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Distances Between Species in Food Webs: Evaluating Alternative Metrics' Predictive Power

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Distances between species in food webs: evaluating alternative metrics' predictive power

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Master of Science in Integrative Biology Thesis

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I. ABSTRACT

The complexity of ecological systems makes it difficult to predict how one species will react to the disturbance of another. Complex systems of species' interactions can be described as ecological networks. One way in which ecological networks can give information concerning one species' response to the perturbation of another is through the quantification of species' proximity to one another in the network. In this study, we evaluate communicability, a topological metric that accounts for all of the direct and indirect interactions between species in a food web without additional information concerning the strengths of species interactions. Communicability is then compared to shortest path distance, a metric only containing information about the shortest path between two species. We found that communicability outperformed shortest path distance in 89% of the significant model treatments (91% were significant) when analyzed using polynomial regression and in 75% of the significant model treatments when analyzed using the linear regression of natural logarithm transformed metric data (58% were significant). Yet, when comparing the effects of varying structural model properties, we found conflicting results between polynomial and linear analysis. Consequently, we were able to conclude that because communicability accounts for the totality of effects based on link structure between two species, it is a better predictor of how a species will respond to a perturbation. However, because of conflicting results in some of our statistical analyses, it is unclear what roles structural network properties play in communicability's predictive abilities.

II. INTRODUCTION

II. 1. Overview

Loss of species and the resulting decline of biodiversity is currently posing a severe threat to ecological communities (Riede et al. 2011), making it increasingly necessary to understand how species' respond to perturbations such as extinctions. It has been a longstanding goal for ecologists to forecast the effects of disturbances caused by the loss of biodiversity on ecological systems in order to aid in conservation efforts and to prevent further species declines from cascading effects (Bodini et al. 2009; Riede et al. 2011). In complex communities, predicting how one species will respond to the perturbation of another is important but challenging because ecological systems are made up of a myriad of interacting components. Some studies have even suggested that this intricacy in realistic communities makes such predictions impossible (Yodzis 1988; Yodzis 2000; Berlow et al. 2009). This complexity presents an additional challenge when it comes to fully understanding conservation problems such as controlling agricultural pests in an environmentally friendly manner, understanding the impacts of over-harvesting a species, or preserving threatened or endangered species.

This study aims to evaluate what role proximity, or the closeness between a pair of species, plays in one species' sensitivity to the perturbation of another species. The objective of this study is to compare two measures of species proximity to determine which one better predicts a species' response to a perturbation in ecological systems. This could improve ecologists' abilities to obtain meaningful information regarding a food web's response to a perturbation using purely information on web topology (structure) even when information on interaction strength is not available. But first, it will be necessary to review a few background topics in depth, including: indirect effects, networks, proximity metrics, and species proximity.

II.2. Indirect Effects

Previous research has shown that most species in a food web are highly connected, suggesting that perturbations have the ability to rapidly percolate through a community (Williams et al. 2002; Byrnes et al. 2007; Dunne 2009). Species in food webs may interact directly or indirectly via a sequence of intervening species interactions (Borrett et al. 2007). Indirect effects play a significant role in generating the structural complexity of species interactions, often being crucial determinants of how a disturbance will affect an ecological community (Montoya et al. 2009).

Trophic cascades are a type of density-mediated indirect effect that are widely observed in nature and are relatively well-studied. In the United States, due to the lack of effective predation, over-grazing by ungulates, such as white-tailed deer and elk, has caused significant disturbances to the local vegetation (Miller et al. 1992; Ripple and Larson 2000; Soulé et al. 2003). Because of this ecological degradation of the plant community, an extensive amount of vegetation has been lost in riparian habitats, removing valuable habitats for beavers (*Castor canadensis*) and also inhibiting the recruitment of new shrub and tree species, which has negatively impacted the songbird population (Ripple and Larson 2000; Soulé et al. 2002). These examples emphasize the prevalence of indirect effects initiated from a trophic cascade and they highlight the importance of transient effects and community network structure in developing better management practices for ecosystems (Estes et al. 1998; Myers et al. 2007).

Several studies have confirmed the importance of indirect effects (Yodzis 1988; Higashi and Patten 1989; Wootton 1992, 1993; Menge 1995; Wootton 2002; Dambacher and Ramos-Jiliberto 2007; Ma and Kazanci 2012; Burns et al. 2014). However, details regarding indirect effects' role in response to perturbations remain lacking. This is partly because indirect effects cause a great deal of complexity, most empirical studies only consider indirect effects from close species (Abrams et al. 1996; Hairston and Hairston 1993; Caldarelli et al. 1998; Post et al. 2000; Barton and Ives 2014).

II. 3. Ecological Networks

II.3.a. General Contribution

Food webs provide a description of species interactions in a community, and valuable insights have been gained by evaluating food webs using a network perspective. A network perspective allows for the quantification of various aspects of the way a complex system is structurally organized, so that the effects, significance and implications of that organization can be studied. Some recent studies have used ecological network structure in order to characterize a species' importance in a food web, aiding in the identification of keystone species (Jordán et al. 2002; Jordán et al. 2006; Jordán et al. 2007; Jordán 2009; Estrada 2007; Torres-Alruiz and Rodríguez 2013). Other studies have used network structure to gain information concerning whole-web properties such as modularity and robustness (Dunne et al. 2002; Curtsdotter et al. 2011; Stouffer and Bascompte 2011). However, there has been a relative lack of focus on pairwise relationships between species.

II.3.b. Necessary Terminology

Networks are represented mathematically as graphs, and we now introduce some terminology needed for the discussion of graph structure. A graph $G = (V, E)$ is a pair of sets where V is the node set (each node will represent a species) and E is the link set (each link corresponds to an interaction between some pair of species) (Estrada and Hatano 2008). For a network with n nodes, an adjacency matrix ($\boldsymbol{A}_{nxn} = A_{ij}$) represents the structural information of a network, with elements A_{ij} denoted as ones or zeros depending on whether the nodes i and j are adjacent or not.

Node degree is the number of links in which a node participates. A *walk* between two nodes, say *p* and *q*, is an alternating sequence of nodes and corresponding links that starts at *p* and ends at *q*. The links and nodes comprising a walk do not have to be distinct (Estrada 2007). A *path* is a walk in which the nodes (and thus links) must be distinct (Estrada 2007). Following Borrett et al. (2006), we will refer to both paths and walks as *pathways*, because we will generally not need to distinguish between the two. The *length* of a walk, path, or pathway equals the number of links that the walk, path, or pathway contains. The shortest walk between two nodes is any walk whose length is less than or equal to the length of any other walk between those nodes. It is routine to see that a shortest walk between two nodes must be a path, and so we refer to such a walk as the "*shortest path*" between nodes. Graphs can vary in complexity, and thus in the amount of knowledge about the system required to construct them. Graphs may be *directed* or *undirected*, and *weighted* or *unweighted* (Ponstein 1966; Bang-Jenson and Gutin 2001; Borrett et al. 2007). A directed network is specified by a set of nodes with oriented links, while an undirected network contains a set of nodes with unoriented links. Information can travel in either direction along a given link in an undirected network but only in one direction on any given link in a directed network. An ecological example of an undirected relationship between two species would be species *A* consuming species *B* with the effects of this direct relationship impacting both species (Dunne 2009). Links can also be given weights to represent the strength or magnitude of the relationship that link represents. However, information regarding interaction strength in real systems is often difficult to obtain (Menge 1997). A network without weights is termed unweighted, and only contains information on the presence or absence of the relationship represented by each link.

In this study we will be focusing on only unweighted and undirected networks. We will also be quantifying the proximity of pairs of species in an ecological network. Proximity of nodes (species) are most often measured by the *shortest path distance* (*SPD*) (Williams et al. 2002), which equals the length of a shortest path between the nodes if at least one path between them exists, and is defined to be infinity if no path between them exists (Caldarelli et al. 1998; Post et al. 2000). In general, SPD is a standard measure in network analysis and there are many alternate algorithms for calculating it (Zahn and Noon 1998; Gallo and Pallottino 1988; Mondou et al. 1991; Cherkassky et al. 1993). However, proximities between species can also be quantified using the metric of *communicability*, which accounts for the totality of pathways between a pair of species. As communicability is more complex and less often used than SPD, we will explain it in further detail in the following section.

II. 3.c. Communicability

Communicability is a topological metric, considering only the link structure of a network and accounting for all possible pathways between two nodes (Estrada et al. 2012). When comparing the two metrics of communicability and SPD, it should be noted that while a high value in communicability implies a greater "coupling" between nodes, a high value in SPD indicates less coupling. Figure 1 depicts an example of an unweighted, undirected network. Here, the shortest path from node 1 to node 4 is one. Yet, longer pathways (i.e. walks) exist, such as: 1→2→3→4 or 1→2→1→4. Through these additional walks between 1 and 4, there is an increased potential for node 1 to influence node 4 because there are more ways for effects to be transmitted. Extra walks, both long and short, between nodes will be expected to increase how coupled they are, making them more responsive, or sensitive, to one another and increasing their communicability. However, longer and shorter walks are not treated equally. Communicability is defined between a pair of nodes by assigning larger weights to shorter walks and smaller weights to longer walks. The *communicability* between two nodes p and q, denoted by $G_{p,q}$, is defined as:

$$G_{p,q} = \sum_{k=1}^{\infty} C_k W_{p,q}^{(k)} \qquad (1).$$

C_k is equal to $\frac{1}{k!}$ and $W_{p,q}^{(k)}$ is the number of walks of length k from p and q. This can be expressed as, $W_{p,q}^{(k)} = A^k[p,q]$ where A is the adjacency matrix of the graph so that

$$G_{p,q} = \sum_{k=1}^{\infty} C_k W_{p,q}^{(k)} = \sum_{k=1}^{\infty} \frac{A^k[p,q]}{k!} = (e^A)_{p,q} \qquad (2).$$

Therefore, the communicability between p and q is the corresponding entry in the matrix exponential function, e^A. It is well known that this function converges for all square matrices A. There are numerous approaches to efficiently computing e^A numerically but we will not discuss that here. The shortest walk(s) between two nodes will always contribute the most to communicability, but longer walks have some contribution as well (Estrada and Hatano 2008). We can calculate the communicability between species 1 and 4 in Figure 1 here:

$$G_{1,4} = \sum_{k=1}^{\infty} C_k W_{1,4}^{(k)} = C_l P_{1,4} + \sum_{k>l} C_k W_{1,4}^{(k)} \qquad (3)$$

Where l is the length of the shortest path between 1 and 4 ($C_l = 1$), $P_{1,4} = W_{1,4}^{(l)}$ and is the number of shortest paths. C_k is equal to $\frac{1}{k!}$, k is some longer walk length, and $W_{1,4}^{(k)}$ is the number of walks of length k between 1 and 4.

In Figure 1, the shortest path from 1 to 4 is one. There are no walks of even length because of the network structure, but there are an infinite number of walks of odd length. For example, there are four walks of length three: (1→2→3→4), (1→2→1→4), (1→4→1→4), and

(1→4→3→4). Likewise, there will be sixteen walks of length five, sixty-four walks of length seven, and so on. These four values can then be plugged into equation 5:

$$G_{1,4} \approx \left(\frac{1}{1!}\right) * 1 + \left(\frac{1}{3!}\right) * 4 + \left(\frac{1}{5!}\right) * 16 + \left(\frac{1}{7!}\right) * 64 \approx 1.8127 \qquad (5)$$

Continuing to add terms to this equation for longer walks will ultimately lead to the communicability in the right-hand side of this equation equaling the communicability found between 1 and 4 in Table 3. Since this is such a small and simple network, the communicability value in equation 5 is already approaching the communicability given in Table 1. Table 1 compares the communicability and SPD of Figure 1. Again, since this is a very simple network, there are only two possible scores for either SPD (1 or 2) or communicability (1.81 or 1.38). The scores in this network for SPD might suggest that the responsiveness between nodes 1 and 4 is twice that of nodes 1 and 3. However, communicability would suggest the responsiveness of nodes 1 and 4 to be 1.3 times greater than species 1 and 3. Furthermore, as webs become larger and more complex, there will be more variety in the relative scores of both communicability and SPD across pairs of nodes.

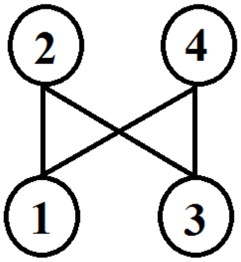

Figure 1: A simple network with nodes.

Table 1: Two matrices comparing the approximate communicability and exact SPD of the small network in Figure 1. For example, the SPD between nodes two and four is 2, while the communicability is approximately 1.381098. A high value for communicability suggests two nodes are more responsive to one another, while a high value for SPD implies less responsive node pairs.

COMMUNICABILITY

SPECIES	**1**	**2**	**3**	**4**
1	-	-	-	-
2	1.81343	-	-	-
3	1.381098	1.81343	-	-
4	1.81343	1.381098	1.81343	-

SPD

SPECIES	**1**	**2**	**3**	**4**
1	0	-	-	-
2	1	0	-	-
3	2	1	0	-
4	1	2	1	0

II.3.d. Species' Proximities in Ecological Networks

Several other studies have evaluated how close species are to one another. The proximity of two species helps to indicate to what extent one species is expected to be affected by the other. Burns et al. (2014) sought to quantify all the direct and indirect paths between a pair of species in a food web in order to evaluate the importance of indirect interactions in transmitting the effects of a perturbation between species. This study relates to ours in that it evaluates pairwise interactions and measures response to pulse perturbations at equilibrium which incorporate all the pathways between species. However, it differs from our study in that they did not specifically test whether dynamic responses seen in their simulations were related to any topological metric, and their models used weighted networks which require information concerning the interaction strengths between species. Berlow et al. (2009) also used dynamic models to assess the equilibrium response of one species to the removal of another in an ecological network. They applied a more topological approach using the shortest path distance between species and found that as degrees of separation between species increased, species were less affected by the removal of the focal species. This agrees with earlier works evaluating the propagation of effects in an ecological system (Strong 1992, Menge 1995). Salas and Borrett (2011) use a directed network modeling the flow of energy between nodes to quantify and compare the overall magnitudes of direct and indirect effects between species. They found that indirect effects were as important as direct effects and even dominated direct flows in the majority of their models. These studies' goals align in many aspects to ours, such as accounting for pathways between species in a pairwise relationship.

II.4. General Approach and Questions

In this study, we constructed dynamic simulation models, which we subjected to perturbations. We compared the relative performance of two topological metrics—communicability and SPD—in predicting species' responses to perturbations of one another. We also specifically looked at a few comparisons between specific web structure treatments that we hypothesized might affect the relative performance of each metric.

We compared treatments varying in node degree, or the number of links in which a node participates. Increased node degree not only added longer pathways between nodes, but it also increased the number of short pathways between two nodes. Since communicability accounts for these additional interactions, we hypothesized that increased node degree would improve communicability's predictive power relative to SPD's.

We hypothesized that model treatments containing node degree heterogeneity would also increase communicability's predictive power relative to SPD's. Node degree heterogeneity increases the chance that some pairs of nodes will be connected by many pathways while other pairs of nodes are connected by a sparse number of pathways. This increased connection between a pair of species would be expected to affect the communicability between nodes, but not the SPD.

Treatments with heterogeneity or “noise” in the interaction strength (magnitude) between nodes would cause some pathways between nodes to be stronger than others, affecting the propagation of effects. In this case, nodes with sparse connections should be more sensitive to variability in pathway magnitude than that of node pairs connected by many pathways. This is because when there are multiple pathways between nodes, there should be more opportunity for variability to cancel out—some pathways would be expected to be stronger than average, while others would be expected to be weaker than average. Moreover, since the difference between “sparsely connected” and “richly connected” pairs of nodes is not reflected in SPD, noise in interaction magnitudes might be expected to improve the relative performance of communicability. For these reasons, we hypothesized communicability would outperform SPD in treatments including noise in interaction strengths.

Lastly, we compared treatments with either a type I or type II functional response. Type I function responses were used in order to prevent time lags. In other treatments, type II functional responses allowed for these time lags and consequently made the system more reactive and increased the potential for effects to propagate throughout a network. We hypothesized that this would increase communicability’s predictive power because communicability would reflect the longer pathways through which stronger effects would be more able to propagate in a type II model. Increased propagation of effects would also make multiple short paths between two nodes have more influence, consequently increasing the relative responsiveness between richly connected nodes relative to sparsely connected nodes and further increasing communicability’s relative predictive power.

III. METHODS

III.1. Dynamic Models

Community dynamics of all the ecological networks were simulated using Lotka-Volterra models:

$$\frac{dR_i}{dt} = rR_i\left(1 - \frac{R_i}{K}\right) - \frac{\sum_j a_{ij}R_iN_j}{1+\sum_i a_{ij}hR_i} \tag{6}$$

$$\frac{dN_j}{dt} = \frac{\sum_i ea_{ij}R_iN_j}{1+\sum_i a_{ij}hR_i} - \frac{\sum_i a_{ji}N_jP_i}{1+\sum_j a_{ji}hN_j} - mN_j \tag{7}$$

$$\frac{dP_i}{dt} = \frac{\sum_j ea_{ji}N_jP_i}{1+\sum_j a_{ji}hN_j} - mP_i \tag{8}$$

Where R_i is the density of resource species i, dR_i/dt is the rate of change of resource species i with respect to time, r is the growth rate of species i, K is the carrying capacity of resource species i, N_j is the density of herbivore species j, dN_j/dt is the rate of change of herbivore species j with respect to time, P_i is the density of predator species i, dP_i/dt is the rate of change of predator species i with respect to time and a_{ij} is the attack rate of predator j on prey i. The handling time for consumer j to catch and consume prey i is h, m is the mortality rate for any non-resource species and e is a measure of conversion efficiency for prey captured to consumer production. Equations 6, 7 and 8 represent type II functional responses that include a handling time of 0.1. A handling time of zero would make these equations have type I functional responses. Parameter values that remained constant in all models can be found in Table 2.

Table 2: Parameter values for population dynamics that remained constant across all treatments.

CONSTANT PARAMETER VALUES	
PRODUCER CARRYING CAPACITY	10
PRODUCER INTRINSIC GROWTH RATE	1.5
STRONG INTERACTION ATTACK RATE	0.3
CONVERSION EFFICIENCY	0.4
CONSUMER MORTALITY	0.3

III.2. Web Construction

Network models (Figure 2) had food webs of either 48 or 108 species constructed with an equal number of species on two or three distinct trophic levels. These sizes were chosen in order to evaluate large food webs as well as smaller ones, simply to assess generality of results. Moreover, since there were an equal number of species on each trophic level, 48 and 108 were easily divisible by 2 and 3 so that food webs of equal size but with a different number of trophic levels could be made. Each species was then connected to precisely one species on the level below it and/or above it (if applicable) by a strong interaction (interaction strength = 0.3). All other connections between species were composed of weaker links to facilitate coexistence. One set of weak links (interaction strength = 0.05 or 0.1) was laid out between a close resource and consumer in a way that guaranteed a fully connected network, while all other weak links (interaction strength = 0.05 or 0.1) were placed randomly between species. For instance, consumer *j* was allotted a strong link to resource *i*, then given a weak link specifically to resource (*i*-1), and lastly assigned weak links to *x* other resource species, where *x* was varied between one, two, or four to compare webs with different node degree. The reason for some models having an interaction strength of 0.05 instead of 0.1 was because networks with a high node degree and increased variability required a weaker attack rate in order for the system to coexist and reach equilibrium sufficiently quickly.

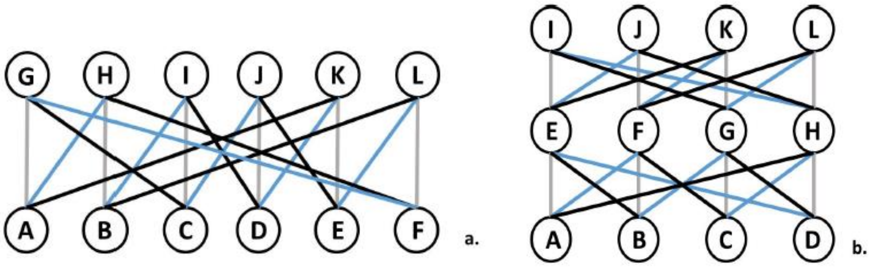

Figure 2: Examples of constructed food webs with species represented as lettered circles with either 2 trophic levels (*a*) or 3 trophic levels (*b*). Links between species characterizing trophic interactions. Gray lines indicate strong interactions, blue lines represent weak interactions placed regularly to guarantee a fully connected web, and black lines indicate randomly-placed weak interactions.

III.3. Simulations

Models were simulated using Euler's formula for a certain number of iterations determined to be sufficient for the system to reach a steady state. A system was considered settled if all the species' densities varied by less than 1% for 100 iterations. However, the number of iterations required to reach equilibrium varied depending on the complexity of the network. In all models, a community disturbance was simulated using a pulse perturbation. The system was allowed to reach a steady state and then one focal species' density was reduced by half at a single point in time, and then the simulations continued until the densities return to equilibrium.

III.4. Treatments and Parameter Space

Model treatments (Table 3) for these simulations varied for a number of different parameters hypothesized to potentially affect communicability's ability to predict how one species responds to the perturbation of another. This added variability in models was accomplished by altering both the structure and dynamics of the network in a variety of different parameters for model treatments.

Food webs of different sizes, 48 or 108 nodes, allowed us to evaluate if network size and increased distances between nodes affected the propagation of effects and thus the predictive power of each metric. Nodes were assigned 3, 4 or 6 links each. These treatments were designed to differ in the number of pathways connecting a given pair of nodes. Some additional model treatments contained node degree heterogeneity. If node degree heterogeneity was included, link-to-node assignments were allowed to vary by either one additional link or by one less link. Thus, a food web with a designated 4 links per node with heterogeneity could have nodes with 3, 4 or 5 links randomly throughout the network. In specified cases, this heterogeneity was allowed to vary by two links (+2). Heterogeneity or “noise” in the interaction strength between nodes was included for both weak and strong attack rates by allowing them to vary by ten percent of their given value. This caused some pathways between nodes to be stronger than others, affecting the propagation of effects. Lastly, type I functional responses (no handling time) were used for food web dynamics in some model treatments. In other treatments, type II functional responses were used (handling time = 0.1).

Table 3: Treatment parameters that varied in each simulation in order to evaluate their influence on the effectiveness of each metric.

TREATMENTS COMPARED	
SIZE (SPECIES NUMBER)	48 or 108
NUMBER OF TROPHIC LEVELS	2 or 3
NODE DEGREE (CONNECTEDNESS)	3, 4 or 6
NODE DEGREE VARIABILITY	+/- 1 or +/- 2
WEAK LINK ATTACK RATE	0.05 or 0.1
VARYING ATTACK RATES (ATTACK RATE HETEROGENEITY)	0% or 10%
TYPE I AND II FUNCTIONAL RESPONSES	handling time = 0 or 0.1
TROPHIC LEVEL OF PERTURBED SPECIES	Resource, herbivore or predator

III.5. Analyses

III.5.a. Quantifying Species' Response to Perturbations

Each species' response to a perturbation was measured as total magnitude of deviation in density from equilibrium, integrated over the time required for the system to return to equilibrium (Burns et al. 2014). Burns et al. (2014) also normalized their metric by dividing by the species' densities. This would be appropriate for their model if species with a low density may have been minimally affected while species with a large density were largely affected, in which case normalization could allow for a better comparison across trophic levels with varying species densities. Normalization would then make these species' responses to a perturbation much more comparable. However, we found that in our models, density and response did not strongly covary, and so normalization did not have the desired effect of making our results more comparable between trophic levels (Figure 2). Rather than making comparisons between species more comparable, normalizing our data actually worsened the predictive power of both metrics with lower correlations and R-squared values. Normalization corrected a potential artifact in Burns et al (2014)'s models but it created an artifact for our models. For these reasons, we chose to not normalize the integral response.

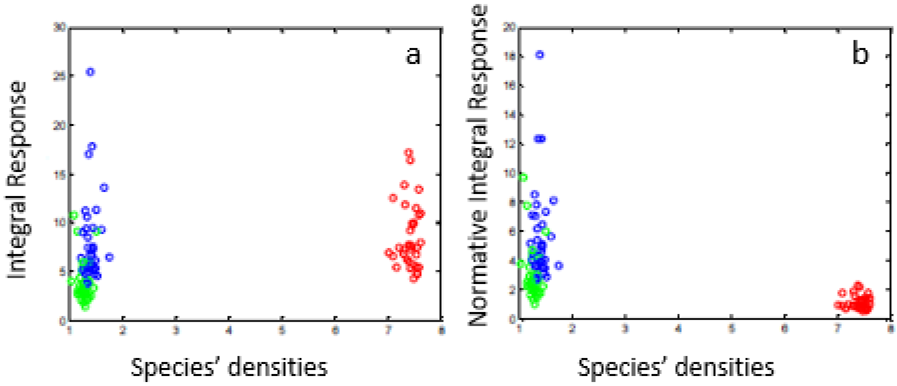

Figure 3: Scatter plots of species' densities versus integral response. Points represent individual species and are color coded based on trophic position. Green circles are resources, blue circles are herbivores, and red circles are predators. Plot *a* has not been normalized, while plot *b* has been normalized. These plots are not intended to show a meaningful relationship between densities and response, but to allow for a comparison between trophic levels and response. Graph *b* shows how normalization created an artifact by making species on different trophic levels less comparable.

III.5.b. Quantifying Correlations between Proximity and Response

We assessed models with variations in a number of different aspects. We began our analysis with an overly simplified web containing 108 species, two links per node, a type II functional response and a perturbed resource. While this model has very little real-world food web complexity, it does allow for a clear visual of each metrics' non-linear response, especially in the case of shortest path distance (Figure 4), which is difficult to see in more complex models. Because of this curvilinear nature, we chose to use the statistical methods of both a polynomial regression analysis as well as a linear regression analysis on metric data that had been transformed using the natural logarithm. We then obtained the R-squared value for each metric from each analysis type in order to compare each metrics' predictive power, generating 16 repetitions for each of the 94 model treatments.

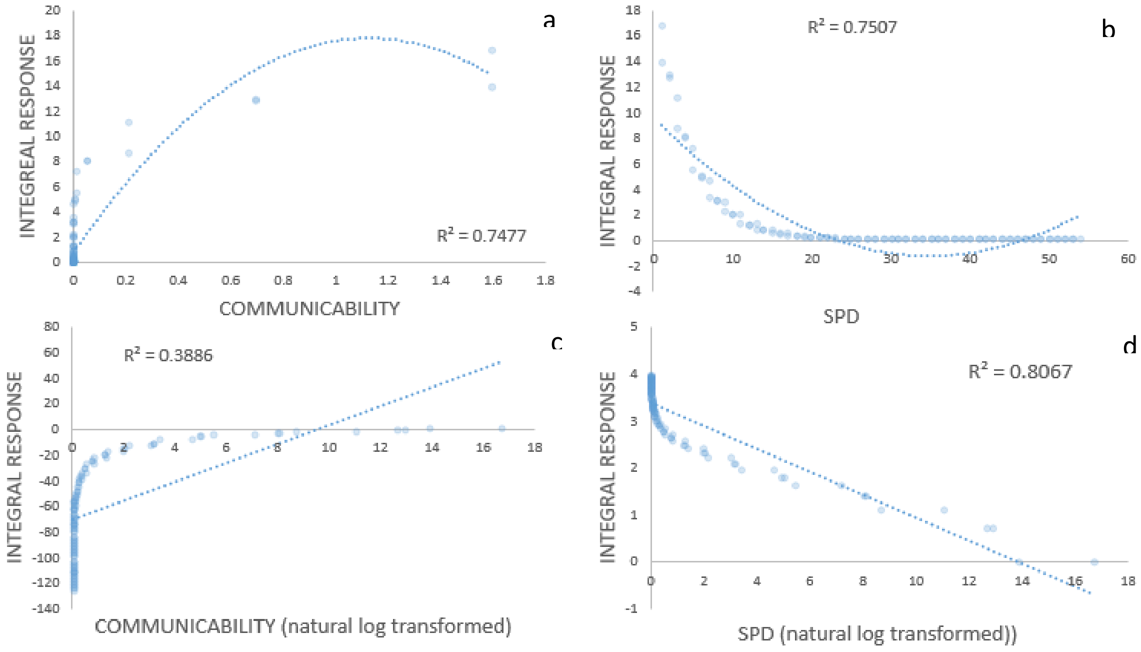

Figure 4: Graphs depicting the proximity metric (communicability or SPD) of each species in relation to its integral response. Each panel shows a different trend line option along with its corresponding R-squared value and equation for polynomial regression *(a*, *b*) and linear regression for natural transformed metrics (*c*, *d*). All points contain transparency, so darker areas indicate a high number of clustered points.

III.5.c. Comparing Metrics' Performance within Treatments

We first sought to evaluate which metric performed best for each of the 94 treatments. Mean R-squared values were compared to determine which metric better predicted each species' response to the perturbation. We then used a paired t-test to analyze whether there was a significant difference between each model treatments' communicability and SPD R-squared values.

III.5.d. Testing Effects of Focal Web Properties on Metrics' Relative Performance

In order to quantify the relative performance of each metric across two different treatment models, we created an easily analyzed ratio by dividing communicability's R-squared value by SPD's R-squared value, and then performed an unpaired t-test to determine if the difference was significant. Treatments that were compared were the same in every aspect except for the particular focal trait being evaluated between the two models.

IV. RESULTS

IV.1. Metrics' Relative Performance within Treatments

In all model treatments analyzed with data from polynomial regression with a perturbed resource, communicability significantly outperformed SPD (Figure 5; Appendix, Table 5). Likewise, in models where a predator was perturbed, communicability also significantly outperformed SPD in all but one treatment (Figure 6; Appendix, Table 6). SPD had a higher value in one treatment but it was not significant. However, in 11% of significant model treatments (76% of model treatments were significant) with a perturbed herbivore and no node degree heterogeneity, SPD significantly outperformed communicability (Figure 7; Appendix, Table 7).

In model treatments analyzed using the linear regression of natural log transformed data with a perturbed resource, communicability outperformed SPD in 94% of the significant models (84% of model treatments were significant) (Figure 8; Appendix, Table 8). Communicability performed best in 84% of the significant model treatments when an herbivore was perturbed (44% of model treatments were significant) (Figure 9; Appendix, Table 9) and 76% of the significant models when a predator was perturbed (44% of model treatments were significant) (Figure 10; Appendix, Table 10). An example from one of the repetitions from one of the model treatments used can be found in Figure 4.

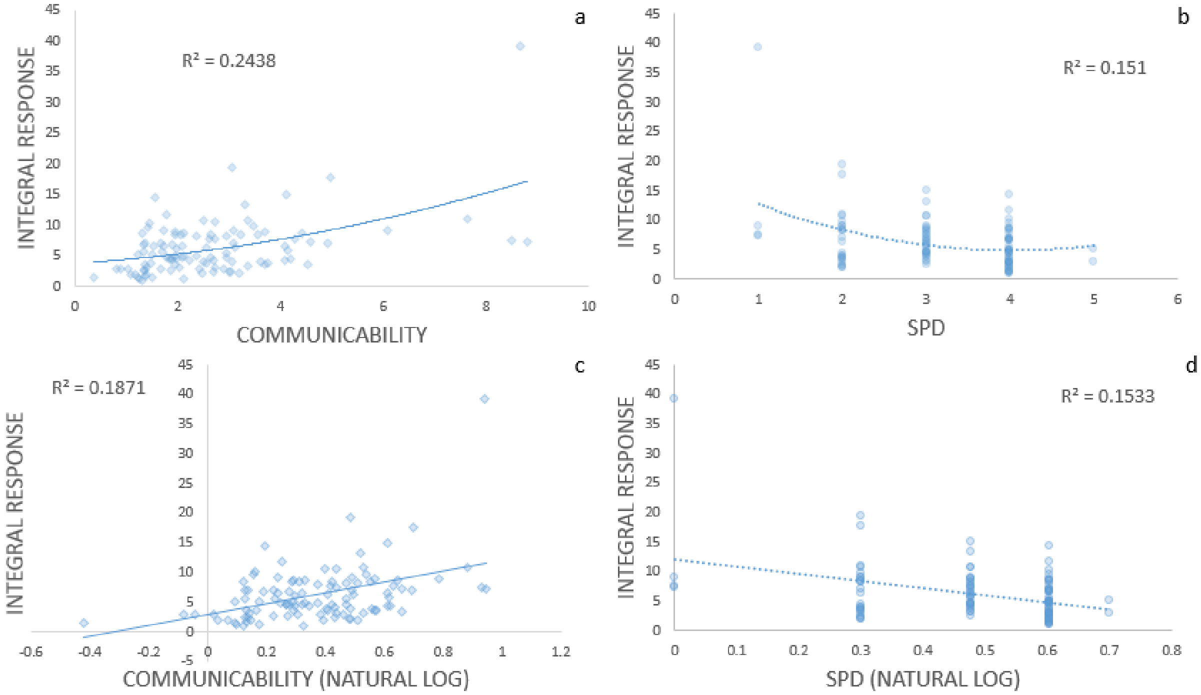

Figure 4: The communicability (diamond points; *a*, *c*) or SPD (circle points; *b*, *d*) of each species plotted against its integral response for a polynomial regression (*a*, *b*) and a linear regression of natural log transformed metric (*c*, *d*). These data were generated by a model of a 3 level food web with 108 species, 4 links per node, node degree heterogeneity, a type II functional response and a perturbed resource.

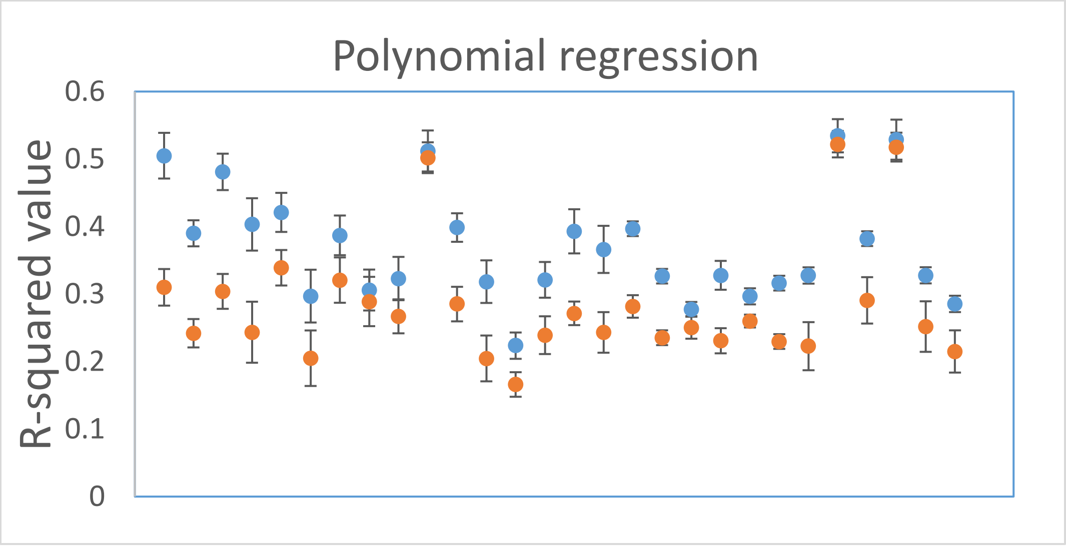

Figure 5: Communicability's (blue points) mean R-squared value for each treatment relative to SPD's (orange points) mean R-squared value for all treatments with a perturbed resource and analyzed using polynomial regression. Error bars indicate standard error. Communicability's R-squared value was significantly higher than SPD's for all treatments.

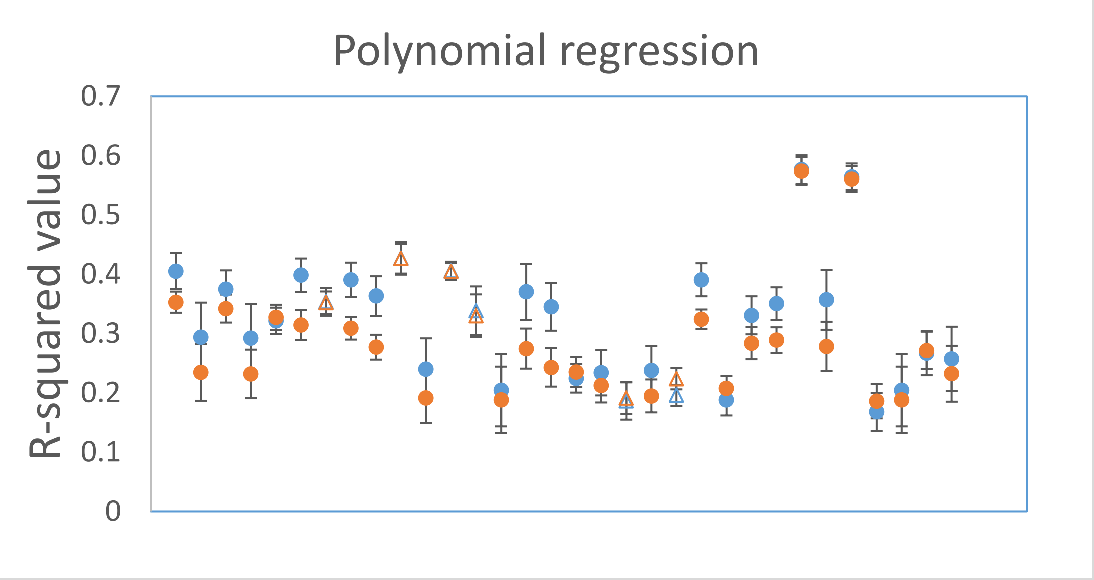

Figure 6: Communicability's (blue points) mean R-squared value for each treatment relative to SPD's (orange points) mean R-squared value for all treatments with a perturbed herbivore and analyzed using polynomial regression. Error bars indicate standard error. Unfilled triangles show treatments where R-squared values for communicability and SPD were not significantly different; filled circles indicate treatments where they were significantly different.

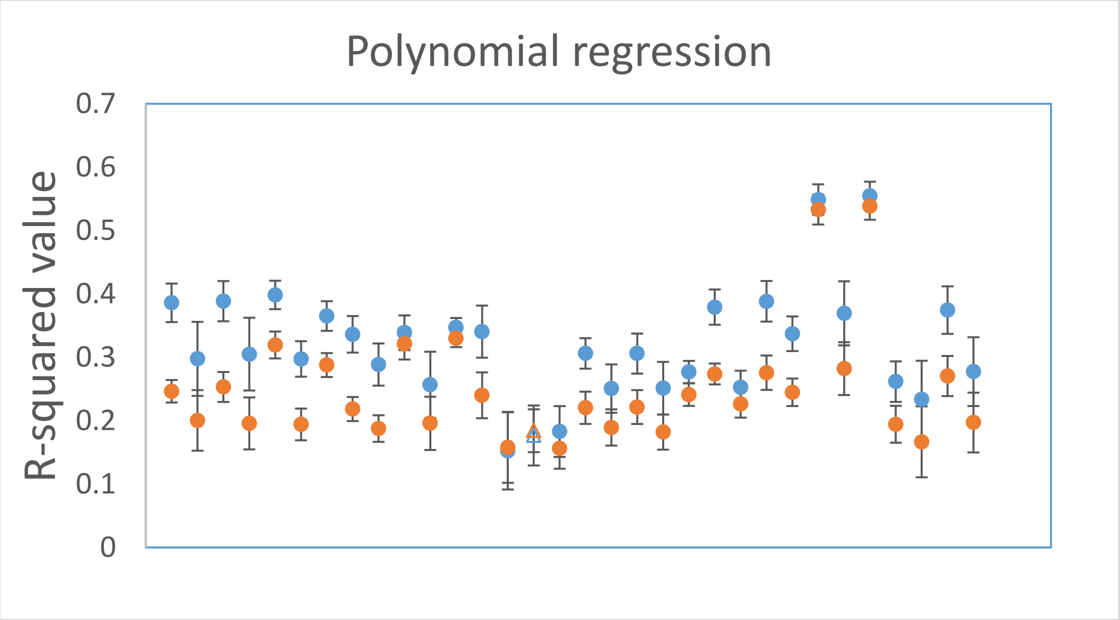

Figure 7: Communicability's (blue points) mean R-squared value for each treatment relative to SPD's (orange points) mean R-squared value for all treatments with a perturbed predator and analyzed using polynomial regression. Error bars and symbol meanings are identical to Figure 6.

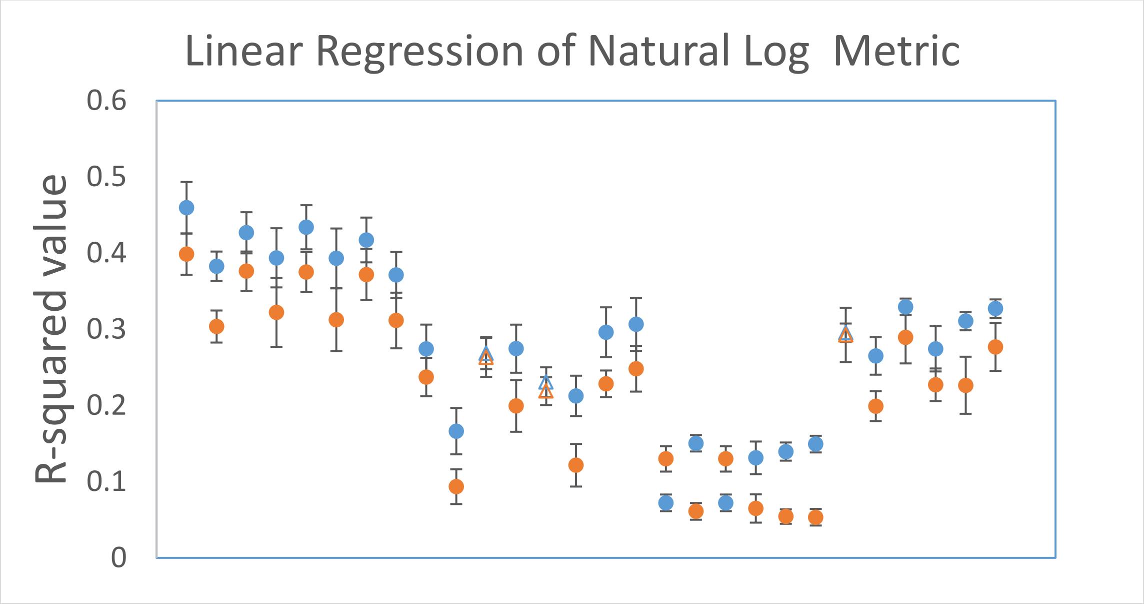

Figure 8: Communicability's (blue points) mean R-squared value for each treatment relative to SPD's (orange points) mean R-squared value for all treatments with a perturbed resource and analyzed using the linear regression of the natural log transformed metric. Error bars indicate standard error. Error bars and symbol meanings are identical to Figure 6.

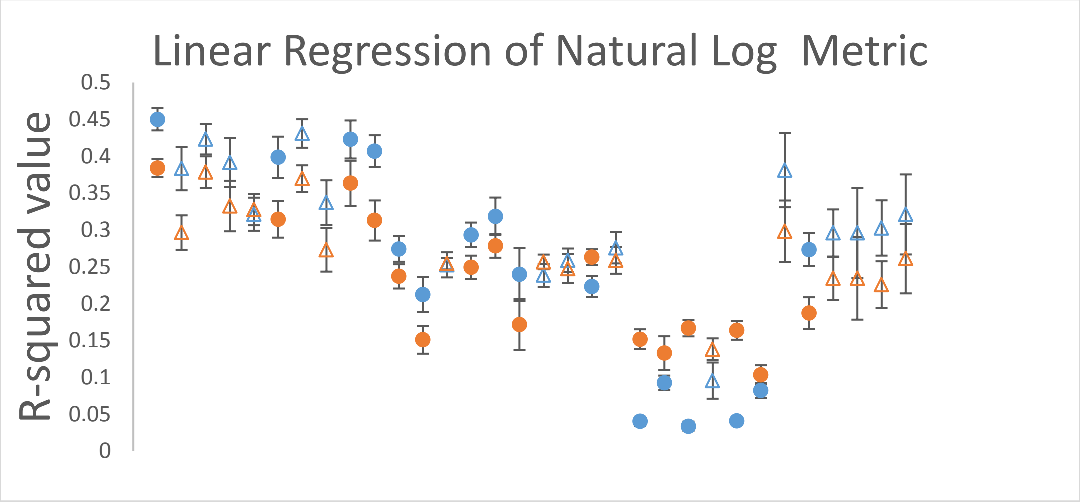

Figure 9: Communicability's (blue points) mean R-squared value for each treatment relative to SPD's (orange points) mean R-squared value for all treatments with a perturbed herbivore and analyzed using the linear regression of the natural log transformed metric. Error bars indicate standard error. Error bars and symbol meanings are identical to Figure 6.

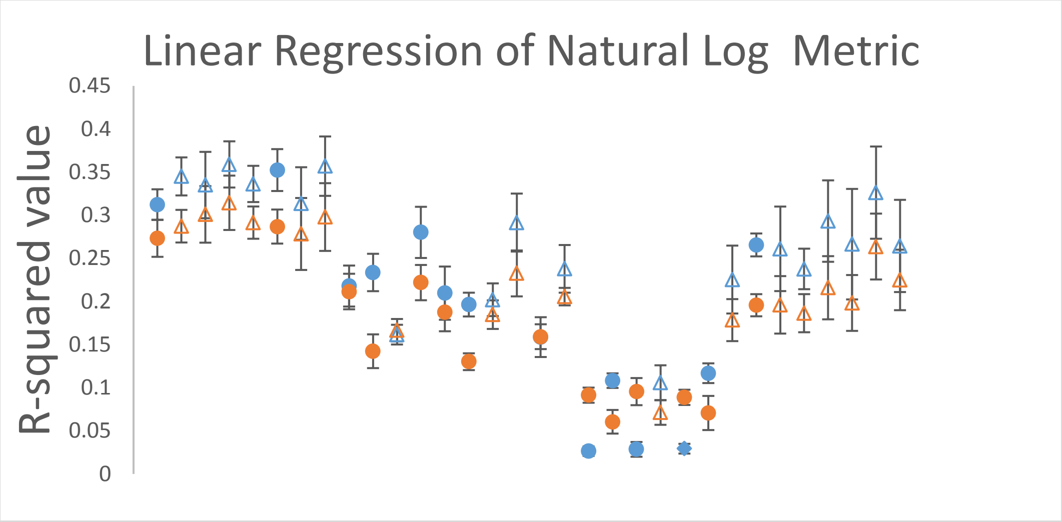

Figure 10: Communicability's (blue points) mean R-squared value for each treatment relative to SPD's (orange points) mean R-squared value for all treatments with a perturbed predator and analyzed using the linear regression of the natural log transformed metric. Error bars indicate standard error. Error bars and symbol meanings are identical to Figure 6.

IV.2. Effects of Focal Web Properties on Metrics' Relative Performances

IV.2.a. Node Degree

With polynomial regression analysis, higher node degree increased communicability's predictive power relative to SPD's in none of the significant cases compared (94% significant cases) (Figure 11; Appendix, Table 11). When these treatments were analyzed using the linear regression of the natural log transformed metrics, communicability's R-squared value improved with node degree in 38% of the significant comparisons (94% significant cases) (Figure 12; Appendix, Table 12).

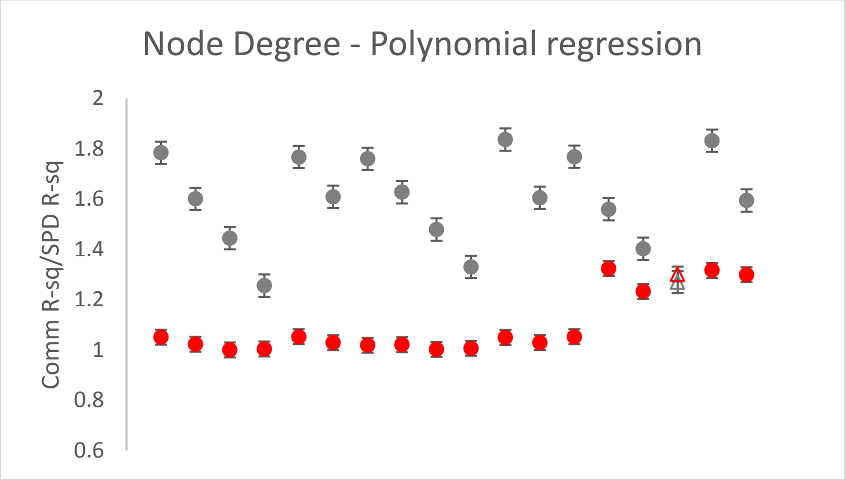

Figure 11: Comparison of treatments with a node degree of 3 (gray points) to treatments with a node degree of 6 (red points). Treatments compared are the same in all aspects excluding what is being compared. The y-axis represents the ratio of the mean communicability R-square divided by the mean SPD R-square for each treatment. Error bars indicate standard error. Unfilled triangles show treatments where R-squared values for communicability and SPD were not significantly different; filled circles indicate treatments where they were significantly different.

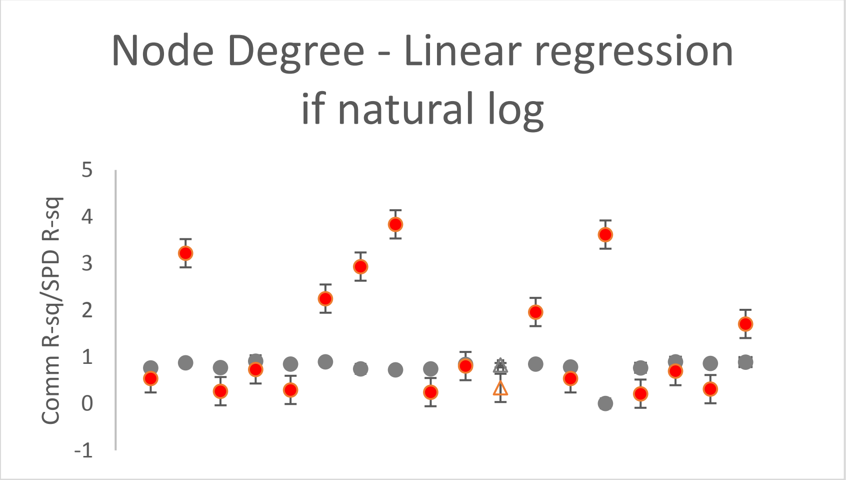

Figure 12: Comparisons of treatments with a node degree of 3 (gray points) to treatments with a node degree of 6 (red points). Treatments compared are the same in all aspects excluding what is being compared. The y-axis represents the ratio of the mean communicability R-square divided by the mean SPD R-square for each treatment Error bars indicate standard error. Error bars and symbol meanings are identical to Figure 11.

IV.2.b. Node Degree Heterogeneity

An additional comparison was performed between treatments that either contained node degree heterogeneity or contained a fixed node degree. With polynomial regression analysis, communicability's performance increased relative to SPD's performance in all significant comparisons (67% significant cases) (Figure 13; Appendix, Table 13). However, with the linear regression of the natural log transformed metrics analysis, only 4 out of the 18 treatments (22%) were significant, and communicability's performance increased with node degree heterogeneity in only one of these four significant case comparisons (Figure 14; Appendix, Table 14).

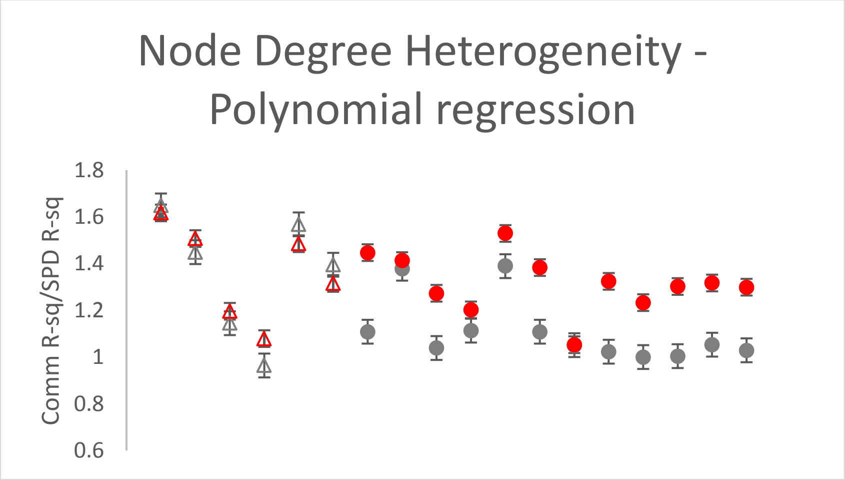

Figure 13: Comparisons of treatments without node degree heterogeneity (gray points) to treatments with node degree heterogeneity (red points). Treatments compared are the same in all aspects excluding what is being compared. The y-axis represents the ratio of the mean communicability R-square divided by the mean SPD R-square for each treatment. Error bars and symbol meanings are identical to Figure 11.

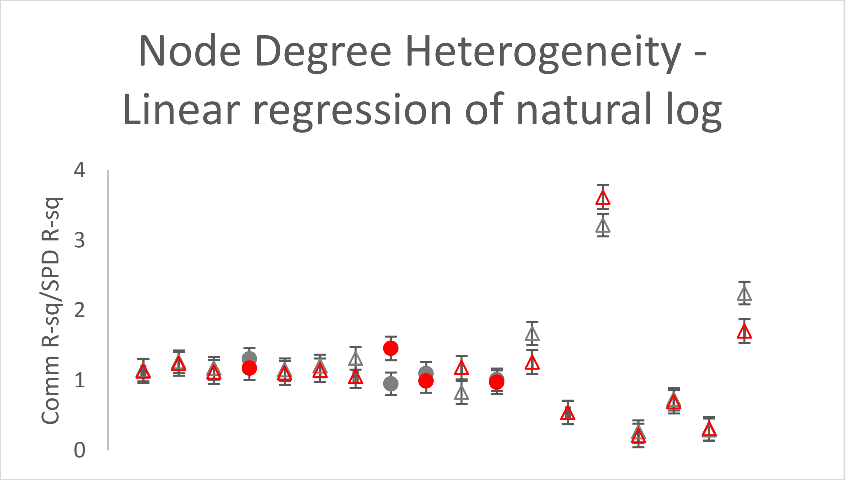

Figure 14: Comparison of treatments without node degree heterogeneity (gray points) to treatments with node degree heterogeneity (red points). Treatments compared are the same in all aspects excluding what is being compared. The y-axis represents the ratio of the mean communicability R-square divided by the mean SPD R-square for each treatment. Error bars and symbol meanings are identical to Figure 11.

IV.2.c. Variation in the Strengths of Species' Interactions ("Noise")

We found that when analyzing R-squared values from the polynomial regression, variability in interaction strength improved communicability's R-squared value relative to SPD's in 63% of the cases compared with significant differences (66% cases were significant) (Figure 15; Appendix, Table 15). However, none of the case comparisons for variability in interaction strength were significant with the linear regression of the natural log transformed metrics analysis (Figure 16; Appendix, Table 16).

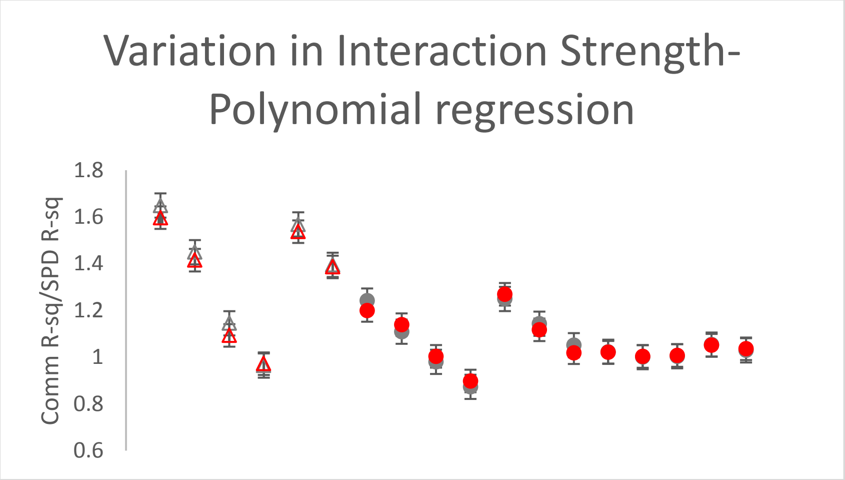

Figure 15: Comparison of treatments without variation in interaction strength (gray points) to treatments with variation in interaction strength (red points). Treatments compared are the same in all aspects excluding what is being compared. The y-axis represents the ratio of the mean communicability R-square divided by the mean SPD R-square for each treatment. Error bars and symbol meanings are identical to Figure 11.

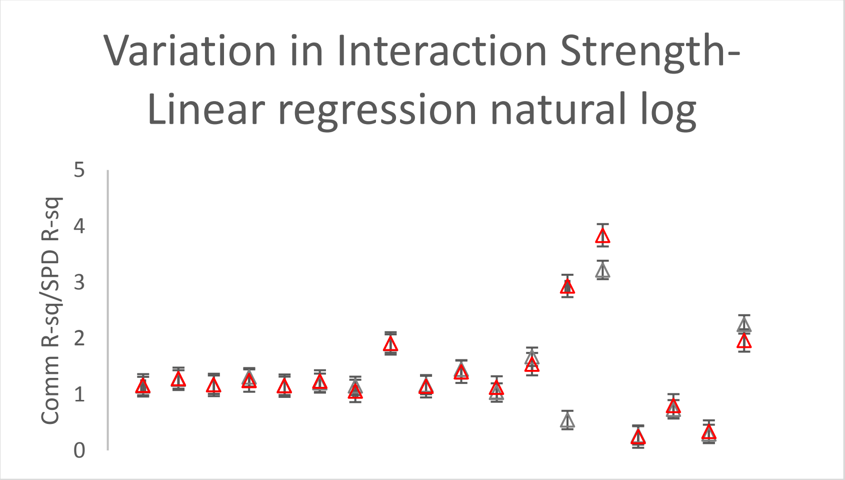

Figure 16: Comparison of treatments without variation in interaction strength (gray points) to treatments with variation in interaction strength (red points). Treatments compared are the same in all aspects excluding what is being compared. The y-axis represents the ratio of the mean communicability R-square divided by the mean SPD R-square for each treatment. Error bars and symbol meanings are identical to Figure 11.

IV.2.d. Functional Response

Lastly, in models analyzed using polynomial regression, communicability's score only improved with a type II functional response in comparison to a type I functional response in 18% of the significant comparisons (72% significant cases) (Figure 17; Appendix, Table 17).

However, in models analyzed using the linear regression of natural log transformed data, communicability improved with a type II functional response in 57% of the model cases compared (71% significant cases) (Figure 18; Appendix, Table 18).

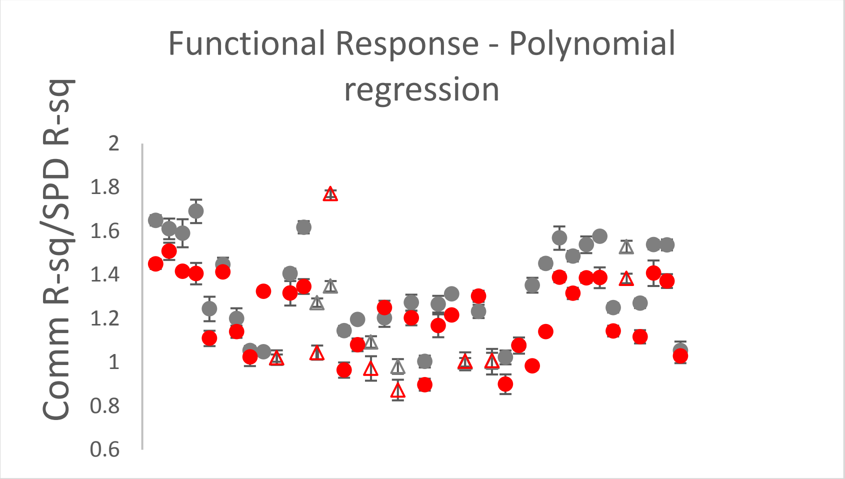

Figure 17: Comparison of treatments with a type I functional response (gray points) to treatments with a type II functional response (red points). Treatments compared are the same in all aspects excluding what is being compared. The y-axis represents the ratio of the mean communicability R-square divided by the mean SPD R-square for each treatment. Error bars and symbol meanings are identical to Figure 11.

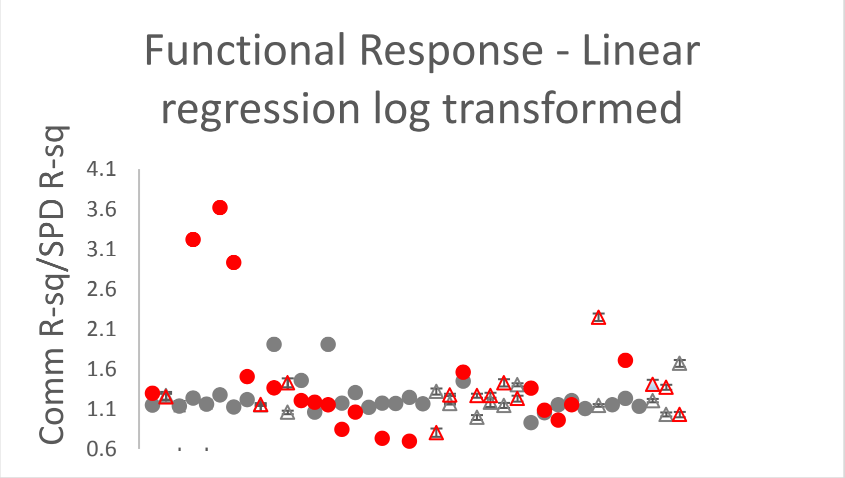

Figure 18: Comparison of treatments with a type I functional response (gray points) to treatments with a type II functional response (red points). Treatments compared are the same in all aspects excluding what is being compared. The y-axis represents the ratio of the mean communicability R-square divided by the mean SPD R-square for each treatment. Error bars and symbol meanings are identical to Figure 11.

V. DISCUSSION

In our results, both communicability and shortest path distance yielded potentially valuable information concerning responses to a perturbation, based solely on network topology. We found that for the polynomial regression analysis as well as for the linear regression analysis on natural log transformed data in the majority of model treatments, communicability tended to outperform SPD in its ability to predict how species in a network responded to a perturbation.

For models analyzed using the polynomial regression analysis, communicability had a higher mean R-squared value compared to shortest path distance's mean R-squared value in 89% of the significant individual model treatments (91%). In models analyzed using the linear regression of natural log transformed data, communicability outperformed SPD in 75% of the significant treatments (58%). This indicates that the fact that communicability takes into account the totality of effects between two species in food web, instead of just the shortest pathway between them, may make it a more valuable means to evaluate the effects of a perturbation on an ecological community. While both statistical methods used had communicability performing best in the majority of the models, communicability outperformed SPD less often when analyzed using the linear regression of natural log transformed data. Moreover, many of the treatments showed no significant difference between communicability and SPD when analyzed using the linear regression of natural log transformed data.

Additionally, we had hypothesized that since communicability contains additional information about multiple and long pathways that it would perform better in model treatments with characteristics such as increased node degree, node degree heterogeneity, variations in interaction strengths, and a type II functional response.

For models analyzed using the polynomial regression, we found our hypotheses to be true for variations in the strength of attack rates and especially for node degree heterogeneity. This supports the idea that communicability's relative performance would improve when pairs of species have more potential to differ in the multiple, long pathways that communicability reflects but SPD does not. These results also agree with previous theoretical work emphasizing the importance of indirect effects when predicting how a community will respond to a disturbance (Higashi and Patten 1989; Borrett et al. 2007; Borrett et al. 2010; Salas and Borrett 2011; Burns et al. 2014). However, contrary to our hypotheses, increased node degree as well as type II functional responses did not improve communicability's predictive power. In fact, they appeared to have the opposite effect.

For model treatment comparisons analyzed using the linear regression of natural log transformed data, we found that node degree heterogeneity as well as variability in interaction strength had no effect on either metric's predictive power since only a few of these treatments were significantly different. However, we did find two treatments in support of two of our hypotheses: increased node degree as well as a type II functional response slightly increased communicability's performance relative to SPD's.

V.1. Future Direction

While both types of statistical analyses found that communicability had a higher predictive power concerning perturbations in a network relative to SPD's predictive power, they also contradicted one another when analyzing the effects of focal treatments on each metric's relative performance. This may be occurring because the shape of the relationship between each metric and the species' integral responses is important for making inferences about the correlations in each type of analysis. Further analysis of these shapes would be necessary to fully understand differences in the results between the two statistical methods.

A solution to the potential problems concerning shape caused by using a regression analysis would be to use a non-parametric statistical test. An ideal option would be the Kendall rank correlation coefficient because, unlike Spearman's rank correlation, it adjusts for ties in rank which can be common with a discrete variable such as SPD.

V.2. Conclusions

A better understanding of the consequences of a species perturbation is pivotal for practical conservation and management purposes. The ability to accurately predict the consequences of these disturbances can help to alleviate any secondary effects of a perturbation and can even aid in preventing future ecological disturbances. While communicability is a somewhat crude metric that omits important aspects of food web interactions, it incorporates much more detail than SPD by accounting for long paths of indirect effects as well as the multiplicity of short paths between a pair of species. The fact that communicability may be calculated based purely on network link structure (without data concerning the strengths of species' interactions) enhances its potential usefulness in real-world situations, where such data may be limited. Further study of the factors affecting communicability's performance may yield new insights into food webs' responses to disturbances.

VI. INTEGRATION OF THE THESIS RESEARCH

Theoretical ecology is in itself a very integrative field of biology. This study involves using mathematical modeling as a means to answer ecologically relevant questions. I used a computer program to run equations that theoretically simulated the dynamics of a hypothetical food web in order to gain better insight into the effects of a perturbation on a food web. While this method is highly quantitative, it allows for studies that either cannot be done in a real-world environment, or would be extremely difficult to perform.

VII. ACKNOWLEDGMENTS

I would first like to thank my major advisor, Dr. Antonio Golubski, for his expertise and patience throughout this experience. I would also like to thank my committee members, Dr. William Ensign, Dr. Erik Westlund, and Dr. Stuart Borrett for all of their helpful input and guidance. Lastly, a thanks to the Kennesaw State University Department of Biological Sciences and the Graduate College for funding and support.

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IX. APPENDIX

Table 4: Key for acronyms in all table headers.

Trph Lvl	Number of trophic levels
LPN	Links per node
NOS	Number of species in food web
VAR	Varying attack rates
WAR	Weak attack rates
FR	Functional Response
NDV	Node degree variation
SP	Species perturbed
Std Error	Standard Error
C- Std	Standard Error for communicability
SPD- Std	Standard Error shortest path distance
Sig	Significant?
Mean Comm R^2 / SPD R^2	The mean communicability R-squared value/ shortest path distance R-square value
Mean w/o VAR	The mean ratio of treatments with varying attack rates
Mean w/ VAR	The mean ratio of treatments without varying attack rates
Mean 3 LPN	The mean ratio of treatments with 3 links per node
Mean 6 LPN	The mean ratio of treatments with6 links per node
Mean w/o NDV	The mean ratio of treatments without node degree variation
Mean w/ NDV	The mean ratio of treatments with node degree variation
R	resource
H	herbivore
P	predator

Table 5: Comparison of model treatments with a perturbed resource. A key for all headings can be found in table 4. The mean communicability and SPD R-squared ratio is highlighted in blue if communicability's value is significantly higher and in orange if SPD is significantly greater.

Polynomial Regression Analysis													
Trph lvls	**LPN**	**NOS**	**WAR**	**FR**	**NDV**	**VAR**	**SP**	**Mean R^2 Comm**	**Mean R^2 SPD**	**C- Std**	**SPD-Std**	**Mean Comm R^2 / SPD R^2**	**Sig**
3	3	108	0.1	I	-	-	R	0.505	0.31	0.042	0.0276	1.649	+
3	3	108	0.1	I	+	-	R	0.39	0.242	0.0444	0.0247	1.61	+
3	3	108	0.1	I	-	+	R	0.481	0.304	0.023	0.0218	1.59	+
3	3	108	0.1	I	+	+	R	0.4032	0.2435	0.046	0.027	1.69	+
3	4	108	0.1	I	-	-	R	0.421	0.339	0.0309	0.0229	1.243872	+
3	4	108	0.05	I	+	-	R	0.297	0.205	0.044	0.0255	1.446661	+
3	4	108	0.1	I	-	+	R	0.387	0.3207	0.0381	0.0248	1.199866	+
3	6	108	0.05	I	-	-	R	0.306	0.289	0.0338	0.030	1.05287	+
3	6	108	0.05	I	+	-	R	0.323	0.267	0.0299	0.041	1.048	+
3	6	108	0.05	I	-	+	R	0.512	0.502	0.0201	0.02	1.019123	+
3	3	48	0.1	I	-	-	R	0.398572	0.285167	0.033	0.0255	1.405817	+
3	3	48	0.1	I	+	-	R	0.31842	0.20467	0.052	0.0366	1.617462	+
3	3	48	0.1	I	-	+	R	0.223585	0.166063	0.074	0.045	1.272804	+
3	3	48	0.1	I	+	+	R	0.321087	0.239113	0.053	0.037	1.347708	+
3	3	108	0.1	II	-	-	R	0.39295	0.271475	0.021	0.0115	1.448806	+
3	3	108	0.1	II	+	-	R	0.366199	0.243213	0.0464	0.0228	1.507336	+
3	3	108	0.1	II	-	+	R	0.3968	0.2817	0.0383	0.0259	1.415341	+
3	3	108	0.1	II	+	+	R	0.326495	0.235348	0.038	0.026	1.405352	+
3	4	108	0.1	II	-	-	R	0.277397	0.250543	0.0356	0.031	1.109101	+
3	4	108	0.05	II	+	-	R	0.327792	0.230822	0.051	0.033	1.413227	+
3	4	108	0.1	II	-	+	R	0.296643	0.260057	0.0368	0.0302	1.139632	+
3	4	108	0.05	II	+	+	R	0.316216	0.22974	0.052	0.0324	1.362158	+
3	4	108	0.05	II	+ 2	-	R	0.327532	0.222813	0.0553	0.035	1.463423	+
3	6	108	0.05	II	-	-	R	0.534526	0.522024	0.0205	0.019	1.023852	+
3	6	108	0.05	II	+	-	R	0.382104	0.290695	0.039974	0.034	1.324248	+
3	6	108	0.05	II	-	+	R	0.528735	0.517715	0.021884	0.0213	1.021231	+
3	3	48	0.1	II	-	-	R	0.327791	0.251847	0.047538	0.037	1.315496	+
3	3	48	0.1	II	+	-	R	0.28543	0.215011	0.042632	0.0312	1.346547	+

Table 6: Comparison of model treatments with a perturbed herbivore. A key for all headings can be found in table 4. The mean communicability and SPD R-squared ratio is highlighted in blue if communicability's value is significantly higher and in orange if SPD is significantly greater.

Polynomial Regression Analysis													
Trph lvls	**LPN**	**NOS**	**WAR**	**FR**	**NDV**	**VAR**	**SP**	**Mean R^2 Comm**	**Mean R^2 SPD**	**C- Std**	**SPD- Std**	**Mean Comm R^2 / SPD R^2**	**Sig**
3	3	108	0.1	I	-	-	H	0.405314	0.353003	0.030409	0.0178	1.144861	+
3	3	108	0.1	I	+	-	H	0.293854	0.234559	0.058378	0.0478	1.195786	+
3	3	108	0.1	I	-	+	H	0.374859	0.342202	0.031673	0.0236	1.092896	+
3	3	108	0.1	I	+	+	H	0.292598	0.23194	0.057384	0.041	1.203193	+
3	4	108	0.1	I	-	-	H	0.321312	0.327456	0.022431	0.0212	0.980978	+
3	4	108	0.05	I	+	-	H	0.398509	0.314523	0.028028	0.025	1.272681	+
3	4	108	0.1	I	-	+	H	0.35348	0.352066	0.023382	0.0189	1.003469	-
3	4	108	0.05	I	+	+	H	0.390748	0.30889	0.028851	0.019	1.265754	+
3	4	108	0.05	I	+ 2	-	H	0.363352	0.277106	0.033275	0.021	1.312044	+
3	6	108	0.05	I	-	-	H	0.426759	0.426179	0.027405	0.025	1.000054	-
3	6	108	0.05	I	+	-	H	0.239639	0.190984	0.052327	0.042	1.232671	+
3	6	108	0.05	I	-	+	H	0.406069	0.404822	0.015123	0.014	1.002771	-
3	3	48	0.1	I	-	-	H	0.338431	0.329944	0.041086	0.036149	1.0224	-
3	3	48	0.1	I	+	-	H	0.204383	0.18831	0.060909	0.055955	1.076451	+
3	3	48	0.1	I	-	+	H	0.370358	0.274667	0.047318	0.033792	1.352422	+
3	3	48	0.1	I	+	+	H	0.345004	0.242942	0.040128	0.032374	1.451974	+
3	3	108	0.1	II	-	-	H	0.224601	0.23505	0.024073	0.025437	0.964371	+
3	3	108	0.1	II	+	-	H	0.233846	0.212386	0.038168	0.028582	1.079824	+
3	3	108	0.1	II	-	+	H	0.186496	0.190976	0.031574	0.026716	0.971827	-
3	3	108	0.1	II	+	+	H	0.237642	0.194865	0.041598	0.027748	1.249805	+
3	4	108	0.1	II	-	-	H	0.19575	0.22377	0.017678	0.017883	0.873162	-
3	4	108	0.05	II	+	-	H	0.390674	0.324126	0.027844	0.016481	1.202311	+
3	4	108	0.1	II	-	+	H	0.188064	0.207101	0.026157	0.021433	0.897622	+
3	4	108	0.05	II	+	+	H	0.330804	0.283761	0.032039	0.0271	1.166916	+
3	4	108	0.05	II	+ 2	-	H	0.350634	0.288865	0.027347	0.02172	1.21629	+
3	6	108	0.05	II	-	-	H	0.576522	0.573905	0.02417	0.023611	1.004437	+
3	6	108	0.05	II	+	-	H	0.357039	0.278307	0.050532	0.04166	1.301607	+
3	6	108	0.05	II	-	+	H	0.564547	0.560636	0.022434	0.021633	1.006795	+
3	3	48	0.1	II	-	-	H	0.16802	0.186173	0.031975	0.029132	0.899697	+
3	3	48	0.1	II	+	-	H	0.204383	0.18831	0.060909	0.055955	1.076451	+
3	3	48	0.1	II	-	+	H	0.267193	0.271553	0.03748	0.031649	0.983262	-
3	3	48	0.1	II	+	+	H	0.257349	0.232348	0.054287	0.047153	1.140404	+

Table 7: Comparison of model treatments with a perturbed predator. A key for all headings can be found in table 4. The mean communicability and SPD R-squared ratio is highlighted in blue if communicability's value is significantly higher and in orange if SPD is significantly greater.

Polynomial Regression Analysis													
Trph lvls	**LPN**	**NOS**	**WAR**	**FR**	**NDV**	**VAR**	**SP**	**Mean R^2 Comm**	**Mean R^2 SPD**	**C- Std**	**SPD- Std**	**Mean Comm R^2 / SPD R^2**	**Sig**
3	3	108	0.1	I	-	-	P	0.386013	0.246473	0.029184	0.015307	1.567831	+
3	3	108	0.1	I	+	-	P	0.297586	0.200488	0.057941	0.034955	1.484947	+
3	3	108	0.1	I	-	+	P	0.388624	0.253256	0.023086	0.013453	1.537367	+
3	3	108	0.1	I	+	+	P	0.305062	0.195766	0.067232	0.03877	1.575189	+
3	4	108	0.1	I	-	-	P	0.398401	0.319484	0.030407	0.022962	1.24888	+
3	4	108	0.05	I	+	-	P	0.297404	0.194148	0.029882	0.017223	1.52857	+
3	4	108	0.1	I	-	+	P	0.365155	0.287769	0.037017	0.027478	1.269582	+
3	4	108	0.05	I	+	+	P	0.336286	0.218426	0.041207	0.025231	1.537848	+
3	4	108	0.05	I	+ 2	-	P	0.288609	0.187661	0.046569	0.029551	1.536839	+
3	6	108	0.05	I	-	-	P	0.338695	0.321511	0.018693	0.016779	1.052881	+
3	6	108	0.05	I	+	-	P	0.256531	0.195839	0.041255	0.032182	1.316631	+
3	6	108	0.05	I	-	+	P	0.346886	0.330085	0.018125	0.016101	1.050278	+
3	3	48	0.1	I	-	-	P	0.34053	0.240106	0.033473	0.027914	1.431587	+
3	3	48	0.1	I	+	-	P	0.152438	0.157983	0.043328	0.03995	0.923645	-
3	3	48	0.1	I	-	+	P	0.176717	0.184217	0.04205	0.030943	1.39641	+
3	3	48	0.1	I	+	+	P	0.182952	0.156618	0.040961	0.033723	1.249549	+
3	3	108	0.1	II	-	-	P	0.306157	0.220415	0.017478	0.014141	1.389	+
3	3	108	0.1	II	+	-	P	0.250644	0.189394	0.042188	0.028422	1.314887	+
3	3	108	0.1	II	-	+	P	0.305884	0.221554	0.023884	0.016604	1.385655	+
3	3	108	0.1	II	+	+	P	0.251232	0.182096	0.042291	0.02332	1.386542	+
3	4	108	0.1	II	-	-	P	0.276718	0.241249	0.029886	0.022705	1.14284	+
3	4	108	0.05	II	+	-	P	0.379211	0.273783	0.035663	0.022349	1.383385	+
3	4	108	0.1	II	-	+	P	0.252727	0.226334	0.020564	0.017189	1.116665	+
3	4	108	0.05	II	+	+	P	0.388396	0.275748	0.045486	0.030743	1.407203	+
3	4	108	0.05	II	+ 2	-	P	0.337201	0.244821	0.039371	0.024353	1.371434	+
3	6	108	0.05	II	-	-	P	0.548768	0.533148	0.013287	0.012825	1.029312	+
3	6	108	0.05	II	+	-	P	0.369452	0.282212	0.049016	0.033326	1.299295	+
3	6	108	0.05	II	-	+	P	0.554635	0.538667	0.023502	0.022093	1.029449	+
3	3	48	0.1	II	-	-	P	0.261697	0.194411	0.047229	0.036627	1.388618	+
3	3	48	0.1	II	+	-	P	0.233682	0.16673	0.064075	0.032371	1.364748	+
3	3	48	0.1	II	-	+	P	0.374522	0.270491	0.053473	0.038184	1.39641	+
3	3	48	0.1	II	+	+	P	0.277469	0.197124	0.053466	0.035085	1.404933	+

Table 8: Comparison of model treatments with a perturbed resource. A key for all headings can be found in table 4. The mean communicability and SPD R-squared ratio is highlighted in blue if communicability's value is significantly higher and in orange if SPD is significantly greater.

Linear Regression Analysis of Natural Log Transformed Metric Data													
Trph lvls	LPN	NOS	WAR	FR	NDV	VAR	SP	Mean R^2 Comm	Mean R^2 SPD	C- Std	SPD-Std	Mean Comm R^2 / SPD R^2	Sig
3	3	108	0.1	I	-	-	R	0.459501	0.398766	0.033851	0.027109	1.147646	+
3	3	108	0.1	I	+	-	R	0.382777	0.303655	0.019297	0.02102	1.265196	+
3	3	108	0.1	I	-	+	R	0.426664	0.376295	0.026987	0.02582	1.134387	+
3	3	108	0.1	I	+	+	R	0.39383	0.322242	0.038803	0.045213	1.236034	+
3	4	108	0.1	I	-	-	R	0.433912	0.37509	0.028943	0.026282	1.160243	+
3	4	108	0.05	I	+	-	R	0.393231	0.31258	0.039102	0.041133	1.276454	+
3	4	108	0.1	I	-	+	R	0.417276	0.371989	0.029386	0.033585	1.126587	+
3	6	108	0.05	I	-	-	R	0.371262	0.311561	0.030316	0.036544	1.216086	+
3	6	108	0.05	I	+	-	R	0.27412	0.2374	0.032089	0.025159	1.150761	+
3	6	108	0.05	I	-	+	R	0.166381	0.093507	0.030363	0.022846	1.905259	+
3	3	48	0.1	I	-	-	R	0.268742	0.263175	0.021129	0.025604	1.056936	-
3	3	48	0.1	I	+	-	R	0.27458	0.19948	0.031556	0.033951	1.455751	+
3	3	48	0.1	I	-	+	R	0.230613	0.218844	0.019484	0.018193	1.06048	-
3	3	48	0.1	I	+	+	R	0.212633	0.121574	0.026475	0.027956	1.908109	+
3	3	108	0.1	II	-	-	R	0.296172	0.228491	0.0327	0.017468	1.293305	+
3	3	108	0.1	II	+	-	R	0.30652	0.248326	0.034926	0.030075	1.250158	+
3	3	108	0.1	II	-	+	R	0.072266	0.12992	0.010905	0.016661	0.541733	+
3	3	108	0.1	II	+	+	R	0.15043	0.061029	0.010782	0.010971	3.217986	+
3	4	108	0.1	II	-	-	R	0.072266	0.12992	0.010905	0.016661	0.541733	+
3	4	108	0.05	II	+	-	R	0.131321	0.06489	0.021375	0.018622	3.617466	+
3	4	108	0.1	II	-	+	R	0.139511	0.054286	0.011927	0.009513	2.932643	+
3	4	108	0.05	II	+	+	R	0.149316	0.05338	0.010927	0.010885	3.835907	+
3	4	108	0.05	II	+ 2	-	R	0.295528	0.292677	0.012085	0.03564	1.035929	-
3	6	108	0.05	II	-	-	R	0.265068	0.199213	0.024598	0.019567	1.503424	+
3	6	108	0.05	II	+	-	R	0.329445	0.289597	0.010908	0.03435	1.154802	+
3	6	108	0.05	II	-	+	R	0.274363	0.227253	0.029686	0.021378	1.362052	+
3	3	48	0.1	II	-	-	R	0.310682	0.226579	0.011967	0.03743	1.427137	+
3	3	48	0.1	II	+	-	R	0.327179	0.276729	0.012101	0.031278	1.206061	+

Table 9: Comparison of model treatments with a perturbed herbivore. A key for all headings can be found in table 4. The mean communicability and SPD R-squared ratio is highlighted in blue if communicability's value is significantly higher and in orange if SPD is significantly greater.

Linear Regression Analysis of Natural Log Transformed Metric Data

Trph lvls	LPN	NOS	WAR	FR	NDV	VAR	SP	Mean R^2 Comm	Mean R^2 SPD	C- Std	SPD- Std	Mean Comm R^2 / SPD R^2	Sig
3	3	108	0.1	I	-	-	H	0.450033	0.3839	0.015035	0.011977	1.172066	+
3	3	108	0.1	I	+	-	H	0.383076	0.296397	0.029375	0.023315	1.304026	-
3	3	108	0.1	I	-	+	H	0.423178	0.378436	0.02079	0.021359	1.118387	-
3	3	108	0.1	I	+	+	H	0.391321	0.332404	0.033123	0.034337	1.174537	-
3	4	108	0.1	I	-	-	H	0.430798	0.369522	0.022431	0.0212	1.167483	-
3	4	108	0.05	I	+	-	H	0.336965	0.272877	0.028028	0.025	1.245378	+
3	4	108	0.1	I	-	+	H	0.422714	0.363316	0.019288	0.018102	1.163839	-
3	4	108	0.05	I	+	+	H	0.406752	0.312732	0.030301	0.029448	1.31874	-
3	4	108	0.05	I	+ 2	-	H	0.274143	0.236909	0.025796	0.030587	1.166121	+
3	6	108	0.05	I	-	-	H	0.212297	0.150907	0.02165	0.027214	1.44541	+
3	6	108	0.05	I	+	-	H	0.252568	0.254215	0.017301	0.016429	0.99277	-
3	6	108	0.05	I	-	+	H	0.29326	0.249281	0.024021	0.018878	1.182858	+
3	3	48	0.1	I	-	-	H	0.31849	0.278254	0.017057	0.007818	1.143758	+
3	3	48	0.1	I	+	-	H	0.239528	0.171713	0.016691	0.015795	1.402278	+
3	3	48	0.1	I	-	+	H	0.238475	0.256537	0.025416	0.015985	0.930187	-
3	3	48	0.1	I	+	+	H	0.258791	0.247493	0.036021	0.034342	1.052845	-
3	3	108	0.1	II	-	-	H	0.223088	0.263047	0.015604	0.009999	0.846558	+
3	3	108	0.1	II	+	-	H	0.275687	0.258667	0.015948	0.019515	1.062616	-
3	3	108	0.1	II	-	+	H	0.04007	0.151689	0.014146	0.010638	0.267099	+
3	3	108	0.1	II	+	+	H	0.092413	0.132711	0.021154	0.01811	0.732763	+
3	4	108	0.1	II	-	-	H	0.03334	0.16669	0.006488	0.013438	0.213173	+
3	4	108	0.05	II	+	-	H	0.095504	0.137976	0.009905	0.022907	0.696694	-
3	4	108	0.1	II	-	+	H	0.040768	0.163646	0.006527	0.011163	0.246499	+
3	4	108	0.05	II	+	+	H	0.082199	0.103555	0.024554	0.014829	0.803814	+
3	4	108	0.05	II	+ 2	-	H	0.381239	0.298233	0.002592	0.012646	1.275841	-
3	6	108	0.05	II	-	-	H	0.273144	0.186951	0.009989	0.012763	1.557691	+
3	6	108	0.05	II	+	-	H	0.295823	0.234216	0.050532	0.04166	1.266378	-
3	6	108	0.05	II	-	+	H	0.295823	0.234216	0.022434	0.021633	1.266378	-
3	3	48	0.1	II	-	-	H	0.302609	0.225724	0.031975	0.029132	1.426775	-
3	3	48	0.1	II	+	-	H	0.320965	0.261005	0.060909	0.055955	1.229891	-
3	3	48	0.1	II	-	+	H	0.36179	0.28691	0.03748	0.031649	1.360051	-
3	3	48	0.1	II	+	+	H	0.354474	0.323948	0.054287	0.047153	1.08489	-

Table 10: Comparison of model treatments with a perturbed predator. A key for all headings can be found in table 4. The mean communicability and SPD R-squared ratio is highlighted in blue if communicability's value is significantly higher and in orange if SPD is significantly greater.

Linear Regression Analysis of Natural Log Transformed Metric Data													
Trph lvls	**LPN**	**NOS**	**WAR**	**FR**	**NDV**	**VAR**	**SP**	**Mean R^2 Comm**	**Mean R^2 SPD**	**C- Std**	**SPD- Std**	**Mean Comm R^2 / SPD R^2**	**Sig**
3	3	108	0.1	I	-	-	P	0.312467	0.273199	0.017648	0.021401	1.151436	+
3	3	108	0.1	I	+	-	P	0.345057	0.287336	0.02204	0.018901	1.205122	-
3	3	108	0.1	I	-	+	P	0.335021	0.301025	0.038476	0.032819	1.105734	-
3	3	108	0.1	I	+	+	P	0.358965	0.314475	0.026788	0.031527	1.143697	-
3	4	108	0.1	I	-	-	P	0.33633	0.291468	0.021004	0.018705	1.154088	-
3	4	108	0.05	I	+	-	P	0.352408	0.286902	0.02428	0.01974	1.229855	+
3	4	108	0.1	I	-	+	P	0.313622	0.278296	0.042072	0.041713	1.134144	-
3	4	108	0.05	I	+	+	P	0.356947	0.297926	0.034437	0.039266	1.20432	-
3	4	108	0.05	I	+ 2	-	P	0.217911	0.211562	0.023771	0.020583	1.032125	+
3	6	108	0.05	I	-	-	P	0.233641	0.142327	0.021665	0.019578	1.669426	+
3	6	108	0.05	I	+	-	P	0.161569	0.166686	0.011428	0.013011	0.973903	-
3	6	108	0.05	I	-	+	P	0.280145	0.221911	0.029671	0.020457	1.263108	+
3	3	48	0.1	I	-	-	P	0.209681	0.187349	0.030856	0.021854	1.122208	+
3	3	48	0.1	I	+	-	P	0.196421	0.130159	0.01378	0.009743	1.538305	+
3	3	48	0.1	I	-	+	P	0.202044	0.18475	0.018988	0.016561	1.078615	-
3	3	48	0.1	I	+	+	P	0.291536	0.232561	0.033623	0.026618	1.253622	-
3	3	108	0.1	II	-	-	P	0.158694	0.159186	0.023087	0.014391	0.962375	+
3	3	108	0.1	II	+	-	P	0.237854	0.205649	0.027641	0.010136	1.152514	-
3	3	108	0.1	II	-	+	P	0.026432	0.091357	0.005477	0.008771	0.293954	+
3	3	108	0.1	II	+	+	P	0.108226	0.060537	0.008448	0.013699	2.246854	+
3	4	108	0.1	II	-	-	P	0.028534	0.095498	0.008564	0.015722	0.310356	+
3	4	108	0.05	II	+	-	P	0.10576	0.071341	0.020277	0.014343	1.705122	-
3	4	108	0.1	II	-	+	P	0.029289	0.088841	0.00564	0.008827	0.336657	+
3	4	108	0.05	II	+	+	P	0.388396	0.275748	0.011447	0.019784	1.407203	+
3	4	108	0.05	II	+ 2	-	P	0.337201	0.244821	0.039371	0.024353	1.371434	-
3	6	108	0.05	II	-	-	P	0.548768	0.533148	0.013287	0.012825	1.029312	+
3	6	108	0.05	II	+	-	P	0.369452	0.282212	0.049016	0.033326	1.299295	-
3	6	108	0.05	II	-	+	P	0.554635	0.538667	0.023502	0.022093	1.029449	-
3	3	48	0.1	II	-	-	P	0.261697	0.194411	0.047229	0.036627	1.388618	-
3	3	48	0.1	II	+	-	P	0.233682	0.16673	0.064075	0.032371	1.364748	-
3	3	48	0.1	II	-	+	P	0.374522	0.270491	0.053473	0.038184	1.39641	-
3	3	48	0.1	II	+	+	P	0.277469	0.197124	0.053466	0.035085	1.404933	-

Table 11: Comparison across model treatments. Treatments compared are the same in every aspect except for node degree. Each row compares the mean of the communicability and SPD R-squared ratio of a model treatment 3 links per node and a treatment with 6 links per node. The mean highlighted in green indicates the treatment that communicability significantly performed better. P-values in bold are not significant. A key for all headings can be found in Table *4*.

Polynomial Regression Analysis											
Trph lvl	**SPT**	**WAR**	**FR**	**NDR**	**VAR**	**SP**	**Mean 3 LPN**	**Std error**	**Mean 6 LPN**	**Std error**	**P-value**
3	108	0.1	I	-	-	R	1.784369	0.091804	1.051	0.0557	0.0191
3	108	0.1	II	-	-	R	1.600855	0.059383	1.023	0.006451	0.0012
3	108	0.1	I	-	-	H	1.444518	0.048404	1.00005	0.005061	2.67E-09
3	108	0.1	II	-	-	H	1.256097	0.057222	1.004	0.007377	1.89E-08
3	108	0.1	I	-	-	P	1.767343	0.069757	1.053	0.00323	2.22E-04
3	108	0.1	II	-	-	P	1.609389	0.048042	1.029	0.005786	1.09E-05
3	108	0.1	I	-	+	R	1.760271	0.137558	1.019	0.05714	0.0129
3	108	0.1	II	-	+	R	1.627066	0.06607	1.021	0.003733	0.00937
3	108	0.1	I	-	+	H	1.479053	0.077637	1.0028	0.002993	0.0029
3	108	0.1	II	-	+	H	1.330628	0.038705	1.007	0.004942	7.19E-04
3	108	0.1	I	-	+	P	1.836964	0.075713	1.05	0.002296	0.0012
3	108	0.1	II	-	+	P	1.605524	0.06839	1.03	0.006425	0.0013
3	108	0.05	I	+	-	R	1.76873	0.094714	1.0529	0.05714	0.0027
3	108	0.05	II	+	-	R	1.559712	0.133072	1.324	0.003733	0.0095
3	108	0.05	I	+	-	H	1.402758	0.152887	1.233	0.002993	4.45E-09
3	108	0.05	II	+	-	H	1.269991	0.152887	1.302	0.004942	**0.0873**
3	108	0.05	I	+	-	P	1.832317	0.104478	1.317	0.002296	6.35E-06
3	108	0.05	II	+	-	P	1.594591	0.172886	1.299	0.006425	2.7E-05

Table 12: Comparison across model treatments. Treatments compared are the same in every aspect except for node degree. Each row compares the mean of the communicability and SPD R-squared ratio of a model treatment 3 links per node and a treatment with 6 links per node. The mean highlighted in green indicates the treatment that communicability significantly performed better. Values highlighted in orange indicate that SPD had a higher value in both treatments. P-values in bold are not significant. A key for all headings can be found in Table *4*.

Linear Regression Analysis of Natural Log Transformed Metric Data											
Trph lvl	**SPT**	**WAR**	**FR**	**NDR**	**VAR**	**SP**	**Mean 3 LPN**	**Std error**	**Mean 6 LPN**	**Std error**	**P-value**
3	108	0.1	I	-	-	R	0.766	0.02296	0.541733	0.038705	2.14E-09
3	108	0.1	II	-	-	R	0.8747	0.0386	3.217986	0.006451	0.01041
3	108	0.1	I	-	-	H	0.7737	0.07404	0.267099	0.05061	1.70E-07
3	108	0.1	II	-	-	H	0.909	0.07212	0.732763	0.07377	3.27E-06
3	108	0.1	I	-	-	P	0.8461	0.09757	0.293954	0.0423	9.81E-04
3	108	0.1	II	-	-	P	0.893	0.04042	2.246854	0.06839	0.008271
3	108	0.1	I	-	+	R	0.7445	0.01558	2.932643	0.0734	2.37E-05
3	108	0.1	II	-	+	R	0.722	0.05807	3.835907	0.003733	0.008995
3	108	0.1	I	-	+	H	0.743	0.03637	0.246499	0.02993	1.61E-08
3	108	0.1	II	-	+	H	0.838	0.038705	0.803814	0.004942	2.04E-03
3	108	0.1	I	-	+	P	0.822	0.075713	0.336657	0.004796	**0.0056**
3	108	0.1	II	-	+	P	0.851	0.06839	1.960388	0.02645	0.008165
3	108	0.05	I	+	-	R	0.7837	0.02714	0.541733	0.05714	0.022507
3	108	0.05	II	+	-	R	0.0057	0.03072	3.617466	0.00713	1.50E-03
3	108	0.05	I	+	-	H	0.768	0.0832	0.213173	0.0953	8.07E-08
3	108	0.05	II	+	-	H	0.897	0.1587	0.696694	0.0472	1.06E-04
3	108	0.05	I	+	-	P	0.859	0.10778	0.310356	0.0926	0.000109
3	108	0.05	II	+	-	P	0.889	0.072886	1.705122	0.06425	1.55E-05

Table 13: Comparison across model treatments. Treatments compared are the same in every aspect except for node degree heterogeneity. Each row compares the mean of the communicability and SPD R-squared ratio of a model treatment without node degree heterogeneity and a treatment with node degree heterogeneity. The mean highlighted in green indicates the treatment that communicability significantly performed better. P-values in bold are not significant. A key for all headings can be found in Table *4*.

Polynomial Regression Analysis											
Trph Lvl	LPN	NOS	WAR	FR	VAR	SP	Mean w/o NDV	Std Error	Mean w/ NDV	Std Error	P-value
3	3	108	0.1	I	-	R	1.649	0.091804	1.617	0.094714	**0.638123**
3	3	108	0.1	II	-	R	1.449	0.059383	1.507	0.133072	**0.440032**
3	3	108	0.1	I	-	H	1.1449	0.048404	1.196	0.152887	**0.54149**
3	3	108	0.1	II	-	H	0.964	0.057222	1.079	0.152887	**0.069952**
3	3	108	0.1	I	-	P	1.568	0.069757	1.485	0.104478	**0.394003**
3	3	108	0.1	II	-	P	1.395	0.048042	1.315	0.172886	**0.293195**
3	4	108	0.05	I	-	R	1.10857	0.168238	1.447	0.037279	4.78E-08
3	4	108	0.05	II	-	R	1.378112	0.024853	1.413	0.076596	0.0012
3	4	108	0.05	I	-	H	1.038756	0.027639	1.273	0.066126	2.67E-09
3	4	108	0.05	II	-	H	1.113182	0.023978	1.202	0.039739	0.006
3	4	108	0.05	I	-	P	1.389001	0.018548	1.529	0.047364	3.57E-04
3	4	108	0.05	II	-	P	1.10857	0.040254	1.383	0.049424	0.0089
3	6	108	0.05	I	-	R	1.051	0.0557	1.0529	0.05714	1.58E-08
3	6	108	0.05	II	-	R	1.023	0.006451	1.324	0.003733	4.26E-09
3	6	108	0.05	I	-	H	1.00005	0.005061	1.233	0.002993	9.38E-06
3	6	108	0.05	II	-	H	1.004	0.007377	1.302	0.004942	6.68E-09
3	6	108	0.05	I	-	P	1.053	0.00323	1.317	0.002296	1.32E-07
3	6	108	0.05	II	-	P	1.029	0.005786	1.299	0.006425	1.30E-07

Table 14: Comparison across model treatments. Treatments compared are the same in every aspect except for node degree heterogeneity. Each row compares the mean of the communicability and SPD R-squared ratio of a model treatment without node degree heterogeneity and a treatment with node degree heterogeneity. The mean highlighted in green indicates the treatment that communicability significantly performed better. P-values in bold are not significant. A key for all headings can be found in Table *4*.

Linear Regression Analysis of Natural Log Transformed Metric Data											
Trph Lvl	**LPN**	**NOS**	**WAR**	**FR**	**VAR**	**SP**	**Mean w/o NDV**	**Std Error**	**Mean w/ NDV**	**Std Error**	**P-value**
3	3	108	0.1	I	-	R	1.147646	0.0174	1.134387	0.05471	**0.723978**
3	3	108	0.1	II	-	R	1.265196	0.0883	1.236034	0.1543	**0.343328**
3	3	108	0.1	I	-	H	1.172066	0.04404	1.118387	0.1887	**0.057857**
3	3	108	0.1	II	-	H	1.304026	0.07292	1.174537	0.152887	0.004998
3	3	108	0.1	I	-	P	1.151436	0.09757	1.105734	0.1478	**0.157064**
3	3	108	0.1	II	-	P	1.205122	0.08042	1.143697	0.172886	**0.13807**
3	4	108	0.05	I	-	R	1.315	0.1238	1.056936	0.037279	**0.313**
3	4	108	0.05	II	-	R	0.95	0.02453	1.455751	0.0596	0.000637
3	4	108	0.05	I	-	H	1.098	0.0239	0.99277	0.06126	2.60E-01
3	4	108	0.05	II	-	H	0.8279	0.03978	1.182858	0.09739	**0.572**
3	4	108	0.05	I	-	P	1.007	0.08548	0.973903	0.04364	4.07E-01
3	4	108	0.05	II	-	P	1.669426	0.0404	1.263108	0.049424	**0.998**
3	6	108	0.05	I	-	R	0.541733	0.057	0.541733	0.0574	**0.788922**
3	6	108	0.05	II	-	R	3.217986	0.0451	3.617466	0.00733	**0.11795**
3	6	108	0.05	I	-	H	0.267099	0.005061	0.213173	0.00993	**0.716113**
3	6	108	0.05	II	-	H	0.732763	0.007357	0.696694	0.00942	**0.753502**
3	6	108	0.05	I	-	P	0.293954	0.0323	0.310356	0.0096	**0.202996**
3	6	108	0.05	II	-	P	2.246854	0.00786	1.705122	0.06425	**0.668669**

Table 15: Comparison across model treatments. Treatments compared are the same in every aspect except for variation in interaction strength. Each row compares the mean of the communicability and SPD R-squared ratio of a model treatment without variation in interaction strengths and a treatment with variations in interaction strength. The mean highlighted in green indicates the treatment that communicability significantly performed better. P-values in bold are not significant. A key for all headings can be found in Table *4*.

Polynomial Regression Analysis											
Trph Lvl	LPN	NOS	WAR	FR	NDV	SP	Mean w/o VAR	Std Error	Mean w/ VAR	Std Error	P-value
3	3	108	0.1	I	-	R	1.649	0.092	1.597	0.13755	**0.3752**
3	3	108	0.1	II	-	R	1.449	0.059	1.415	0.06607	**0.5076**
3	3	108	0.1	I	-	H	1.1449	0.048	1.093	0.07763	**0.1112**
3	3	108	0.1	II	-	H	0.964	0.057	0.972	0.03870	**0.8787**
3	3	108	0.1	I	-	P	1.568	0.0698	1.537	0.07571	**0.5456**
3	3	108	0.1	II	-	P	1.395	0.048	1.386	0.06839	**0.8154**
3	4	108	0.1	I	-	R	1.242	0.168	1.1999	0.06348	**0.0797**
3	4	108	0.1	II	-	R	1.109	0.0249	1.139	0.0382	1.56E-01
3	4	108	0.1	I	-	H	0.98	0.028	1.0035	0.03044	3.29E-01
3	4	108	0.1	II	-	H	0.873	0.024	0.898	0.03727	3.85E-01
3	4	108	0.1	I	-	P	1.249	0.019	1.269	0.05067	5.01E-01
3	4	108	0.1	II	-	P	1.143	0.04	1.117	0.04385	2.23E-01
3	6	108	0.05	I	-	R	1.051	0.056	1.019	0.05714	4.74E-09
3	6	108	0.05	II	-	R	1.023	0.0065	1.021	0.00373	3.91E-01
3	6	108	0.05	I	-	H	1.00005	0.0051	1.0028	0.00299	5.54E-01
3	6	108	0.05	II	-	H	1.004	0.0074	1.007	0.00494	1.05E-01
3	6	108	0.05	I	-	P	1.05357	0.003	1.0512	0.00229	5.60E-01
3	6	108	0.05	II	-	P	1.02914	0.0058	1.0358	0.00642	9.65E-01

Table 16: Comparison across model treatments. Treatments compared are the same in every aspect except for variation in interaction strength. Each row compares the mean of the communicability and SPD R-squared ratio of a model treatment without variation in interaction strengths and a treatment with variations in interaction strength. The mean highlighted in green indicates the treatment that communicability significantly performed better. P-values in bold are not significant. A key for all headings can be found in Table *4*.

Linear Regression Analysis of Natural Log Transformed Metric Data											
Trph Lvl	**LPN**	**NOS**	**WAR**	**FR**	**NDV**	**SP**	**Mean w/o VAR**	**Std Error**	**Mean w/ VAR**	**Std Error**	**P-value**
3	3	108	0.1	I	-	R	1.147646	0.04392	1.160243	0.0755	**0.598327**
3	3	108	0.1	II	-	R	1.265196	0.0119	1.276454	0.08707	**0.818267**
3	3	108	0.1	I	-	H	1.172066	0.02368	1.167483	0.063	**0.883189**
3	3	108	0.1	II	-	H	1.304026	0.0377	1.245378	0.0340	**0.176928**
3	3	108	0.1	I	-	P	1.151436	0.06298	1.154088	0.0571	**0.935645**
3	3	108	0.1	II	-	P	1.205122	0.0848	1.229855	0.08339	**0.542534**
3	4	108	0.1	I	-	R	1.150761	0.1368	1.06048	0.0448	**0.224817**
3	4	108	0.1	II	-	R	1.905259	0.02539	1.908109	0.0382	**0.986828**
3	4	108	0.1	I	-	H	1.166121	0.01128	1.143758	0.01044	**0.77872**
3	4	108	0.1	II	-	H	1.44541	0.0124	1.402278	0.01027	**0.632473**
3	4	108	0.1	I	-	P	1.032125	0.03319	1.122208	0.08067	**0.270208**
3	4	108	0.1	II	-	P	1.669426	0.0674	1.538305	0.0985	**0.208758**
3	6	108	0.05	I	-	R	0.541733	0.0956	2.932643	0.0524	**0.163107**
3	6	108	0.05	II	-	R	3.217986	0.0965	3.835907	0.0373	**0.515384**
3	6	108	0.05	I	-	H	0.267099	0.0351	0.246499	0.0289	**0.294678**
3	6	108	0.05	II	-	H	0.732763	0.00454	0.803814	0.0394	**0.497157**
3	6	108	0.05	I	-	P	0.293954	0.00983	0.336657	0.0038	**0.491294**
3	6	108	0.05	II	-	P	2.246854	0.00358	1.960388	0.0782	**0.326136**

Table 17: Comparison across model treatments. Treatments compared are the same in every aspect except for functional response. Each row compares the mean of the communicability and SPD R-squared ratio of a model with type I functional response and a treatment with type II functional response. The mean highlighted in green indicates the treatment that communicability significantly performed better. P-values in bold are not significant. A key for all headings can be found in Table *4*.

Polynomial Regression Analysis											
Trph lvls	**LPN**	**NOS**	**WAR**	**NDV**	**VAR**	**SP**	**Mean w/ type I**	**Std Error**	**Mean w/ type II**	**Std Error**	**P-value**
3	3	108	0.1	-	-	R	1.649	0.023502	1.448806	0.022093	0.000446
3	3	108	0.1	+	-	R	1.61	0.047229	1.507336	0.039371	1.58E-08
3	3	108	0.1	-	+	R	1.59	0.064075	1.415341	0.013287	0.00152
3	3	108	0.1	+	+	R	1.69	0.053473	1.405352	0.049016	9.59E-03
3	4	108	0.1	-	-	R	1.243872	0.055955	1.109101	0.035085	0.005546
3	4	108	0.05	+	-	R	1.446661	0.031649	1.413227	0.016101	0.004507
3	4	108	0.1	-	+	R	1.199866	0.047153	1.139632	0.027914	0.002324
3	6	108	0.05	-	-	R	1.05287	0.021854	1.023852	0.041255	1.59E-07
3	6	108	0.05	+	-	R	1.048	0.009743	1.324248	0.018125	1.58E-08
3	6	108	0.05	-	+	R	1.019123	0.016561	1.021231	0.033473	**0.215744**
3	3	48	0.1	-	-	R	1.405817	0.022431	1.315496	0.055955	0.007515
3	3	48	0.1	+	-	R	1.617462	0.028028	1.346547	0.033792	0.002736
3	3	48	0.1	-	+	R	1.272804	0.019288	1.04426	0.032374	**0.230461**
3	3	48	0.1	+	+	R	1.347708	0.023771	1.770753	0.015307	**0.512014**
3	3	108	0.1	-	-	H	1.144861	0.021665	0.964371	0.034955	0.000771
3	3	108	0.1	+	-	H	1.195786	0.011428	1.079824	0.029132	0.004978
3	3	108	0.1	-	+	H	1.092896	0.026282	0.971827	0.055955	**0.308326**
3	3	108	0.1	+	+	H	1.203193	0.041133	1.249805	0.031649	0.007078
3	4	108	0.1	-	-	H	0.980978	0.033585	0.873162	0.047153	**0.156834**
3	4	108	0.05	+	-	H	1.272681	0.036544	1.202311	0.033275	3.55E-03
3	4	108	0.1	-	+	H	1.003469	0.027107	0.897622	0.027405	2.48E-04
3	4	108	0.05	+	+	H	1.265754	0.038021	1.166916	0.052327	1.33E-02
3	4	108	0.05	2	-	H	1.312044	0.009999	1.21629	0.015123	0.011486
3	6	108	0.05	-	-	H	1.000054	0.019515	1.004437	0.041086	**0.091881**
3	6	108	0.05	+	-	H	1.232671	0.030409	1.301607	0.0255	**0.132477**
3	6	108	0.05	-	+	H	1.002771	0.058378	1.006795	0.0366	1.27E-08
3	3	48	0.1	-	-	H	1.0224	0.031673	0.899697	0.045	2.33E-07
3	3	48	0.1	+	-	H	1.076451	0.019	1.076451	0.037	**0.094812**
3	3	48	0.1	-	+	H	1.352422	0.034	0.983262	0.0178	**0.206042**
3	3	48	0.1	+	+	H	1.451974	0.0213	1.140404	0.0115	3.29E-06
3	3	108	0.1	-	-	P	1.567831	0.053389	1.389	0.0228	**0.290072**
3	3	108	0.1	+	-	P	1.484947	0.024073	1.314887	0.0259	0.042366
3	3	108	0.1	-	+	P	1.537367	0.038168	1.385655	0.021884	**0.06105**
3	3	108	0.1	+	+	P	1.575189	0.016481	1.386542	0.047538	2.31E-05
3	4	108	0.1	-	-	P	1.24888	0.021433	1.14284	0.0247	0.023425
3	4	108	0.05	+	-	P	1.52857	0.0271	1.383385	0.0218	**0.537183**
3	4	108	0.1	-	+	P	1.269582	0.02172	1.116665	0.030409	0.000166
3	4	108	0.05	+	+	P	1.537848	0.021	1.407203	0.058378	2.42E-06
3	4	108	0.05	2	-	P	1.536839	0.025	1.371434	0.031673	2.17E-05
3	6	108	0.05	-	-	P	1.052881	0.042	1.029312	0.033275	4.23E-07
3	6	108	0.05	+	-	P	1.316631	0.0115	1.299295	0.027405	**0.674519**
3	6	108	0.05	-	+	P	1.050278	0.0228	1.029449	0.052327	4.95E-05
3	3	48	0.1	-	-	P	1.431587	0.0259	1.388618	0.057941	1.27E-08
3	3	48	0.1	+	-	P	0.923645	0.0276	1.364748	0.015307	2.88E-08
3	3	48	0.1	-	+	P	1.39641	0.0247	1.45798	0.034955	9.94E-09
3	3	48	0.1	+	+	P	1.249549	0.0218	1.404933	0.013453	1.21E-07

Table 18: Comparison across model treatments. Treatments compared are the same in every aspect except for functional response. Each row compares the mean of the communicability and SPD R-squared ratio of a model with type I functional response and a treatment with type II functional response. The mean highlighted in green indicates the treatment that communicability significantly performed better. P-values in bold are not significant. A key for all headings can be found in Table *4*.

Linear Regression of Natural Log Transformation											
Trph lvls	**LPN**	**NOS**	**WAR**	**NDV**	**VAR**	**SP**	**Mean w/ type I**	**Std Error**	**Mean w/ type II**	**Std Error**	**P-value**
3	3	108	0.1	-	-	R	1.147646	0.026987	1.293305	0.055955	0.005012
3	3	108	0.1	+	-	R	1.265196	0.038803	1.250158	0.031649	**0.140467**
3	3	108	0.1	-	+	R	1.134387	0.028943	0.541733	0.034342	0.006652
3	3	108	0.1	+	+	R	1.236034	0.032089	3.217986	0.021401	0.14671
3	4	108	0.1	-	-	R	1.160243	0.030363	0.541733	0.018901	3.66E-05
3	4	108	0.05	+	-	R	1.276454	0.021129	3.617466	0.022434	0.00985
3	4	108	0.1	-	+	R	1.126587	0.021375	2.932643	0.031975	5.11E-07
3	6	108	0.05	-	-	R	1.216086	0.011927	1.503424	0.060909	0.007477
3	6	108	0.05	+	-	R	1.150761	0.024598	1.154802	0.03748	0.033655
3	6	108	0.05	-	+	R	1.905259	0.010908	1.362052	0.021854	**0.329906**
3	3	48	0.1	-	-	R	1.056936	0.030587	1.427137	0.009743	0.002964
3	3	48	0.1	+	-	R	1.455751	0.027214	1.206061	0.016561	**0.214457**
3	3	48	0.1	-	+	R	1.06048	0.016429	1.182311	0.026618	0.016266
3	3	48	0.1	+	+	R	1.908109	0.018878	1.149164	0.014391	0.004077
3	3	108	0.1	-	-	H	1.172066	0.012646	0.846558	0.010136	0.001683
3	3	108	0.1	+	-	H	1.304026	0.012763	1.062616	0.008771	0.010114
3	3	108	0.1	-	+	H	1.118387	0.04166	0.267099	0.16673	0.041623
3	3	108	0.1	+	+	H	1.174537	0.021633	0.732763	0.270491	0.005647
3	4	108	0.1	-	-	H	1.167483	0.023771	0.213173	0.197124	0.002475
3	4	108	0.05	+	-	H	1.245378	0.021665	0.696694	0.011977	0.007542
3	4	108	0.1	-	+	H	1.163839	0.011428	0.246499	0.023315	0.004528
3	4	108	0.05	+	+	H	1.31874	0.008771	0.803814	0.021359	0.033333
3	4	108	0.05	2	-	H	1.166121	0.013699	1.275841	0.012646	0.005798
3	6	108	0.05	-	-	H	1.44541	0.015722	1.557691	0.012763	1.73E-07
3	6	108	0.05	+	-	H	0.99277	0.024353	1.266378	0.04166	2.30E-05
3	6	108	0.05	-	+	H	1.182858	0.012825	1.266378	0.02582	2.67E-12
3	3	48	0.1	-	-	H	1.143758	0.033326	1.426775	0.045213	0.030904
3	3	48	0.1	+	-	H	1.402278	0.022093	1.229891	0.026282	**0.198355**
3	3	48	0.1	-	+	H	0.930187	0.029671	1.360051	0.034926	**0.081204**
3	3	48	0.1	+	+	H	1.052845	0.030856	1.08489	0.010905	0.005151
3	3	108	0.1	-	-	P	1.151436	0.01378	0.962375	0.010782	**0.192474**
3	3	108	0.1	+	-	P	1.205122	0.018988	1.152514	0.027956	**0.237869**
3	3	108	0.1	-	+	P	1.105734	0.095498	0.293954	0.011977	**0.056082**
3	3	108	0.1	+	+	P	1.143697	0.071341	2.246854	0.023315	**0.269988**
3	4	108	0.1	-	-	P	1.154088	0.088841	0.310356	0.226579	5.01E-08
3	4	108	0.05	+	-	P	1.229855	0.275748	1.705122	0.276729	0.00104
3	4	108	0.1	-	+	P	1.134144	0.018102	0.336657	0.023315	0.003764
3	4	108	0.05	+	+	P	1.20432	0.029448	1.407203	0.021359	1.77E-06
3	4	108	0.05	2	-	P	1.032125	0.030587	1.371434	0.263047	0.040936
3	6	108	0.05	-	-	P	1.669426	0.027214	1.029312	0.009989	**0.110352**
3	6	108	0.05	+	-	P	0.973903	0.021633	1.299295	0.050532	4.05E-05
3	6	108	0.05	-	+	P	1.263108	0.029132	1.029449	0.022434	2.55E-05
3	3	48	0.1	-	-	P	1.122208	0.055955	1.388618	0.031649	2.53E-06
3	3	48	0.1	+	-	P	1.538305	0.049016	1.364748	0.047153	**0.182888**
3	3	48	0.1	-	+	P	1.078615	0.023502	1.39641	0.014391	**0.939171**
3	3	48	0.1	+	+	P	1.253622	0.047229	1.404933	0.023315	**0.237665**