. R package version 0.2.0. https://CRAN.R-project.org/package=fluxweb
7. Gauzens, B., Barnes, A., Giling, D. P., Hines, J., Jochum, M., Lefcheck, J. S., Rosenbaum, B., Wang, S., Brose, U. (2018). Fluxweb: An R package to easily estimate energy fluxes in food webs. *Methods in Ecology and Evolution, 10*(2), 270-279. doi:10.1111/2041-210X.13109
8. Hulme, P. E. (2016). Climate change and biological invasions: evidence, expectations, and response options. *Biological Reviews*, *92*(3), 1297-13. doi:10.1111/brv.12282
9. Ives, A. R., & Carpenter, S. R. (2007). Stability and Diversity of Ecosystems. *Science*, *317*(5834), 58-62. doi:10.1126/science.1133258
10. Koslicki, D., Gibbon, D., Novak, M. (2020). PressPurt: Indeterminacy of Networks via Press Perturbations. R package version 1.0.2. https://CRAN.R-project.org/package=PressPurt
11. Koslicki, D., Novak, M. (2018). Exact Probabilities for the Indeterminacy of Complex Networks as Perceived Through Press Perturbations. *Journal of Mathematical Biology, 76*, 877-909. doi:10.1007/s00285-017-1163-0
12. May, R. M. (1972). Will a large complex system be stable?. *Nature*, *238*, 413-414. doi: 10.1038/238413a0
13. Menge, B, A. (1995). Indirect effects in marine rocky intertidal interaction webs: patterns and importance, *Ecological Monographs*, *65*, 21-74. doi: 10.2307/2937158
14. Novak, M, Wootton, J, T., Doak, D. F., Emmerson, M, Estes, J. A., Tinker, M. T. (2011). Predicting community responses to perturbations in the face of imperfect knowledge of network complexity, *Ecology*, *92*, 836-846. doi: 10.1890/10-1354.1
15. Novak, M., Yeakel, J. D., Noble, A. E., Doak, D. F., Emmerson, M., Estes, J. A., Jacob, U., Tinker, M. T., Wootton, J. T. (2016). Characterizing Species Interactions to Understand Press Perturbations: What Is the Community Matrix?, *Annual Review of Ecology, Evolution, and Systematics*, *47*, 409-432. doi: 10.1146/annurev-ecolsys-032416-010215
16. Power, M. E. (1992). Top-down and bottom-up forces in food webs: Do plants have primacy?, *Ecology*, *73*, 733-746. doi: 10.2307/1940153

17. Proulx, S. R., Promislow, D. E. L., Phillips, P. C. (2005). Network Thinking in ecology and evolution. *Trends in Ecology and Evolution*, *20*(6), 345-353. doi:10.1016/j.tree.2005.04.004
18. Shevtsov, J., Rael, R. (2015). Indirect Energy Flows in Niche Model Food Webs: Effects of Size and Connectance. *PLoS One*, *10*(10). doi: 10.1371/journal.pone.0137829
19. Williams, R. J., Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, *404*. doi: 10.1038/35004572
20. Yodzis, P. (1988). The Indeterminacy of Ecological Interactions as Perceived Through Perturbation Experiments. *Ecology*, *69*(2), 508-515. doi:10.2307/1940449

Appendix

Gradated Tables

Overall, at higher levels of interaction strength uncertainty the original web generally had the highest values for the diagonal and lower triangle interactions (Table 5 and 9). For the upper triangle interactions removing Sp. 1 produced higher values (Table 13). Removing Sp. 10 and adding a basal species also routinely produce values greater than the original web, specifically for the upper and lower triangle interactions (Table 9 and 13), but more so at low levels of interaction strength uncertainty.

Diagonal (0.1)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.000	0.003	0.027	0.209	0.045
Sp. 1 Removed	0.000	0.000	0.017	0.108	0.127	0.043
Sp. 2 Removed	0.000	0.000	0.000	0.000	0.022	0.002
Sp. 3 Removed	0.000	0.004	0.006	0.048	0.062	0.021
Sp. 4 Removed	0.000	0.000	0.000	0.044	0.130	0.033
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.000	0.000
Sp. 6 Removed	0.000	0.000	0.000	0.000	0.040	0.004
Sp. 7 Removed	0.000	0.000	0.000	0.002	0.006	0.001
Sp. 8 Removed	0.000	0.000	0.000	0.001	0.034	0.006
Sp. 9 Removed	0.000	0.000	0.000	0.000	0.034	0.004
Sp. 10 Removed	0.000	0.002	0.014	0.113	0.172	0.052
Basal Added	0.000	0.000	0.004	0.038	0.113	0.025
Int. Added	0.000	0.000	0.001	0.003	0.008	0.002
Apex Added	0.000	0.000	0.000	0.000	0.024	0.004

Gradated tables express the probability of a mispredicted response (rounded to three decimal places), and are shaded based on closeness to the original web value. The gradient to the left was employed. The center gray color represents values from the original web. The red represents a value below the original value (lower probability of an incorrect prediction), while the blue represents a value above the original value (higher probability of an incorrect prediction). Each column is done on its own scale. Meaning, in each column the largest value is given the darkest blue color, and the smallest value is give the darkest red color, unless all of the value are either greater than or lesser than the original value, which is always gray.

Table 2. Diagonal (0.1)- The only web that consistently produced values larger than the original was removing Sp. 10, though the medians for removing Sp. 1 and 3 were also greater than in the original web.

Diagonal (1)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.000	0.086	0.133	0.306	0.103
Sp. 1 Removed	0.000	0.004	0.091	0.153	0.203	0.083
Sp. 2 Removed	0.000	0.000	0.000	0.001	0.024	0.003
Sp. 3 Removed	0.002	0.006	0.015	0.118	0.167	0.055
Sp. 4 Removed	0.000	0.000	0.000	0.097	0.257	0.063
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.000	0.000
Sp. 6 Removed	0.000	0.000	0.002	0.004	0.080	0.011
Sp. 7 Removed	0.000	0.000	0.005	0.010	0.013	0.005
Sp. 8 Removed	0.000	0.000	0.034	0.037	0.084	0.031
Sp. 9 Removed	0.000	0.000	0.000	0.037	0.062	0.017
Sp. 10 Removed	0.000	0.008	0.056	0.134	0.194	0.075
Basal Added	0.007	0.020	0.029	0.087	0.238	0.065
Int. Added	0.000	0.007	0.012	0.020	0.034	0.014
Apex Added	0.000	0.000	0.001	0.012	0.148	0.029

Table 3. Diagonal (1)- All webs, with the exception of removing Sp. 1 generally produced lower values than the original web.

Diagonal (10)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.022	0.180	0.194	0.341	0.147
Sp. 1 Removed	0.000	0.027	0.169	0.208	0.228	0.122
Sp. 2 Removed	0.000	0.000	0.009	0.011	0.025	0.008
Sp. 3 Removed	0.000	0.016	0.109	0.161	0.204	0.092
Sp. 4 Removed	0.000	0.009	0.023	0.107	0.304	0.080
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.060	0.009
Sp. 6 Removed	0.013	0.022	0.026	0.030	0.150	0.039
Sp. 7 Removed	0.000	0.005	0.027	0.058	0.079	0.034
Sp. 8 Removed	0.000	0.036	0.042	0.089	0.143	0.057
Sp. 9 Removed	0.000	0.012	0.021	0.037	0.224	0.063
Sp. 10 Removed	0.000	0.037	0.135	0.172	0.207	0.107
Basal Added	0.012	0.038	0.056	0.176	0.264	0.108
Int. Added	0.000	0.034	0.056	0.106	0.123	0.063
Apex Added	0.000	0.005	0.011	0.057	0.284	0.065

Table 4. Diagonal (10)- Removing Sp. 2, 3, 4, 5, 7, 9, and adding an apex predator all produced lower values than the original web for all values except the minimum. The original web had the largest median and mean values.

Diagonal (100)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.025	0.183	0.198	0.342	0.150
Sp. 1 Removed	0.000	0.031	0.170	0.216	0.229	0.124
Sp. 2 Removed	0.000	0.000	0.009	0.013	0.025	0.010
Sp. 3 Removed	0.000	0.017	0.119	0.170	0.206	0.095
Sp. 4 Removed	0.000	0.010	0.027	0.108	0.305	0.081
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.071	0.011
Sp. 6 Removed	0.013	0.023	0.029	0.032	0.154	0.041
Sp. 7 Removed	0.000	0.005	0.030	0.063	0.089	0.037
Sp. 8 Removed	0.000	0.038	0.046	0.091	0.145	0.059
Sp. 9 Removed	0.000	0.014	0.023	0.037	0.234	0.066
Sp. 10 Removed	0.000	0.039	0.136	0.179	0.210	0.109
Basal Added	0.013	0.038	0.061	0.187	0.265	0.111
Int. Added	0.000	0.038	0.059	0.114	0.132	0.067
Apex Added	0.000	0.006	0.013	0.059	0.293	0.068

Table 5. Diagonal (100)- Removing Sp. 2, 3, 4, 5, 7, 9, and adding an apex predator all produced lower values than the original web for all values, except the minimum. The original web had the largest median and mean values.

Lower (0.1)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.000	0.000	0.033	0.188	0.032
Sp. 1 Removed	0.000	0.001	0.004	0.008	0.158	0.022
Sp. 2 Removed	0.000	0.000	0.000	0.017	0.039	0.009
Sp. 3 Removed	0.000	0.005	0.006	0.013	0.074	0.015
Sp. 4 Removed	0.000	0.000	0.000	0.014	0.020	0.006
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.000	0.000
Sp. 6 Removed	0.000	0.000	0.008	0.041	0.060	0.020
Sp. 7 Removed	0.000	0.000	0.000	0.000	0.011	0.002
Sp. 8 Removed	0.000	0.004	0.020	0.041	0.068	0.026
Sp. 9 Removed	0.000	0.000	0.000	0.000	0.140	0.016
Sp. 10 Removed	0.000	0.008	0.025	0.082	0.187	0.056
Basal Added	0.000	0.002	0.009	0.039	0.134	0.027
Int. Added	0.000	0.000	0.002	0.004	0.040	0.005
Apex Added	0.000	0.000	0.000	0.001	0.222	0.022

Table 6. Lower Triangle (0.1)- Removing Sp. 10 generated consistently higher values than the original web, the only such web where this was true. Thought, removing Sp. 8 and adding a basal species both produced higher 1st quartile values, medians, and 3rd quartile values higher than the original. Removing Sp. 6 produced a higher median and 3rd quartile value than the original, while removing Sp. 1 and three produced higher 1st quartile values and medians than the original.

Lower (1)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.002	0.022	0.125	0.324	0.083
Sp. 1 Removed	0.000	0.009	0.019	0.065	0.307	0.064
Sp. 2 Removed	0.000	0.002	0.018	0.058	0.152	0.036
Sp. 3 Removed	0.000	0.007	0.012	0.130	0.249	0.073
Sp. 4 Removed	0.000	0.001	0.005	0.022	0.048	0.015
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.000	0.000
Sp. 6 Removed	0.000	0.013	0.033	0.065	0.131	0.044
Sp. 7 Removed	0.000	0.001	0.004	0.023	0.060	0.014
Sp. 8 Removed	0.000	0.037	0.044	0.068	0.116	0.048
Sp. 9 Removed	0.000	0.000	0.002	0.014	0.285	0.046
Sp. 10 Removed	0.000	0.041	0.055	0.200	0.285	0.111
Basal Added	0.005	0.021	0.031	0.158	0.272	0.086
Int. Added	0.001	0.008	0.015	0.024	0.144	0.025
Apex Added	0.000	0.002	0.013	0.019	0.331	0.052

Table 7. Lower Triangle (1)- Removing Sp. 10 and adding a basal species generally produced higher results than the original web, while removing Sp. 2, 4, 5, 7, and 9 produced lower or equivalent values across the board.

Lower (10)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.001	0.122	0.176	0.237	0.380	0.179
Sp. 1 Removed	0.000	0.083	0.148	0.173	0.350	0.137
Sp. 2 Removed	0.000	0.008	0.049	0.160	0.285	0.092
Sp. 3 Removed	0.000	0.042	0.100	0.234	0.288	0.131
Sp. 4 Removed	0.000	0.009	0.020	0.063	0.084	0.034
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.004	0.001
Sp. 6 Removed	0.013	0.045	0.078	0.137	0.265	0.098
Sp. 7 Removed	0.000	0.013	0.035	0.088	0.201	0.062
Sp. 8 Removed	0.000	0.036	0.081	0.103	0.145	0.074
Sp. 9 Removed	0.008	0.016	0.030	0.063	0.315	0.078
Sp. 10 Removed	0.001	0.084	0.135	0.272	0.322	0.161
Basal Added	0.024	0.054	0.118	0.250	0.310	0.145
Int. Added	0.008	0.033	0.071	0.090	0.262	0.072
Apex Added	0.001	0.036	0.069	0.122	0.364	0.100

Table 8. Lower Triangle (10)- Removing Sp. 1, 2, 3, 4, 5, 7, 8, 9, and adding an apex predator all produced lower values than the original web for all values except the minimum. The original web had the largest median and mean values.

Lower (100)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.001	0.132	0.195	0.243	0.381	0.186
Sp. 1 Removed	0.000	0.086	0.160	0.184	0.351	0.142
Sp. 2 Removed	0.000	0.010	0.049	0.167	0.297	0.095
Sp. 3 Removed	0.000	0.044	0.109	0.240	0.293	0.135
Sp. 4 Removed	0.000	0.010	0.020	0.072	0.085	0.035
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.005	0.001
Sp. 6 Removed	0.015	0.047	0.082	0.145	0.275	0.102
Sp. 7 Removed	0.000	0.014	0.038	0.098	0.214	0.067
Sp. 8 Removed	0.000	0.036	0.082	0.107	0.148	0.075
Sp. 9 Removed	0.009	0.018	0.032	0.066	0.316	0.080
Sp. 10 Removed	0.001	0.088	0.140	0.274	0.325	0.164
Basal Added	0.026	0.057	0.129	0.253	0.315	0.148
Int. Added	0.008	0.035	0.074	0.096	0.267	0.076
Apex Added	0.001	0.037	0.073	0.131	0.365	0.104

Table 9. Lower Triangle (100)- Removing Sp. 1, 2, 3, 4, 5, 7, 8, 9, and adding an apex predator all produced lower values than the original web for all values except the minimum. The original web had the largest median and mean values.

Upper (0.1)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.000	0.000	0.017	0.160	0.027
Sp. 1 Removed	0.000	0.003	0.008	0.060	0.177	0.041
Sp. 2 Removed	0.000	0.000	0.000	0.017	0.042	0.010
Sp. 3 Removed	0.000	0.005	0.006	0.016	0.117	0.025
Sp. 4 Removed	0.000	0.000	0.000	0.016	0.020	0.007
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.000	0.000
Sp. 6 Removed	0.000	0.000	0.000	0.030	0.071	0.017
Sp. 7 Removed	0.000	0.000	0.014	0.033	0.151	0.030
Sp. 8 Removed	0.000	0.013	0.023	0.046	0.169	0.042
Sp. 9 Removed	0.000	0.000	0.000	0.000	0.167	0.015
Sp. 10 Removed	0.000	0.000	0.020	0.055	0.156	0.042
Basal Added	0.000	0.004	0.023	0.060	0.143	0.037
Int. Added	0.000	0.000	0.000	0.006	0.228	0.028
Apex Added	0.000	0.000	0.000	0.008	0.096	0.011

Table 10. Upper Triangle (0.1)- Removing Sp. 1, 7, 8, 10, and adding a basal species all produced consistently larger results than the original web.

Upper (1)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.001	0.018	0.114	0.242	0.075
Sp. 1 Removed	0.000	0.021	0.068	0.232	0.295	0.115
Sp. 2 Removed	0.000	0.004	0.026	0.062	0.152	0.043
Sp. 3 Removed	0.007	0.008	0.020	0.129	0.269	0.074
Sp. 4 Removed	0.000	0.004	0.028	0.037	0.069	0.025
Sp. 5 Removed	0.000	0.000	0.000	0.000	0.000	0.000
Sp. 6 Removed	0.000	0.009	0.020	0.044	0.138	0.038
Sp. 7 Removed	0.000	0.006	0.051	0.130	0.287	0.078
Sp. 8 Removed	0.000	0.016	0.063	0.110	0.225	0.075
Sp. 9 Removed	0.000	0.000	0.000	0.016	0.308	0.035
Sp. 10 Removed	0.000	0.000	0.045	0.121	0.253	0.077
Basal Added	0.003	0.024	0.082	0.185	0.289	0.108
Int. Added	0.000	0.000	0.010	0.039	0.335	0.060
Apex Added	0.000	0.003	0.013	0.098	0.247	0.053

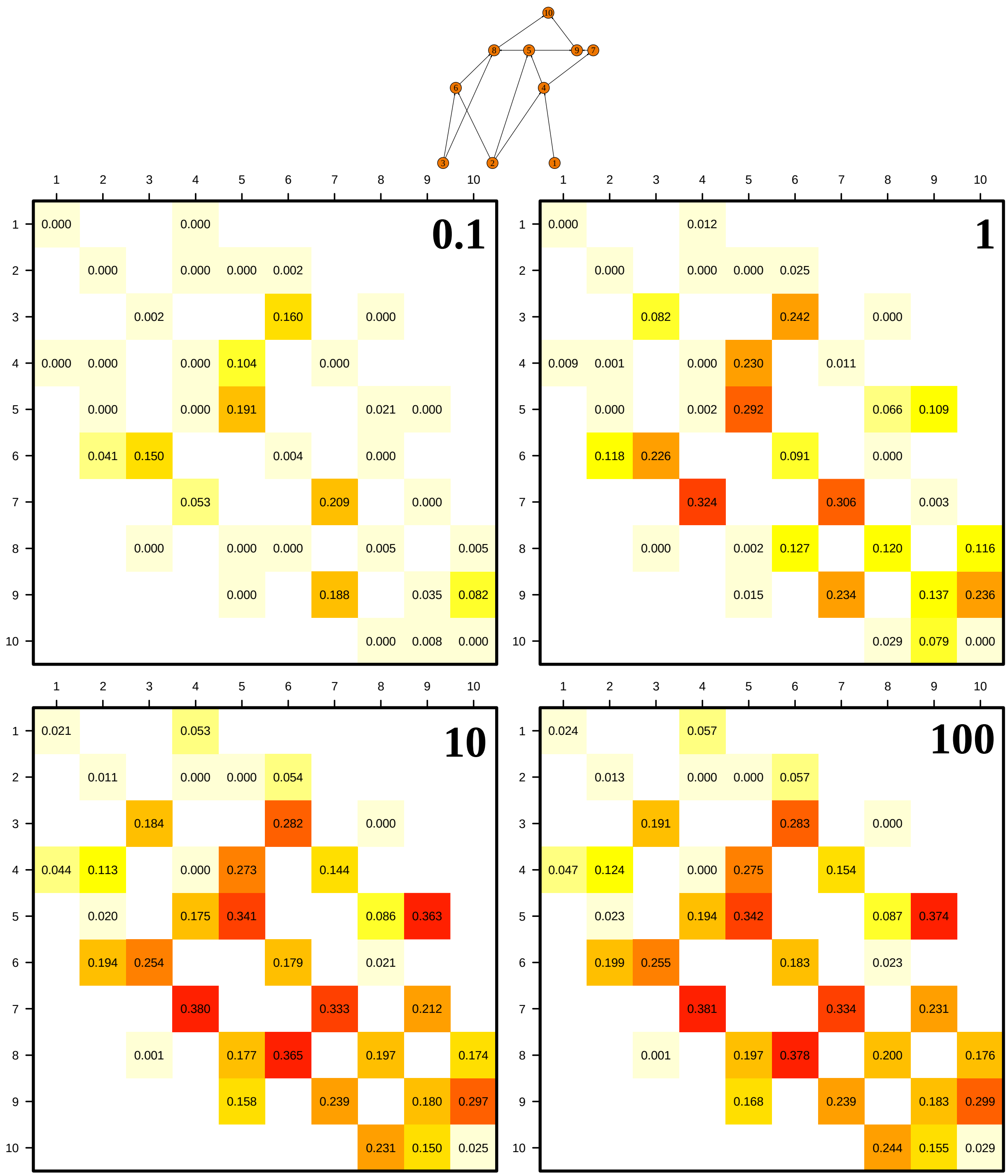
Table 11. Upper Triangle (1)- Removing Sp. 1, 3, and 7, as well as adding a basal species all produced larger or equivalent results for all values than the original web. The opposite was true for removing Sp. 5.

Upper (10)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.029	0.115	0.257	0.363	0.140
Sp. 1 Removed	0.010	0.093	0.204	0.289	0.379	0.189
Sp. 2 Removed	0.001	0.012	0.050	0.179	0.285	0.108
Sp. 3 Removed	0.013	0.031	0.074	0.199	0.316	0.125
Sp. 4 Removed	0.001	0.014	0.031	0.090	0.168	0.053
Sp. 5 Removed	0.000	0.000	0.000	0.002	0.060	0.011
Sp. 6 Removed	0.012	0.026	0.040	0.071	0.275	0.077
Sp. 7 Removed	0.002	0.033	0.100	0.216	0.326	0.130
Sp. 8 Removed	0.000	0.024	0.109	0.157	0.233	0.100
Sp. 9 Removed	0.000	0.006	0.016	0.073	0.355	0.063
Sp. 10 Removed	0.005	0.034	0.089	0.151	0.366	0.117
Basal Added	0.014	0.084	0.143	0.225	0.388	0.162
Int. Added	0.000	0.033	0.060	0.141	0.400	0.107
Apex Added	0.001	0.016	0.061	0.157	0.341	0.096

Table 12. Upper Triangle (10)- Removing Sp. 1 produced larger values across the board than the original, while the same can be said for adding a basal species, third quartile value notwithstanding. Removing Sp. 2, 4, 5, 9, and adding an apex predator all generally produced lower values than the original web.

Upper (100)	Minimum	1st Quartile	Median	3rd Quartile	Maximum	Mean
Original	0.000	0.032	0.120	0.264	0.374	0.144
Sp. 1 Removed	0.010	0.100	0.219	0.301	0.381	0.194
Sp. 2 Removed	0.001	0.015	0.051	0.182	0.297	0.112
Sp. 3 Removed	0.014	0.032	0.084	0.202	0.318	0.128
Sp. 4 Removed	0.001	0.015	0.031	0.091	0.180	0.055
Sp. 5 Removed	0.000	0.000	0.000	0.003	0.066	0.012
Sp. 6 Removed	0.013	0.026	0.042	0.074	0.286	0.080
Sp. 7 Removed	0.002	0.033	0.106	0.223	0.327	0.133
Sp. 8 Removed	0.000	0.024	0.110	0.159	0.233	0.101
Sp. 9 Removed	0.000	0.007	0.018	0.078	0.356	0.065
Sp. 10 Removed	0.005	0.037	0.090	0.158	0.373	0.120
Basal Added	0.016	0.093	0.146	0.228	0.392	0.166
Int. Added	0.000	0.037	0.063	0.146	0.402	0.111
Apex Added	0.001	0.016	0.064	0.161	0.345	0.099

Table 13. Upper Triangle (100)- Removing Sp. 1 produced larger values than the original across the board. The same can be said for adding a basal species, third quartile value notwithstanding. Removing Sp. 2, 4, 5, 9, and adding an apex predator all generally produced lower values than the original web.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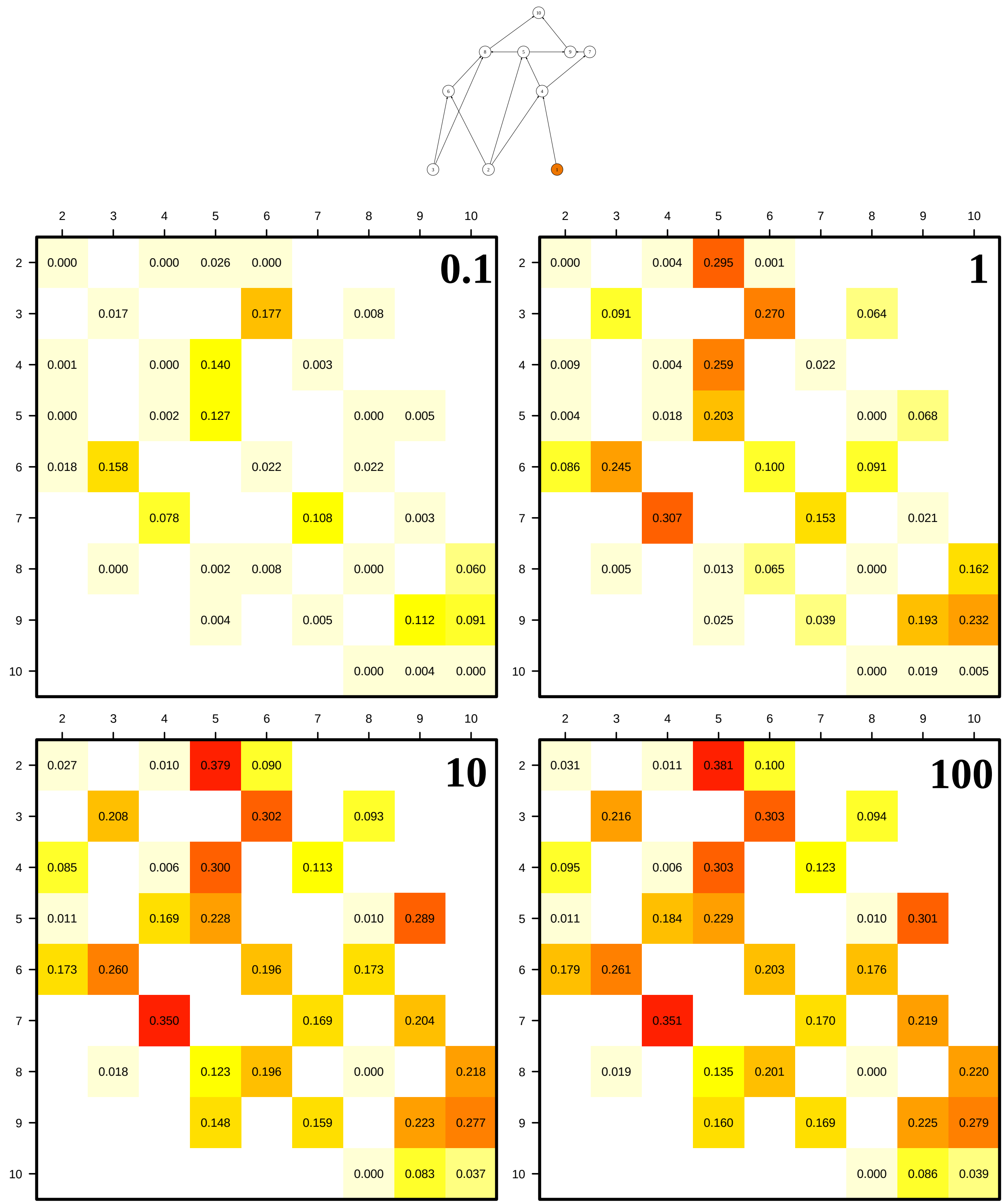
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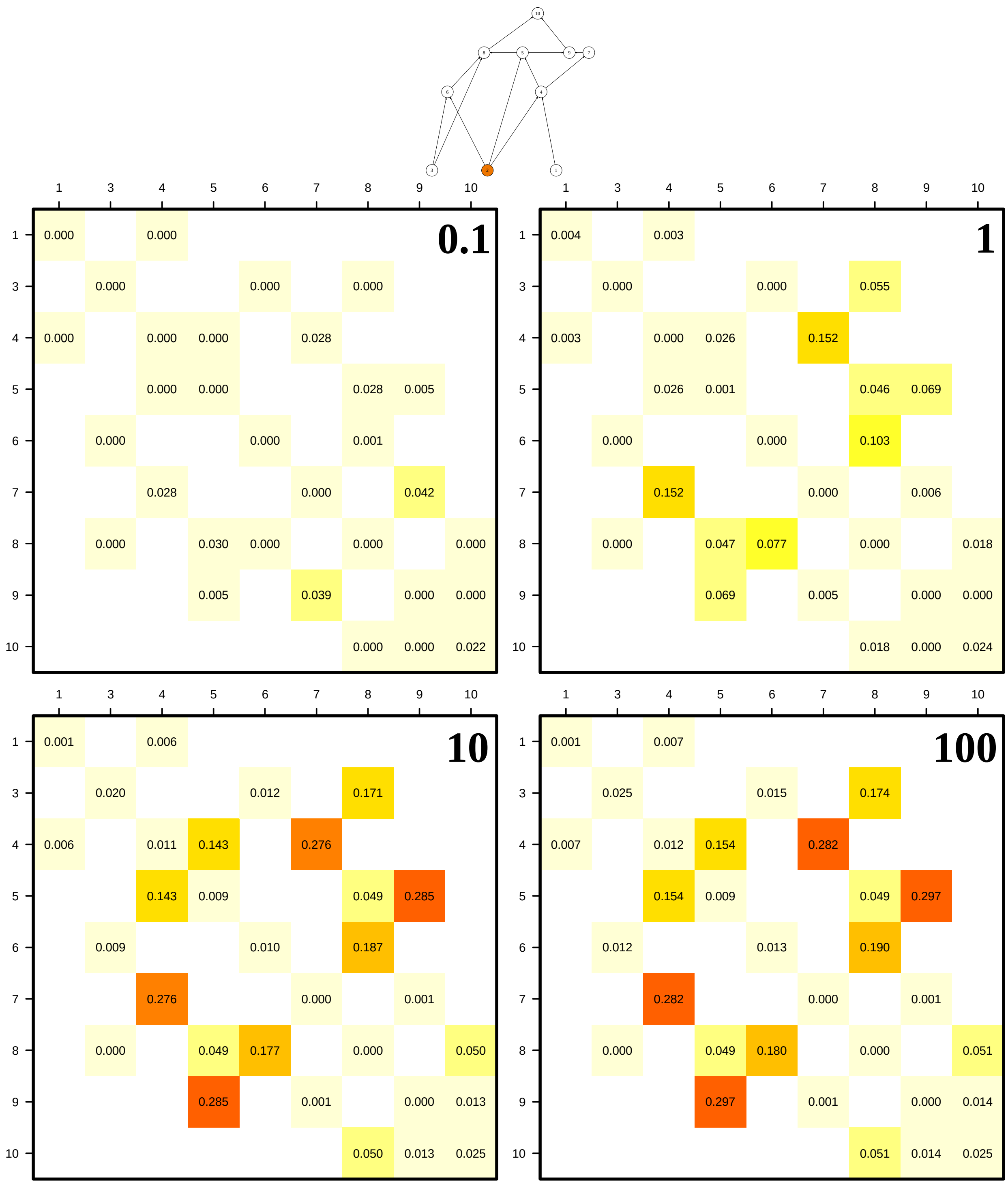
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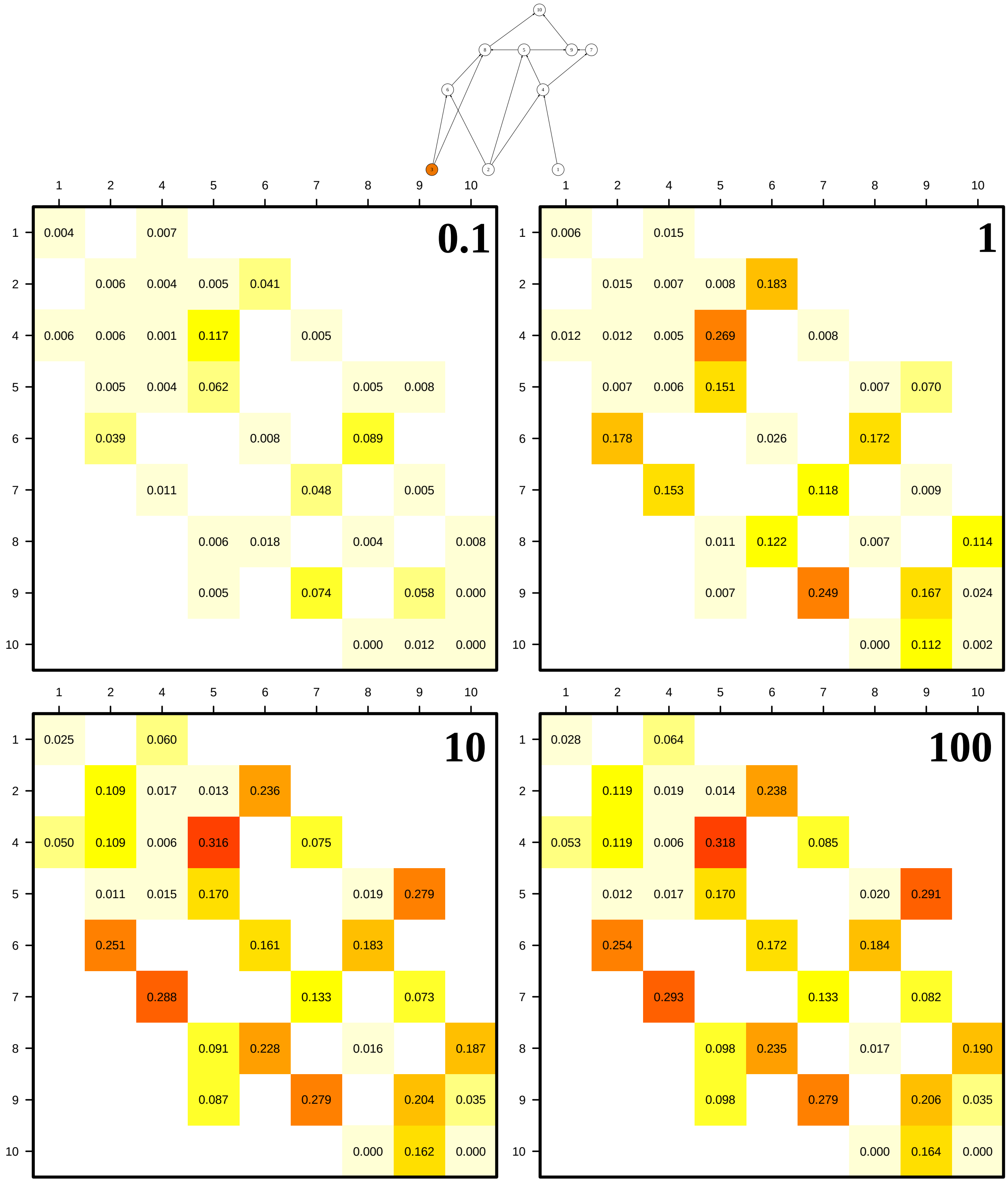
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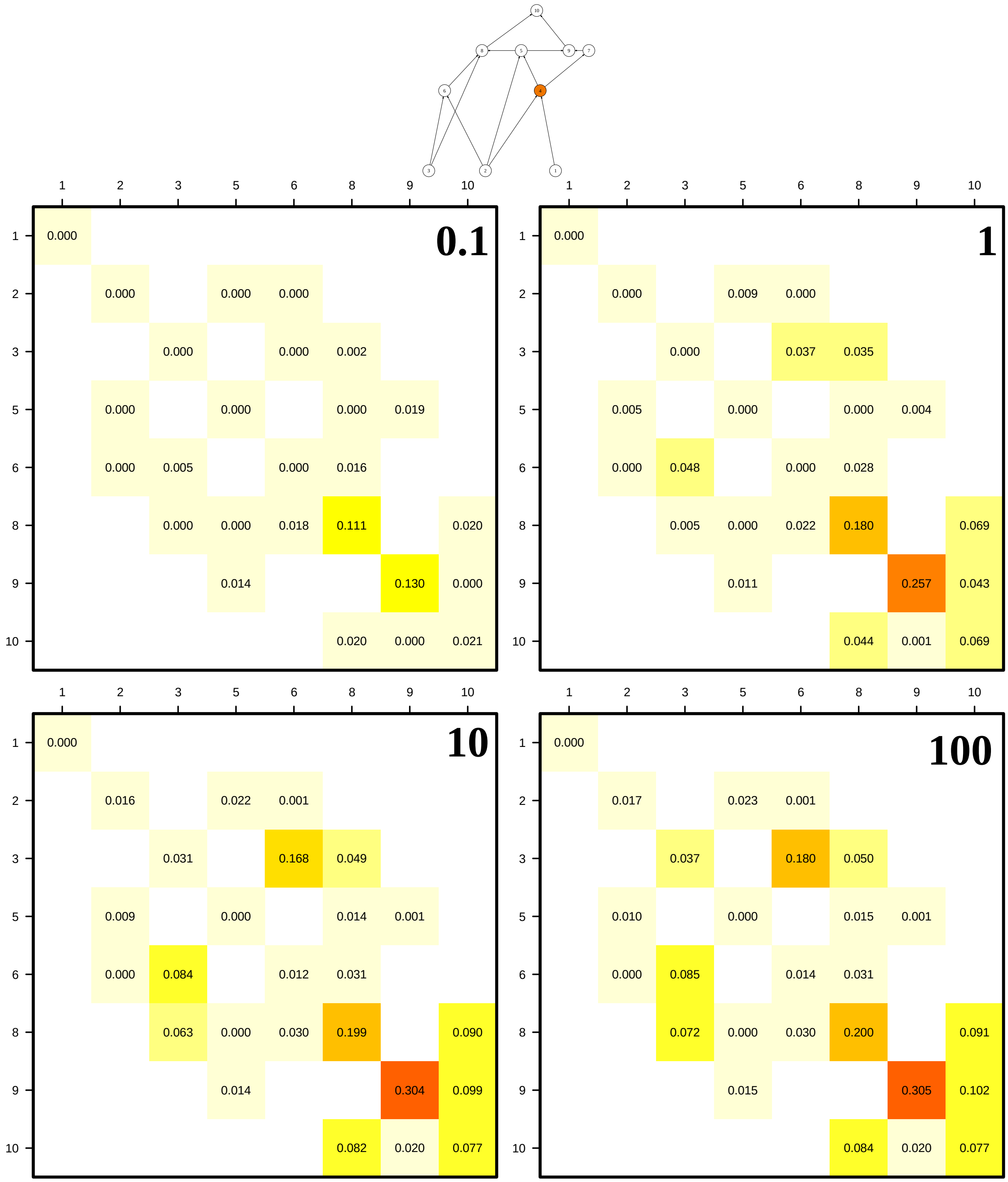
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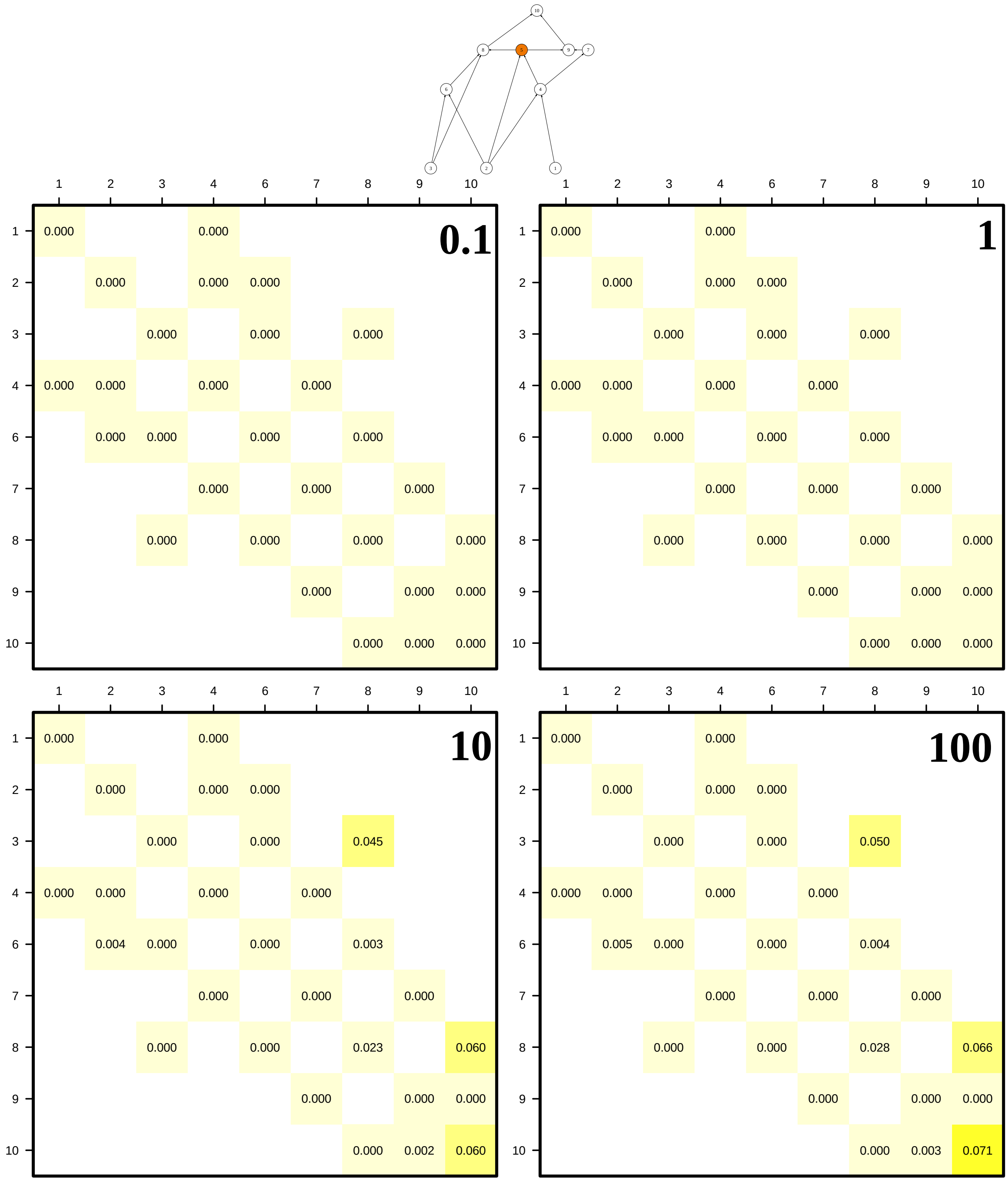
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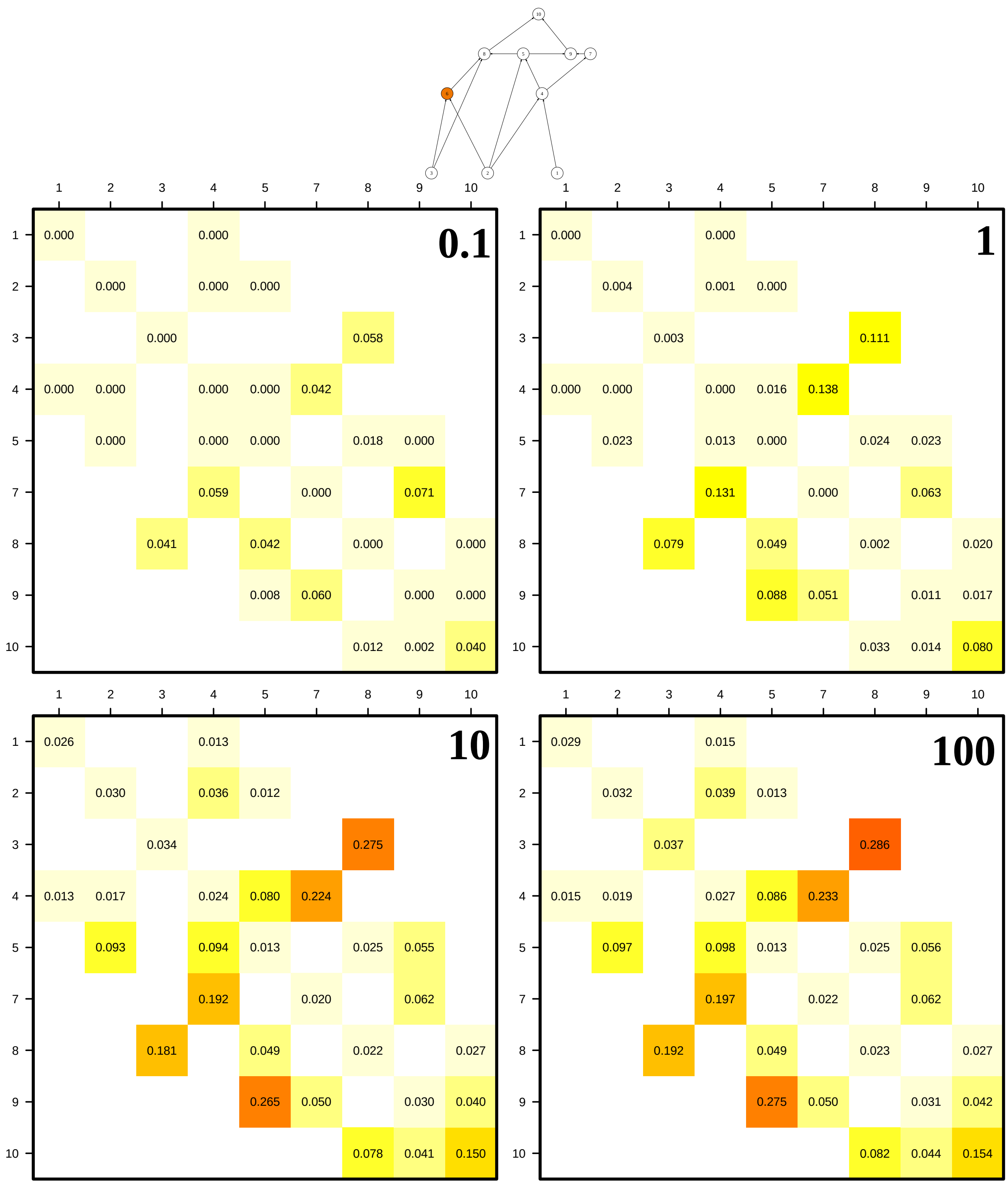
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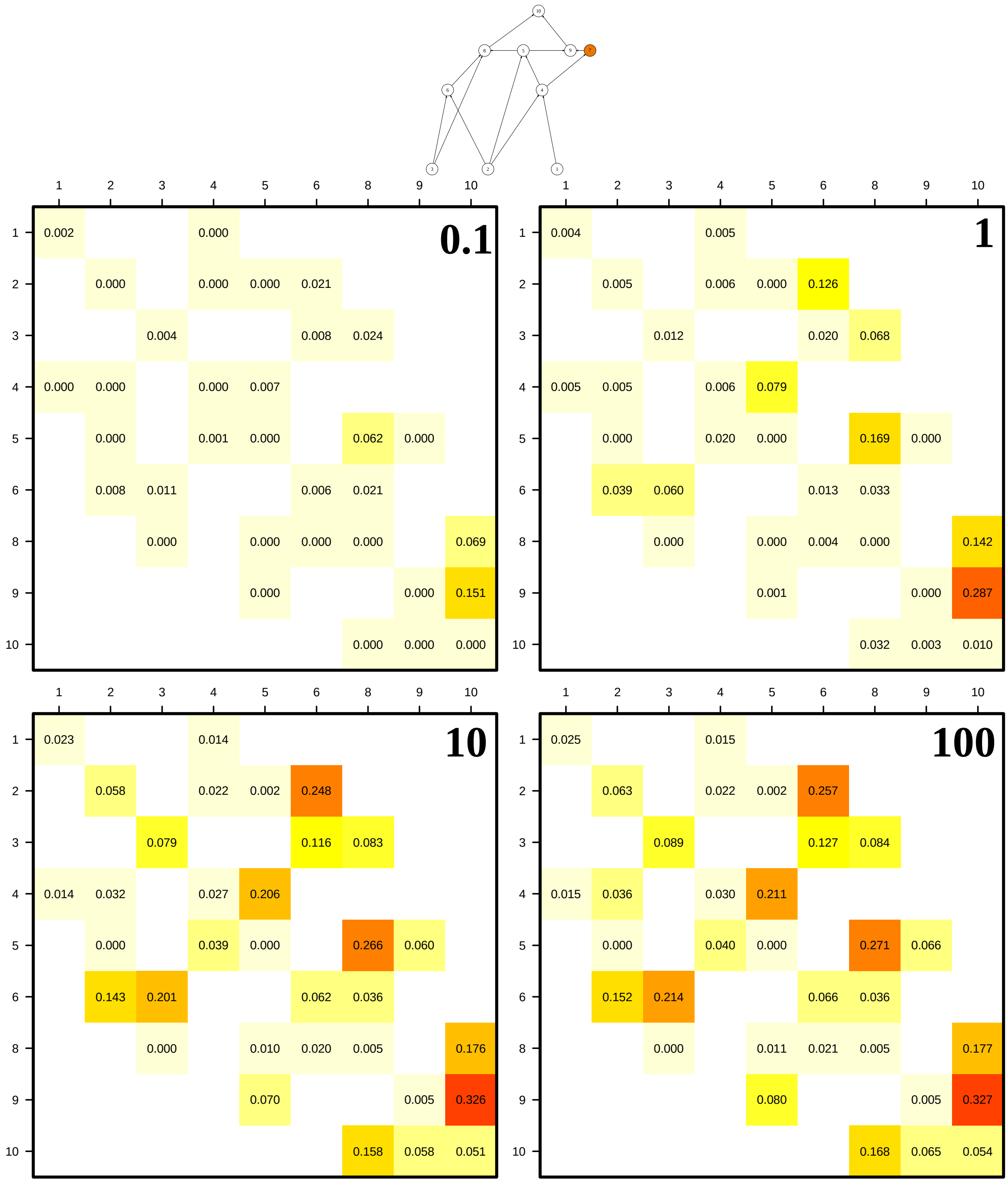

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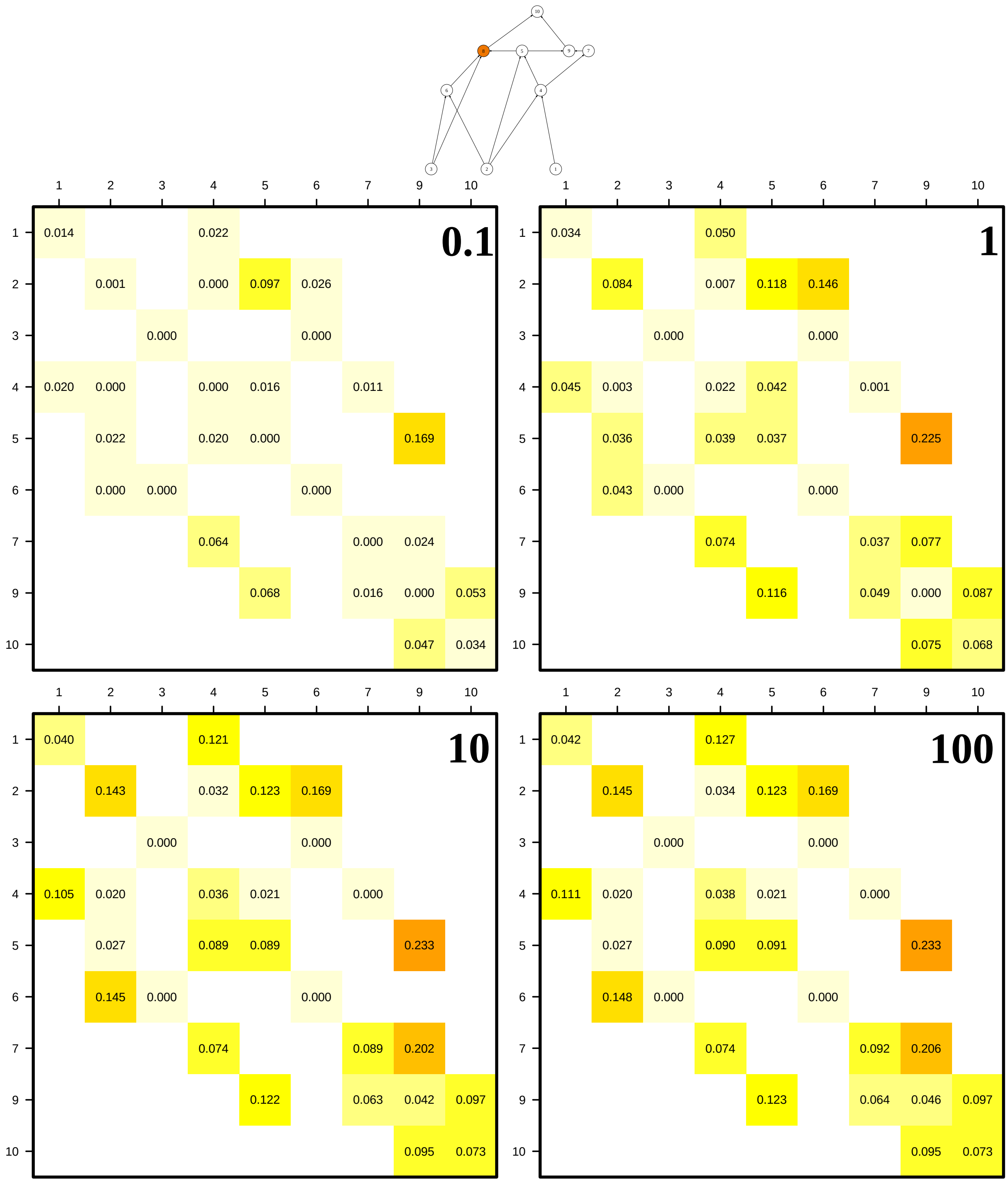
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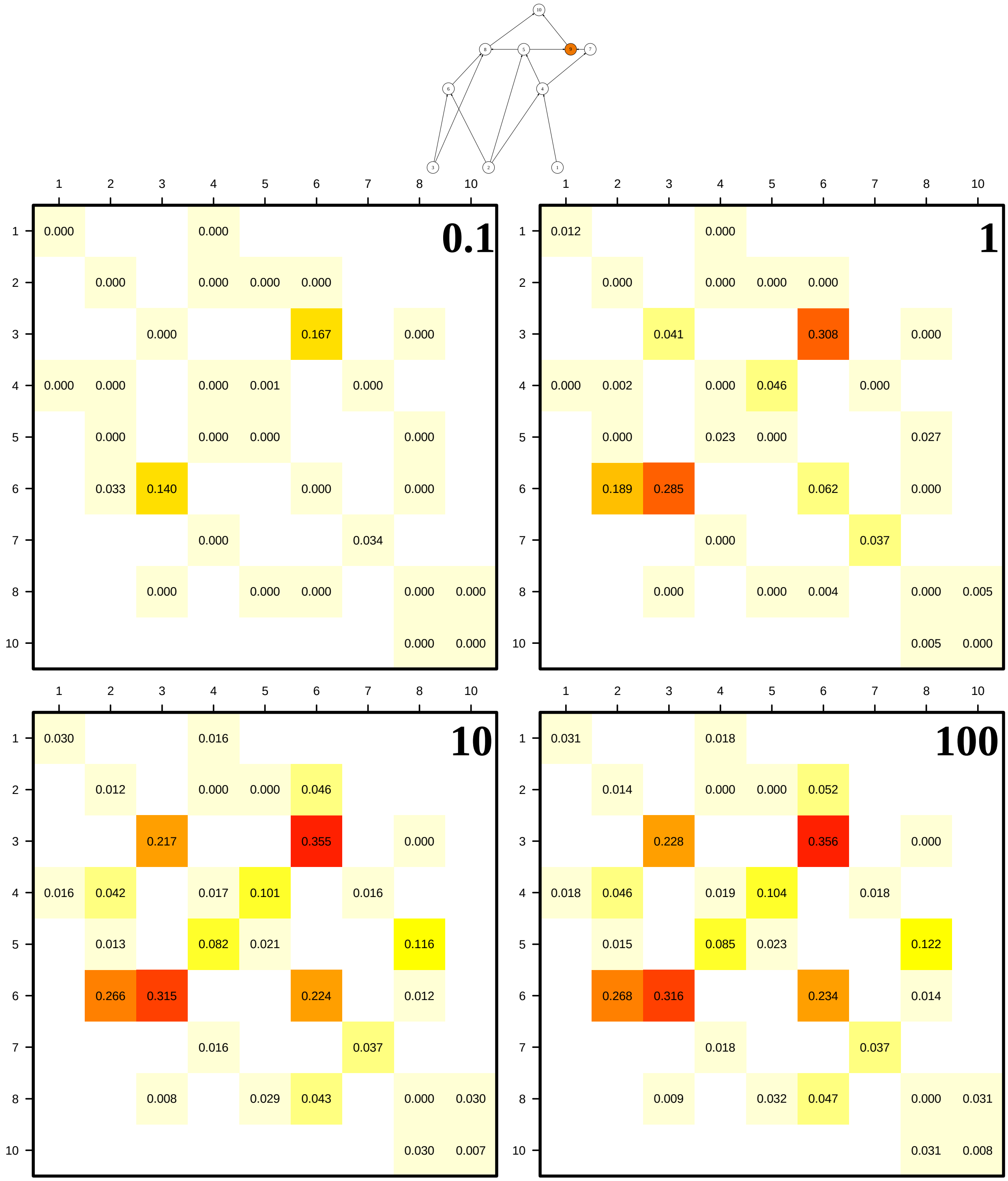
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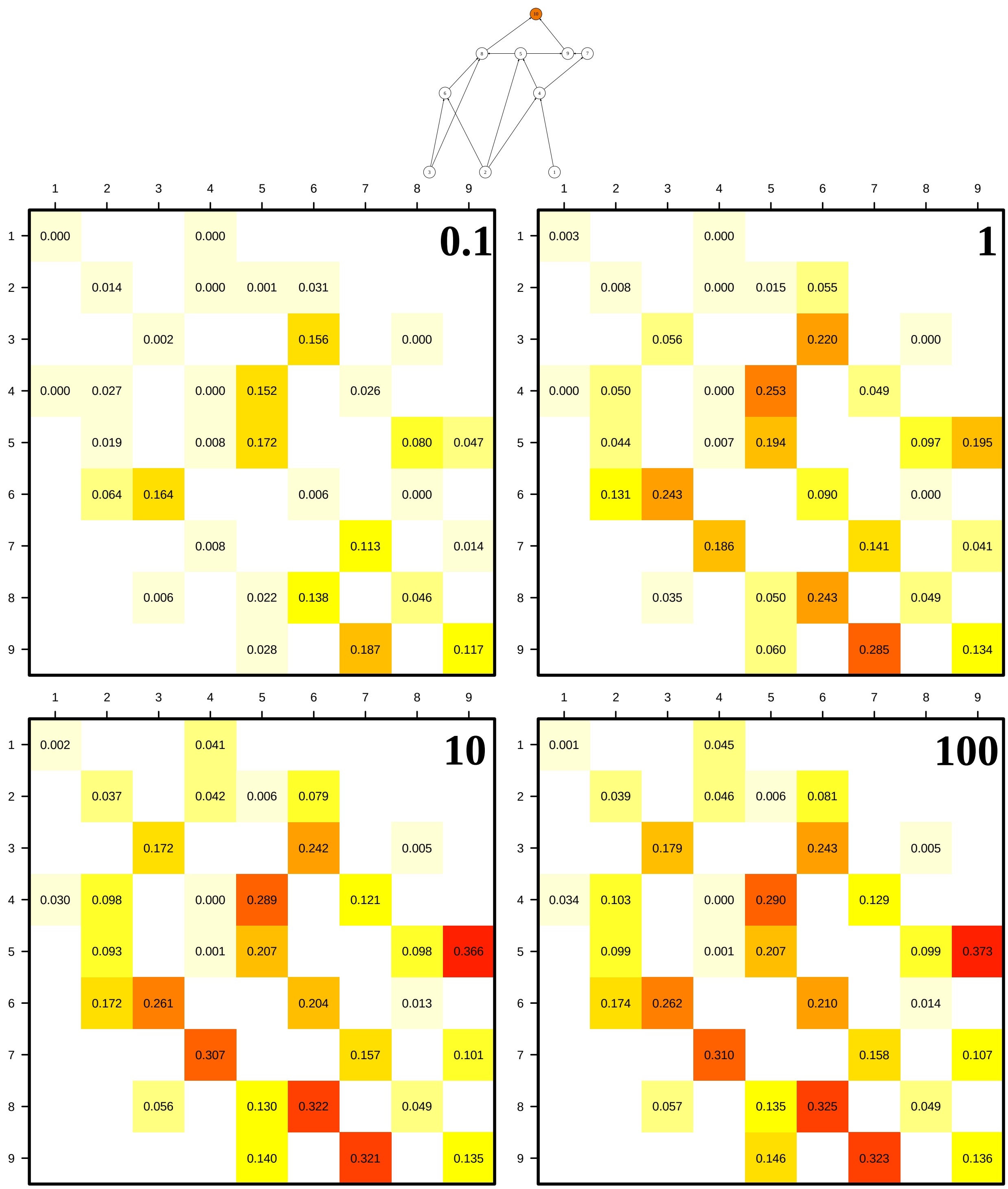
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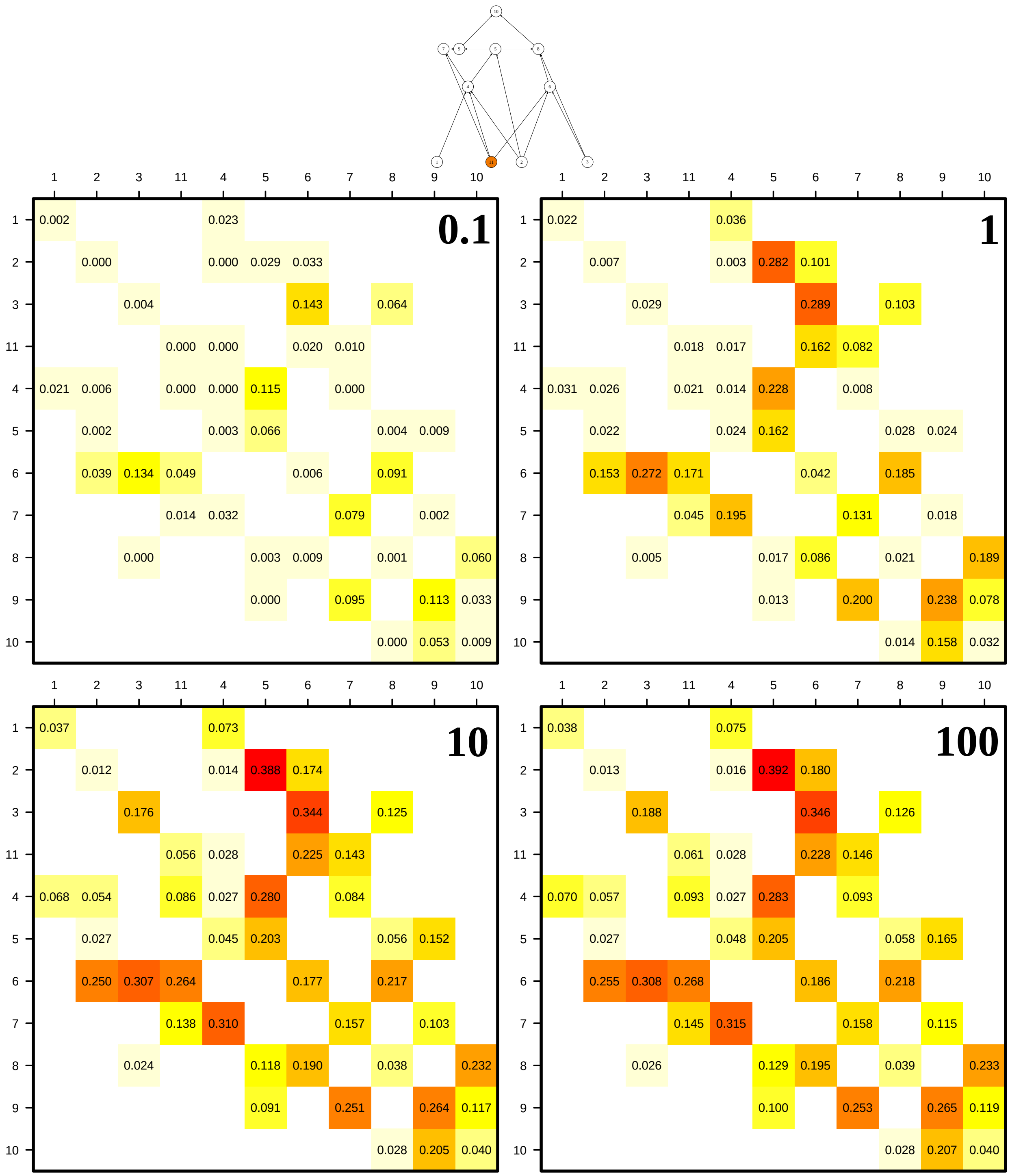
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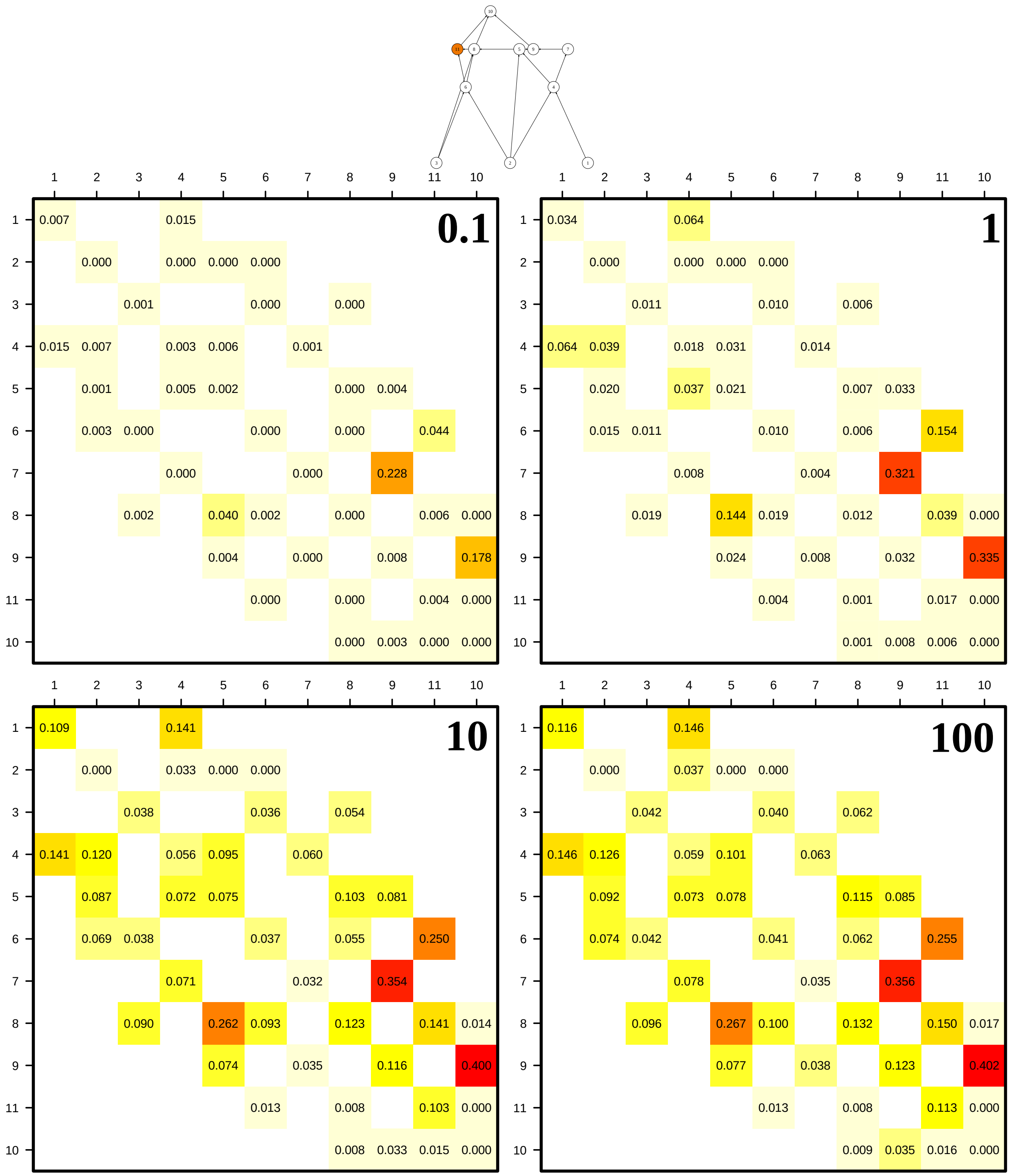
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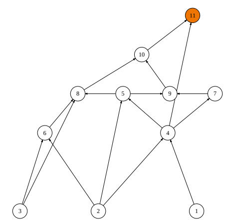
0.078 0.035 0.356
0.096 0.267 0.100 0.132 0.150 0.017
0.077 0.038 0.123 0.402
0.013 0.008 0.113 0.000
0.009 0.035 0.016 0.000



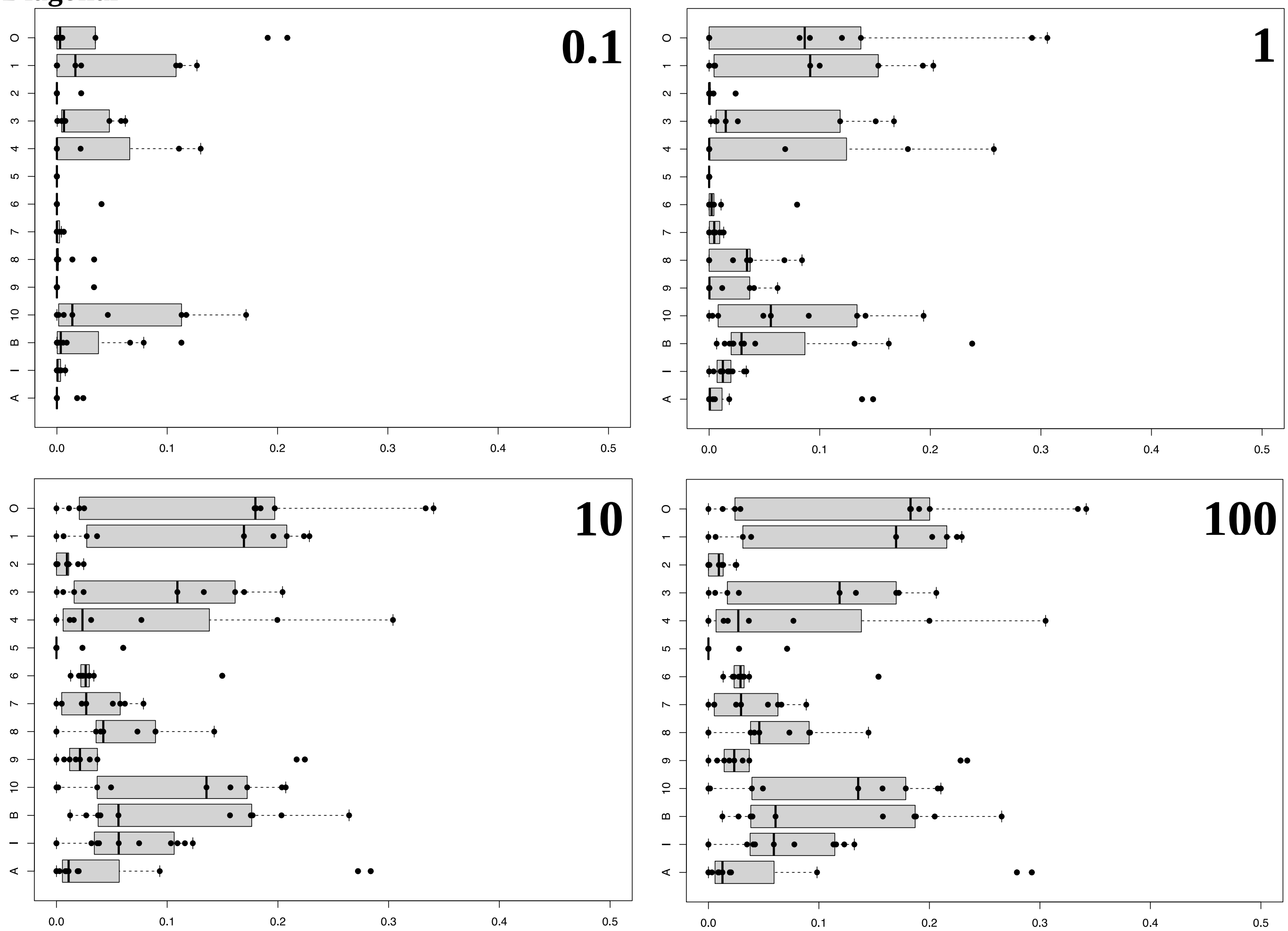
0.1	1	2	3	4	5	6	7	8	9	10	11
1	0.000			0.000							
2		0.000		0.000	0.000	0.012					
3			0.018			0.096		0.000			
4	0.000	0.000		0.000	0.006		0.000				0.000
5		0.000		0.003	0.000			0.003	0.000		
6		0.032	0.222			0.024		0.000			
7				0.000			0.000		0.046		
8			0.000		0.096	0.000		0.000		0.000	
9					0.000		0.000		0.000	0.019	
10								0.000	0.000	0.000	0.000
11				0.000						0.000	0.000

1	1	2	3	4	5	6	7	8	9	10	11
1	0.001			0.002							
2		0.018		0.000	0.008	0.094					
3			0.138			0.247		0.004			
4	0.002	0.004		0.000	0.111		0.005				0.019
5		0.015		0.020	0.005			0.057	0.002		
6		0.145	0.331			0.148		0.018			
7				0.002			0.003		0.110		
8			0.018		0.244	0.015		0.000		0.007	
9					0.017		0.011		0.000	0.165	
10								0.005	0.001	0.000	0.000
11				0.002						0.000	0.000

10	1	2	3	4	5	6	7	8	9	10	11
1	0.009			0.001							
2		0.093		0.012	0.057	0.152					
3			0.284			0.341		0.017			
4	0.001	0.059		0.008	0.198		0.044				0.066
5		0.089		0.043	0.019			0.171	0.028		
6		0.214	0.364			0.272		0.104			
7				0.014			0.020		0.129		
8			0.130		0.282	0.090		0.011		0.005	
9					0.120		0.078		0.003	0.214	
10								0.047	0.012	0.000	0.003
11				0.049						0.004	0.000

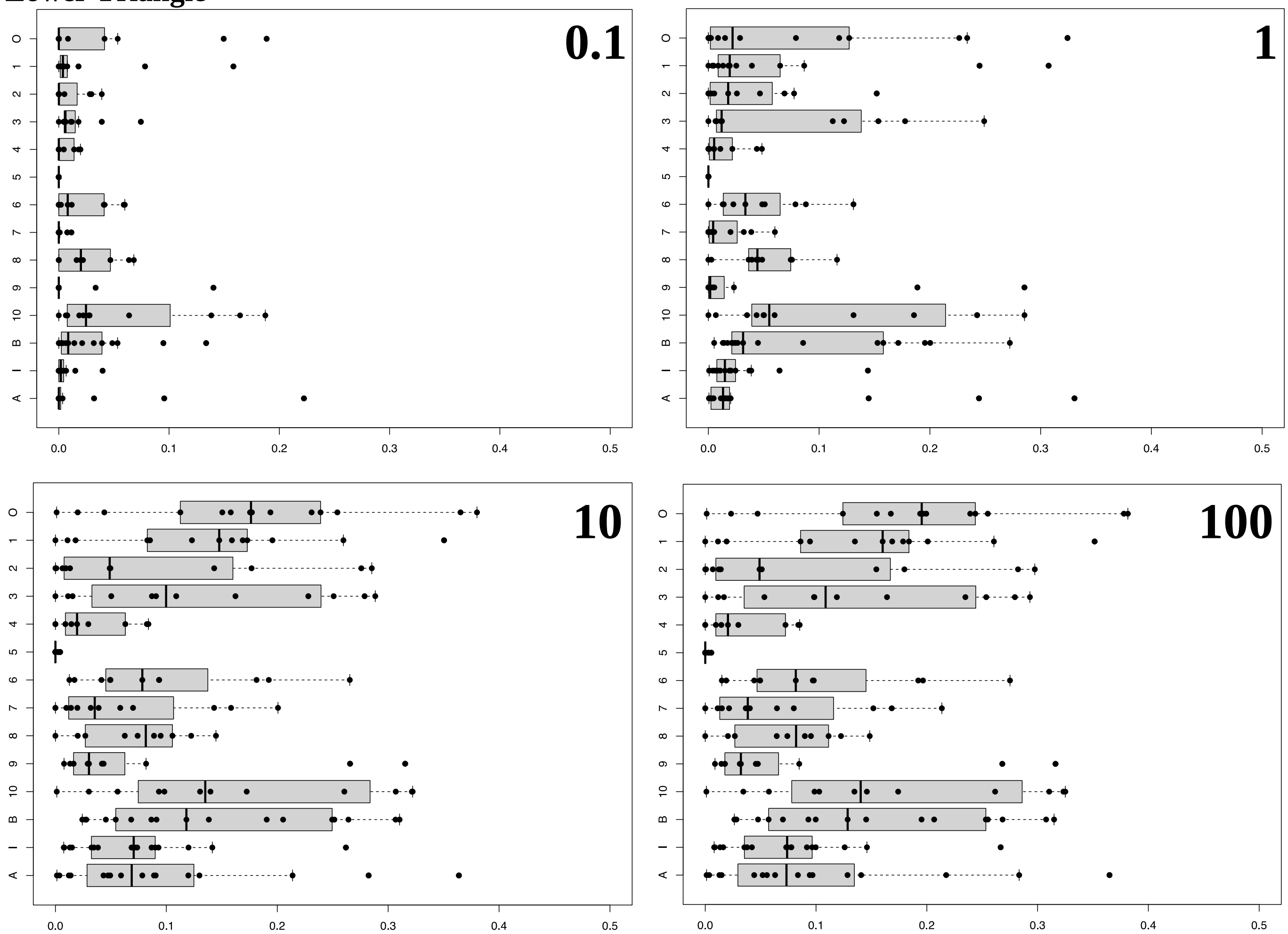
100	1	2	3	4	5	6	7	8	9	10	11
1	0.010			0.001							
2		0.098		0.013	0.060	0.156					
3			0.293			0.345		0.017			
4	0.001	0.063		0.009	0.202		0.046				0.068
5		0.094		0.044	0.019			0.178	0.030		
6		0.217	0.365			0.279		0.111			
7				0.015			0.021		0.129		
8			0.141		0.283	0.097		0.013		0.004	
9					0.128		0.084		0.003	0.215	
10								0.052	0.013	0.000	0.003
11				0.056						0.004	0.000

Diagonal



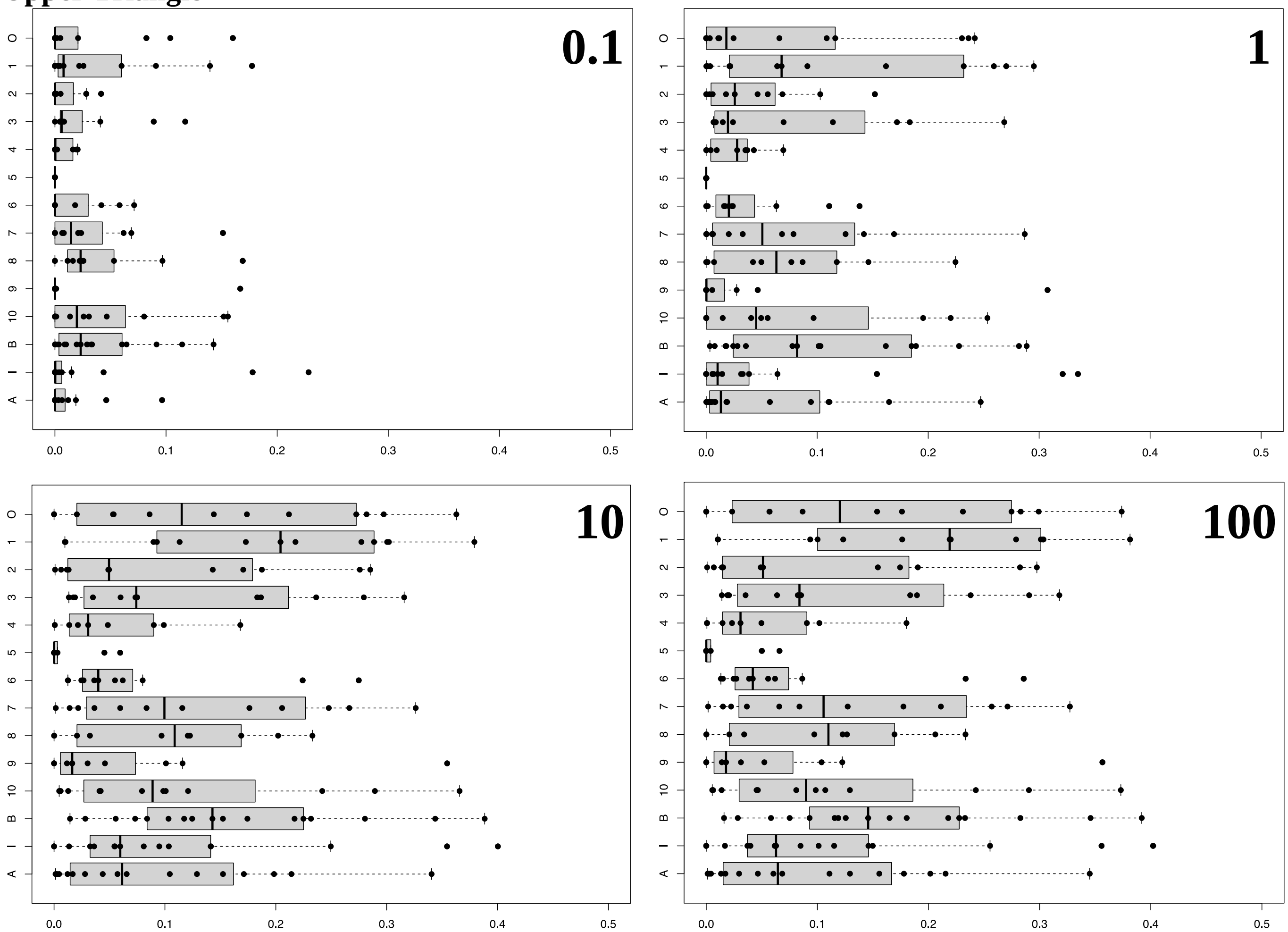
Percent of Mispredicted Responses

Lower Triangle



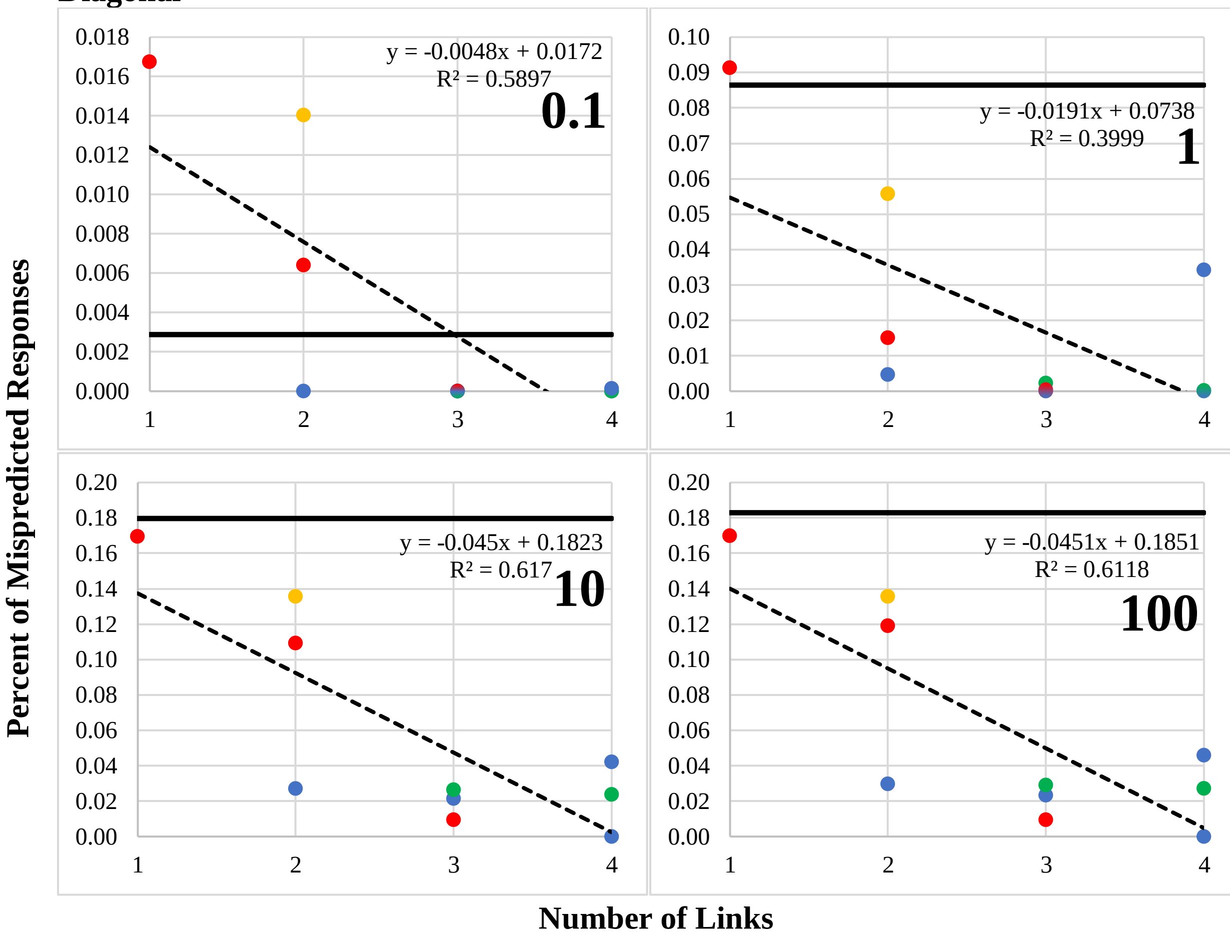
Percent of Mispredicted Responses

Upper Triangle



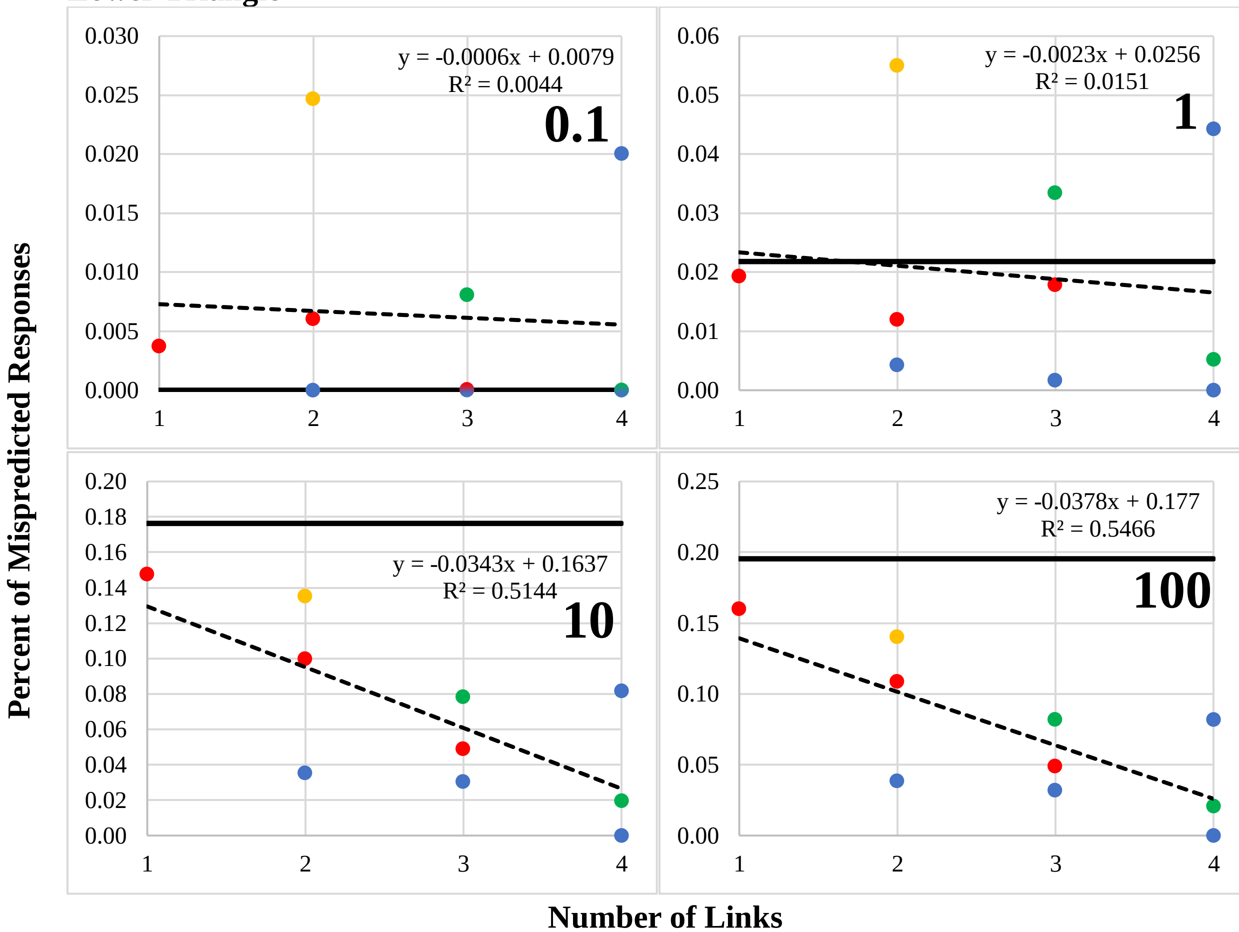
Percent of Mispredicted Responses

Diagonal



y = -0.0048x + 0.0172
R² = 0.5897
0.1
y = -0.0191x + 0.0738
R² = 0.3999
1
y = -0.045x + 0.1823
R² = 0.617
10
y = -0.0451x + 0.1851
R² = 0.6118
100
Percent of Mispredicted Responses
Number of Links

Lower Triangle



Upper Triangle