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Ecological Flow Analysis of Network Collapse II: Indicators of ecosystem level vulnerability

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Abstract: Using donor-controlled, bottom-up equations to describe network collapse we systematically investigate the impact each species has on the survival or extinction of other species. Short of extinction, one can determine the integrated losses experienced by the ecosystem. These losses are aggregated into system level indicators, such as entropy, average gain/loss, average time to extinction, etc. The methodology is applied to 18 ecological flow networks available in the literature. We calculate the correlations between various indicators and determine high positive correlation between: number of nodes & maximal trophic level; connectedness & average entropy losses; number of nodes & average number of extinct nodes; and, maximum trophic level & evenness of links. A high negative correlation was found between: number of nodes & connectedness; connectedness & maximal trophic level; maximum tropic level & average entropy loss; and, connectedness & evenness of flows. Lastly, a low correlation was found between: average number of extinct compartments & evenness of flows; number of nodes & evenness of stocks; and, evenness of flows & evenness of stocks.

***Keywords**:* Ecological Network Analysis; Ecosystem Flows; Extinction; Indicators; Vulnerability

1.0 INTRODUCTION

Ecological food webs are analyzed in order to understand structural and functional properties derived from the exchange of energy between trophic levels. In the companion paper, *Ecological Flow Analysis of Network Collapse I: New methodology to investigate network collapse dynamics*, we use the Cone Spring ecosystem model (Tilly, 1968) to introduce a methodology to assess the network response to collapse of each species. We found that the collapse may be such that either the entire system eventually goes extinct, or that some compartments go extinct while others do not. When extinction occurs, this approach also allows one to calculate the time to extinction and by introducing a discounting factor the overall utility of each compartment to the collapsed condition. When extinction does not occur, the biomass compartments in the ecological system may converge to a new steady state or some may grow unboundedly.

To demonstrate these results, Figure 1 shows the Cone Spring ecosystem decomposed in the various impacts from collapse of other compartments. In some cases (solid shaded) the compartment loses biomass resulting from the other collapse and in some cases (checkered shading) the compartment gains biomass. The center color represents each particular node. For example, plants are reddish brown, and show a large impact (greater than 50%) on the detritus, bacteria, and detrital feeders. The fifth compartment, carnivores, is mostly controlled by the bacteria compartment (blue-green).

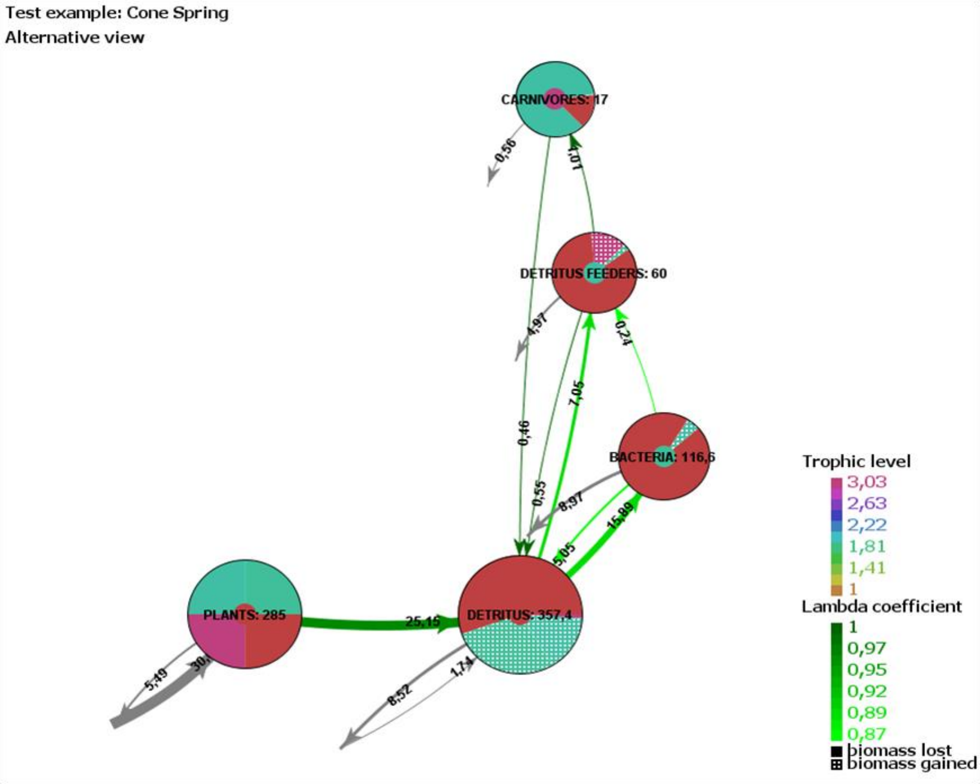

Figure 1. Response of each compartment to the collapse of the other compartments.

In this paper, we propose a series of indicators that describe in more detail the ecosystem response to collapse. These indicators are categorized as vulnerability indicators and structural indicators. Vulnerability is related to the change in biomass and the likelihood of extinction.

The biomass factors include:

- total entropy
- impact evenness
- average relative change
- average relative loss
- average relative gain

The extinction factors include:

- number of extinct compartments
- fraction of extinct compartments
- average time to extinction

Structural indicators are derived from the topology of the network, as well the flow and storage distribution. These indicators are given as:

- number of compartments
- connectivity
- maximum trophic level

- evenness of links
- evenness of stocks
- fraction of weak links

1.1 Data Sources

One of the challenges of testing food web indicators is the lack of data of existing ecological networks that have quantified flow values. There is a significant effort needed to construct these networks (Fath et al., 2007) and only a limited number of good data sets are available in the literature. This paucity of data has instigated the development of community assembly rules (Williams and Martinez, 2000; Halnes et al. 2007) to generate realistic data from heuristics about how food webs are connected. However, these assembly rules typically only generate the network topology and not the flow values needed for our analysis. One approach could be to assign fractional flow probabilities (such as 10%) to each trophic link as a first approximation (see Fath, 2004), but it is better to use empirical data sets if available. While it is preferable to acquire additional empirical network data, there is a bias introduced based on the degree of aggregation and in the treatment of the detrital compartments. Here, we utilize a set of 18 empirically derived ecosystem models available in the EcoPath with EcoSim (Christensen and Walters, 2004; www.ecopath.org/models) database which gives full information on the flows and stocks in each network.

The mean and variance is calculated for the indicators 1) Impact evenness, 2) Average relative change, 3) Average relative loss, 4) Average relative gain, 5) Number of extinct compartments, 6) Fraction of extinct compartments, and 7) Average time to extinction. For example, looking at the last indicator, average time to extinction, the mean is the average time for other compartments to collapse after the removal of the initial compartment (for details on the time to extinction see companion paper Ecological Flow Analysis of Network Collapse I: New methodology to investigate network collapse dynamics). This counts only those compartments which collapse as a result of the compartment removal. The variance is second momentum associated with the uncertainty of the mean. We determine whether positive or negative correlations exist between the indicators listed above and summarize the conclusions below.

2.0 RESULTS

Using the 18 ecosystem networks available accompanying the EcoPath software, indicator values are calculated and averages obtained. Table 1 provides the summary results of the collapse analysis. We see that connectivity had the most high positive correlations on three different categories and the fraction of weak links had the most number of high negative correlations. Looking across rows shows that the mean impact evenness was highly affected by 5 of the 6 structural indicators. Only evenness of stocks did not influence it. Details of these results are explained below.

3.0 CONCLUSIONS

The results clearly show that the collapse of each compartment has a variable impact on the other compartments in the network. The structural properties provide a measure of the overall robustness of the network to perturbation. We consider in detail when there is biomass loss and when there is extinction.

3.1 Population

The more populated the ecosystem, the higher the probability of the existence of dominated compartments; in the case of high ecosystem connectivity, the collapse of some compartment effects the other compartments in equal measure. Collapse of high trophic levels' compartments produces crucial influence on the ecosystem. The higher the maximum trophic level the less the uncertainty of the average losses distribution. High population of the ecosystem increases uncertainty of the average relative losses distribution, while the high system connectivity on the contrary reduces this uncertainty.

Table 1. Computed indicator values for the 18 ecosystem networks which measure the overall robustness of the ecological network to perturbations.

		Structural Indicators					
		# of compart-ments	***Connect-ivity***	***Maximum trophic level***	***Link evenness***	***Stock evenness***	***Weak links fraction***
Total entropy		-0.18	0.39	-0.25	-0.29	-0.17	-0.39
Impact evenness	***mean***	-0.55	0.76	-0.60	-0.51	0.11	-0.59
	variance	-0.42	0.43	-0.23	-0.30	0.05	-0.75
Average relative change	***mean***	0.01	-0.21	0.07	0.30	0.40	-0.02
	variance	0.13	-0.29	0.22	0.41	0.31	-0.04
Average relative loss	***mean***	0.42	-0.27	0.12	0.57	0.15	0.37
	variance	-0.59	0.72	-0.48	-0.45	0.01	-0.78
Average relative gain	***mean***	-0.28	0.26	-0.45	-0.43	0.29	0.05
	variance	0.18	-0.35	0.44	0.59	0.01	-0.05
Number of extinct compart-ments	***mean***	0.72	-0.31	0.05	0.02	0.17	0.50
	variance	-0.05	-0.04	0.17	0.01	-0.04	-0.37
Fraction of extinct compart-ments	***mean***	0.46	-0.11	-0.08	-0.04	0.36	0.43
	variance	-0.42	0.64	-0.38	-0.35	0.21	-0.81
Average time to extinction	***mean***	-0.39	0.43	-0.23	-0.19	-0.10	-0.79
	variance	-0.40	0.39	-0.18	-0.58	0.03	-0.57

>0.5 - high positive correlation

<-0.5 - high negative correlation

>-0.05, <0.05 - low correlation

3.2 Stocks and flows

If the evenness of energy flows is low, then the probability of the existence of a dominant compartment is high (collapse of dominant compartment produces crucial influence on the ecosystem). If the evenness of links is higher, then the relative losses are greater, but the uncertainty of the losses distribution is less. Flow evenness is also related to the information content which defines the network, implying lower uncertainty. The high evenness of ecosystem links and stocks tend to increase the average relative changes and its distribution uncertainty.

3.3 Weak Links

Weak links are often very important for establishing strongly connected components and ensuring the full connectivity and transfer of energy in the ecosystem. Therefore, it is not surprising that they can have a dominant impact on the collapse dynamic. Specifically, the more ecosystem links that are weak, the more uneven the compartments' collapse impacts. A larger number of weak links increases the average losses and its distribution uncertainty.

3.4 Extinction

In cases when we observe extinction, the more compartments there are in the ecosystem the higher is the absolute and relative quantity of extinct compartments. System connectivity does not influence significantly the number of extinct compartments, but high connectivity increases the average time to extinction and uncertainty of its distribution. Maximum trophic level does not affect the extinction associated indicators. Furthermore, evenness of links does not influence the extinction indicators, except the fact that with high links evenness decreases the average time to extinction distribution uncertainty. Evenness of stocks does not affect the number of extinct compartments and the average time to extinction, but the high value of this indicator tends to increase the fraction of extinct compartments. Lastly, the more links that are weak the more is the absolute and relative numbers of extinct compartments and the less is the uncertainty of these indicators' distributions. The weakness of links decreases the time to extinction and its distribution uncertainty.

3.5 Next steps

It is important for environmental management to have a deep and reliable toolbox of ecological indicators. The indicators presented in this paper attempt to shed light on the energetic, network, and temporal (in terms of extinction) characteristics of the ecosystem data. The ecosystem models were first converted to simulation models using the approach described in the earlier paper. There are certain biases inherent in these approaches, such as the donor-controlled approach used places considerable significance to the compartments that play a role in energy acquisition (primarily plants). Therefore, the approach is called "bottom-up". Interestingly, it was not the maximum trophic level had a noticeable correlation with only two of the indicators.

This work is only the first step in marrying the network simulation approach above and the calculation of usable ecological indicators from those results. We intend to continue to explore and test these indicators, in particular, with some attention to the cross-type (e.g., network v. biomass or temporal v. network) correlations. In the future, we will also consider other empirical datasets such as those available at ATLSS website (Across Trophic Level System Simulation).

REFERENCES

Christensen, V., and Walters, C.J., Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling, 172*, 109–139, 2004.

Fath, B.D., Network analysis applied to large-scale cyber-ecosystems. *Ecological Modelling 171*, 329–337, 2004.

Fath, B.D., Scharler, U., Ulanowicz, R.E., and Hannon, B.. Ecological Network Analysis: Network Construction. *Ecological Modelling 208*, 49–55 2007.

Halnes, G., Fath, B.D., and Liljenström, H., The modified niche model: Including a detritus compartment in simple structural food web models. *Ecological Modelling 208*, 9–16 2007.

Tilly, L. J., The Structure and Dynamics of Cone Spring. *Ecological Monographs, 38*, 169–197, 1968.

Williams, R.J., and Martinez, N.D., Simple rules yield complex food webs. *Nature 404*, 180–183, 2000.