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Ecological Flow Analysis of Network Collapse I: New methodology to investigate network collapse dynamics

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Abstract: This research builds on standard ecological network analysis techniques in order to investigate the impact of removing species (nodes) on the remaining of the network species. The flow network is expressed as a system of dynamical equations such that the removal of one node has time-forward impacts on the remaining nodes. The approach allows one to determine the gain or loss experienced by each other compartment in the model and the time for such impact to occur. The general methodology is demonstrated on the Cone Spring Ecosystem. These results indicate that collapse of certain species exert more control on the overall network organization. We also investigate model sensitivity to determine discount rate robustness and discuss further research.

Keywords: Collapse; Discount Factor; Donor-controlled Models; Ecological Network Analysis; Extinction time; Food Webs;

1 INTRODUCTION

A food web is a conceptualization of the energy interactions in an ecosystem. It provides a means to identify how species are interconnected by the supply and utilization of energy exchange with each other and also with the external environment. The term “species” is often used to mean “trophic species”, defined as the set of biological species that utilize energy that has been processed a similar number of biotic transformations. There is ample literature on how to aggregate species into conceptual species groups or compartments (Solow and Beet, 1998; Krause et al., 2003) either strictly defined as “trophic species”, or less strictly as “similar species”, having more or less the same roles in terms of diet and predation. Food webs have been extensively studied in terms of the stability and indirect network interactions (May, 2000; McCann, 2000; Patten, 1985). Here, we suggest an approach to quantify the potential impact of collapse of a particular compartment or the environment on the other compartments in the network. The compartment represents the state variables of interest as given by their stock (amount) and input output flow relations.

Specifically, we assume a finite speed of energy drift between compartments and view the food web as a discrete-time dynamical system. This implies that during each time period the compartments and the environment exchange portions of energy (flows) which results in changes in the compartment’s stocks. If the system

is in steady state, then both the energy flows and stocks remain the same in each time period. A collapse of any compartment or the environment in some time period moves the system away from its steady state and the “domino” effect of changes in flows and stocks due to collapse starts to occur over all subsequent time periods. Along the collapse dynamics, network compartments may receive different energy inflows as compared with those in the steady state. Hence, they face the necessity to set up regulation rules which describes the compartment’s adaptation to changes in the energy inflows. We examine three types of regulation rules in our work: 1) donor-controlled approach, 2) recipient-controlled approach and 3) meeting-and-equivalence approach (Kazanci 2006). The donor-controlled approach defines a linear relation between a stock and each of its out-coming flow. On the contrary, the recipient-controlled approach defines a linear relation between a stock and each incoming flow. Finally, the meeting-and-equivalence approach claims that a flow from one compartment to another is proportional to the product of both stocks.

For each network compartment, the collapse dynamic determines a time series of losses in the energy stocks. To quantify the negative impact of that series of energy losses on the compartment, we impose a positive discount effect. Based on that, we define a compartment’s utility to be the weighted sum of the energy stocks in the present period and in all the subsequent periods, with the weights decreasing over time. As discussed, the collapse dynamics of any compartment determines losses in utility for other compartments. These pair-wise collapse-loss relationships form a matrix of relative integrated discounted losses, a model of the network’s sensitivity to collapses in all individual compartments. The matrix of losses is obviously a function of the initial stationary flows and the regulation rules.

2.0 EXAMPLE – CONE SPRING ECOSYSTEM

This new collapse investigation methodology is demonstrated using data from the Cone Spring Ecosystem (Tilly, 1968), a very well studied model and one of the early quantified food web systems. Compartments are connected by transaction of the energy flows between them (Figure 1). These pair-wise couplings are the basis for the internal network structure. The sum of all throughflows is called Total System Throughflow (TST) and is an important measure of the total energy (power) passing through the network. For the Cone Spring ecosystem $TST = 30626 \text{ kcal m}^{-2}\text{y}^{-1}$. The connectivity oriented from columns-to-rows is given in the corresponding agency matrix where a “1” represents a direct link and zero no direct link between each pair-wise set of compartments:

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 & 0 \\ 1 & 1 & 1 & 1 & 0 \end{bmatrix} \quad (1)$$

And, the internal flows can be compacted into the corresponding flow matrix, F:

$$F = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 5205 \\ 0 & 75 & 0 & 0 & 2309 \\ 0 & 0 & 370 & 0 & 0 \\ 8881 & 1600 & 200 & 167 & 0 \end{bmatrix} \quad (2)$$

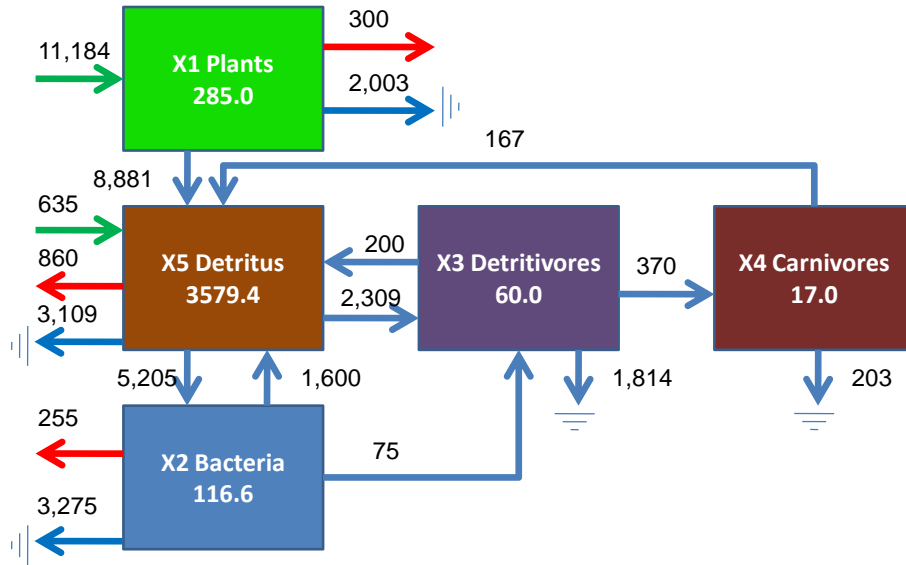


Fig. 1: The network of energy flows in the Cone Spring ecosystem where X1 = Plants; X2 = Bacteria; X3 = Detritivores; X4 = Carnivores; and X5 = Detritus. All flows are in units of $\text{kcal m}^{-2}\text{y}^{-1}$. Biomasses (values inside compartments) are in kcal m^{-2} . Arrows not originating from a compartment represent external inputs. All arrows not terminating into a compartment represent exports of still useable energy. Numbers near ground symbols represent respired (degraded) energy.

Applying the three regulation rules mentioned above one can generate a system of 5 differential equations. Methodologically, we show dx_1/dt for each rule type and leave the rest to the reader.

1) donor-controlled approach:

$$\frac{dx_1}{dt} = z_1 - c_{51}x_1 - r_1 - y_1$$

2) recipient-controlled approach

$$\frac{dx_1}{dt} = z_1 - c_{51}x_5 - r_1 - y_1$$

3) meeting-and-equivalence approach

$$\frac{dx_1}{dt} = z_1 - c_{51}x_1x_5 - r_1 - y_1$$

Where z_1 is the input flow from the environment to compartment 1, y_1 is the loss term to the environment from compartment 1, and r_1 is the respiration loss from compartment 1. The value of the coefficient c_{51} varies depending on the equation type used.

The model system was simulated using the three equation types mentioned above. Only the donor-controlled approach was stable in the neighborhood of the steady state while the recipient-controlled and meeting-and-equivalence approaches did not reach stable steady states. Therefore, the donor-controlled approach was used throughout the rest of the analysis.

3.0 RESULTS

Model results demonstrate the down stream impact that the collapse of each compartment has on the rest of the model. Clearly, in this model, the plants compartment, X1 plays the role of the major input source of energy for the other compartments. Losing that compartment will significantly affect the others (Figure 2). Note, however, the other compartments do not go to zero because they retain some energy flow entering through compartment X5, detritus. The results for all collapses are not shown, but note the interesting variable response with the collapse of the detritivores, compartment X3 (Figure 3). The plants are unaffected by the collapse of the detritivores, whereas, the bacteria and detritus both benefit reaching a higher stable level. The carnivores are negatively impacted reaching a lower stable state because they lose a potential source of inflow.

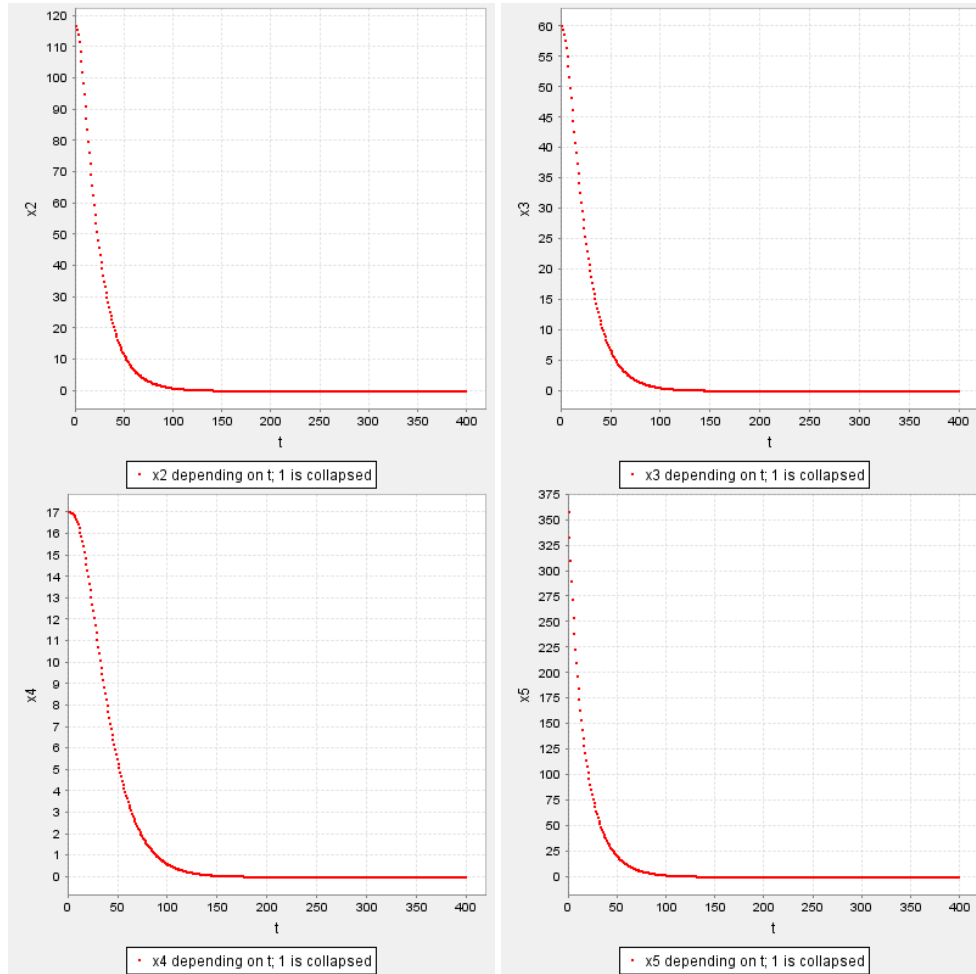


Figure 2 represents the time trajectories of the collapse dynamics of stocks when compartment 1 (plants) collapses. This leads to asymptotically diminishing of all other stocks (bacteria, detritivores, carnivores and detritus).

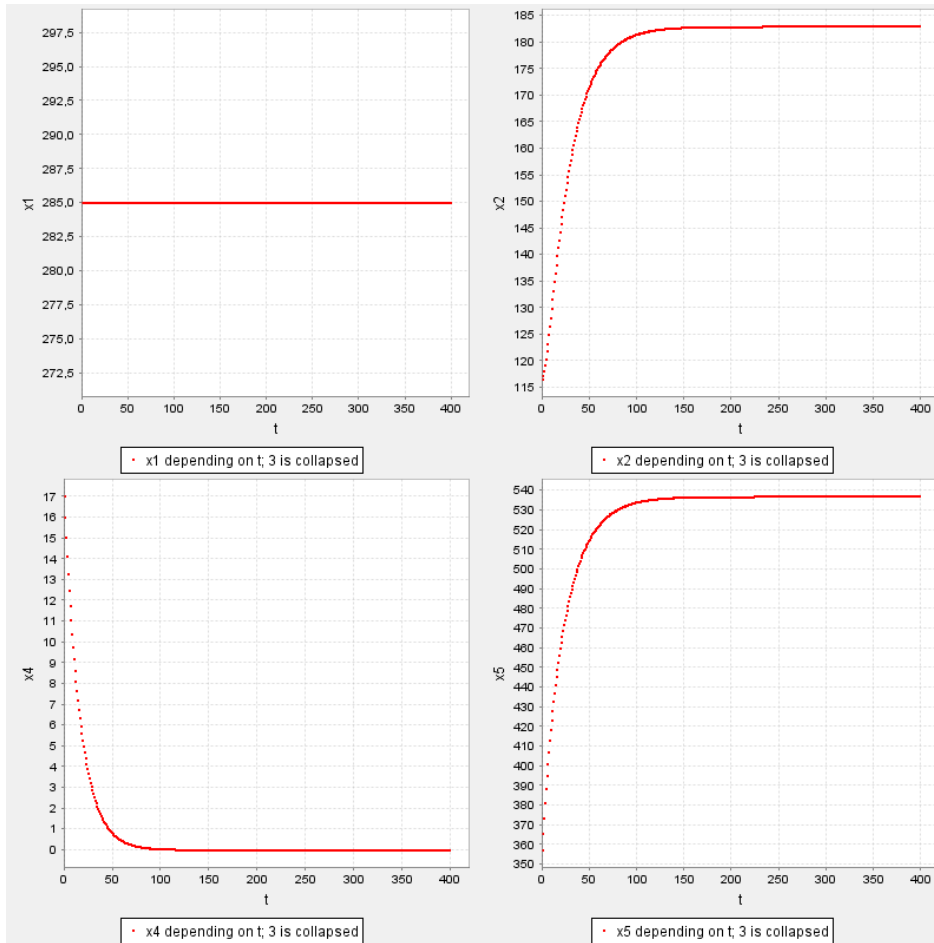


Figure 3: The collapse dynamics (stocks) when compartment 3 (detritivores) collapses. 3a is impact on X1, 3b is impact on X2, 3c is impact on X4, and 3d is impact on X5.

3.1 Extinction Times

The collapse of certain compartments may lead to the disappearance or extinction of other species. Since these are dynamic processes, one could ascertain the speed of the loss. These extinction times for each compartment are given in Table 1. The entire simulation was run for 400 time steps. The shorter the extinction time the faster the compartment disappeared. Specifically, Table 1 shows the time if any to extinction of other species with the removal of the focal species (listed along the columns). The diagonal is zero because by definition the extinction is instantaneous when that compartment is removed. For example, when the plants compartment is removed (X1) the detritivores (x3) disappear after 271 time steps, the carnivores (X4) after 277 time steps, and the bacteria (X2) after 285 time steps. The detritus (X5) do not go extinct after removal of the plants as they are maintained by their own source of external energy.

Table 1: The extinction matrix for the model involving “bottom-up” approach (the entire time interval T=400).

	1 (plants)	2(bacteria)	3 (detritivores)	4 (carnivores)	5 (detritus)
1 (plants)	0	-	-	-	-
2(bacteria)	285	0	-	-	-
3 (detritivores)	271	-	0	-	-
4 (carnivores)	277	-	196	0	-
5 (detritus)	-	-	-	-	0

Removal of the other compartments only results in their own loss, with the exception of detritivores whose loss causes the extinction of the carnivores after 196 time steps. The donor-controlled approach is referred to as “bottom-up” since the flow is always downstream from the point of origin through the rest of the system.

3.2 Discount rate

Lastly, we consider the situation in which the compartments are able to adapt to the changing conditions in the network, thereby affecting their own response to the collapse. In this manner the importance of the energy inflows lowers over time. To simulate this we introduce a discounting coefficient, ρ , similar to an economic discount rate, which considers the compartment's utility as the discounted sum of instantaneous stocks over the infinite time horizon (Samuelson, 1937; Gollier, 2002). Then, we define the loss in utility of compartment j due to collapse of compartment m . The ratio of the utility loss and the utility in the steady state gives the relative loss in utility of compartment j due to collapse of compartment m . Letting m and j vary over the energy network we define a matrix of relative utility losses. To demonstrate this methodology, results are given in Figure 4 for the relative losses of compartment 5 (detritus) due to collapses of other compartments. We see that when the plants collapse, compartment 5 loses its biomass thus the discounted relative loss is positive and converges to 0 with an increase in ρ . Collapse of compartment 2 (bacteria) and compartment 3 (detritivores) make compartment 5 (detritus) gain its biomass and thus the discounted relative loss is negative and converges to 0 with an increase of ρ . Collapse of compartment 4 (carnivores) also makes compartment 5 (detritus) gain the biomass in the long-run, after initially declining. That is why for $\rho=0$ (future losses are as important as current ones) the relative loss is negative, i.e., gaining biomass in the long run dominates the immediate but short-term drop in the biomass. However, the relative discounted loss becomes positive with the increase in ρ indicating the importance of the immediate drop of the biomass. When the biomass is gained, the non-discounted relative loss to compartment 5 (detritus) is the biggest when compartment 2 (bacteria) collapses (about 180%), the non-discounted relative loss to compartment 5 (detritus) when compartment 3 (detritivores) collapses is about 50%, and the non-discounted relative loss to compartment 5 (detritus) when compartment 4 (carnivores) collapses is only about 2%. With the increase in ρ however, the difference between relative losses diminishes. When the biomass is lost, i.e., when compartment 1 (plants) collapses, the non-discounted relative loss to compartment 5 (detritus) is almost 100% because compartment 5 (detritus) converges to a zero equilibrium in the long run. When discounted this loss becomes less important and therefore, the relative loss decreases.

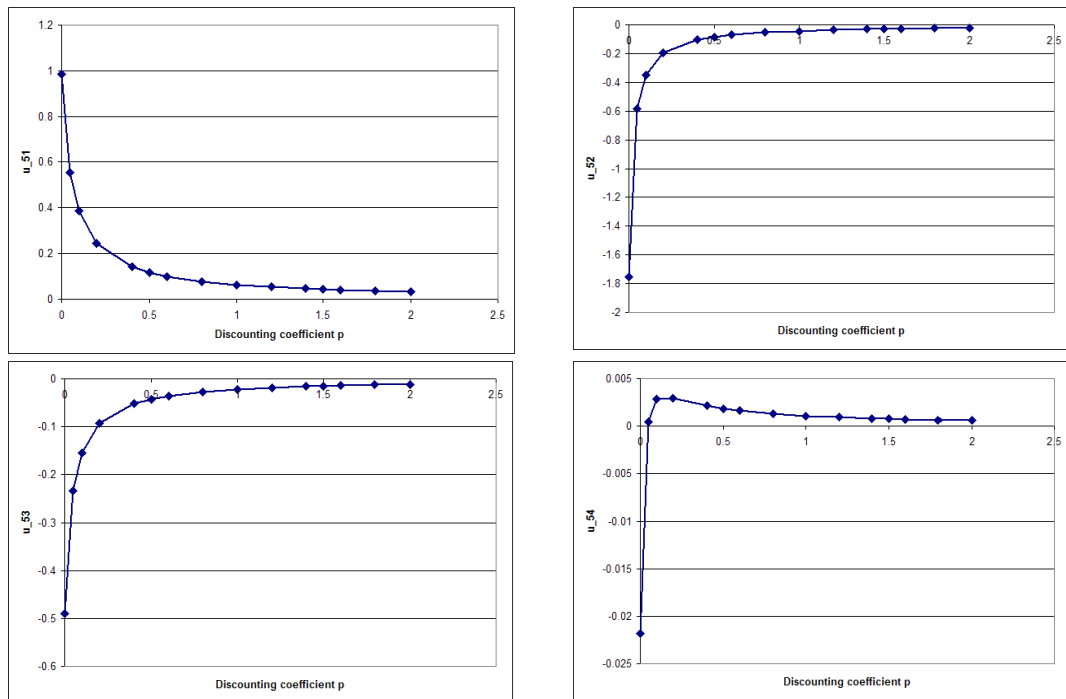


Figure 4. Relative losses of compartment 5 (detritus) due to collapses of other compartment over the entire time interval ($T=400$) with respect to the discount coefficient ρ .

4.0 Conclusions and Recommendations

In this paper, we introduce a methodology to construct and simulate models using ecological food web data. Equations are derived from the static network using a linear, donor-controlled approach. By systematically removing each compartment we generate the time series for decay of the other network compartments. We see the impact of nodal collapse and can report the time to extinction of each compartment that disappears. In this example of the Cone Spring ecosystem, where there is not much cycling (Finn Cycling Index = 9.2%), the flows are strongly dominated by the primary producers making their collapse most noticeable.

In the case of monotonic stock dynamics (either growing or diminishing stock), the relative loss preserves its sign (positive or negative correspondingly) regardless from the discounting parameter. Non-monotonic dynamics may lead to changes in a sign of the relative loss, putting dominance to the dynamical trend which the compartment follows immediately after the collapse; that allows for differentiation. In magnitude the relative loss converges to zero with the increase in the discounting parameter, normally, for $\rho > 1$ all relative losses are negligibly small. If a compartment does not grow exponentially, then without discounting the relative loss does not exceed 200% in magnitude when the biomass is gained. Lastly, bacteria experiences the least relative losses from all collapses and collapse of the carnivores brings the least relative loss to bacteria and detritus (about 2%). In the next paper, we develop specific vulnerability indicators based on these results.

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