GRAPHS, NETWORKS, EXTINCTION AND PALEOCOMMUNITY FOOD WEBS

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"Certainly, let us learn proving, but also let us learn guessing." (Polya, 1954, p. vi)

ABSTRACT

Food webs represent the trophic interactions among species in communities. Those interactions both structure and are structured by species richness, ecological diversity, and evolutionary processes. Geological and macroevolutionary timescales are therefore important to the understanding of food web dynamics, and there is a need for proper reconstruction and analysis of paleocommunity food webs. The fossil record presents many challenges, but the problem may be approached with combinatoric analysis, and graph and network theories. This paper is a brief introduction to the aspects of those disciplines relevant to the study of paleo-food webs, and explores several probabilistic and numerical approaches.

INTRODUCTION

THIS contribution an introduction for students of paleontology to graph and network theories, and an exploration of their current and potential applications to paleo-food web analysis. The theories are closely related, with networks comprising a subset of graphs, and both have proven to be powerful and intuitive approaches to the representation of relationships and interactions. Current trends in science and society have led to a proliferation of rich datasets that capture interactions among entities, and network theory has become a fundamental part of the scientific toolkit. Ecology amassed a tremendous amount of information in the 20th century on the interactions of organisms with their environments and each other. Since then, a growing number of ecologists have been assembling this information to understand the complexity of real-world ecological systems. Those systems, including food webs, are true complex systems since properties may emerge from the assembled systems that are not apparent or easily predicted from the individual parts. Network theory is a powerful tool in the analysis of these complex biological systems. It can also be extended to understanding the history of complex systems on geological timescales, where communities and ecosystems are exposed to low frequency, high impact interactions with the geophysical world, and systems themselves vary because of evolutionary change and long-term fluctuations of system composition.

The increasingly frequent combination of empiricism and quantitative theory in paleontology is justification enough for including graphs and networks in this short course volume, but I will focus on current and potential applications to paleo-food web analysis. The chapter will develop brief introductions to graph and network theories using food webs throughout as examples, and finally will examine paleocommunity food webs and the combinatoric network CEG (Cascading Extinction on Graphs) model (Roopnarine, 2006). Development of this final section requires exercises in combinatorics and counting, both of which form the basis of much of probability theory, a central topic in this volume. Emphasis is placed on the unique challenges of constructing and analyzing paleo-food webs, and the application of these food webs to analyses of extinction. Examples will be presented throughout, mathematical when necessary and real-world when possible. The paper is not an exhaustive review of graph or network theory, combinatorics, nor of network food webs, but is intended as an accessible introduction from which a solid foundation may be built for deeper exploration of these topics. A significantly more biological and paleobiological treatment of paleo-food webs is presented in Roopnarine (2009), while here I will focus on the more technical aspects. The paper assumes that readers have at least an introductory undergraduate course in probability and statistics or equivalent.

GRAPHS

A food web is a summary of interspecific trophic interactions. A mathematical graph is the combination of two sets, commonly written G(V, E), where the elements of E are relationships among the elements of V. Both concepts may be expressed graphically as diagrams of relationships among species or elements, an exercise that makes clear the relationship between the real-world biological system and the abstract mathematical one. The area of mathematics dealing with graphs is known as graph theory, familiarity with which proves very useful in the exploration and analysis of not only food webs, but of any real-world system (biological and otherwise) that can be expressed as relationships or interactions among discrete entities. Examples of other systems include networks of genomic interactions, metabolic networks, and phylogenetic trees.

Examine the simple food webs illustrated in Figure 1. The circles represent species, and the links between them are interspecific interactions. Describing these systems mathematically as G(V,E), the elements of E are relationships among the elements of V. The elements of V are typically referred to as *vertices* or *nodes*, and their relationships, or the elements of E, are referred to as *edges* or *links*. Edges are written as pairs of vertices, for example $\{v_1,v_2\}$, where v_1 and v_2 are vertices in G (that is, $v_1 \in V$ and $v_2 \in V$). Species in the food web are therefore nodes, and trophic interactions or links are edges.

The first web (Fig. 1.1) is a system of non-interacting species. It could function only if embedded within a larger system of species with which these species interacted, or if all three species were autotrophic. Such a graph where no vertices or nodes are connected (E is an empty set) is an *unconnected* graph, one with some edges is *connected* (Fig. 1.2), while a graph with all vertices connected (Fig. 1.3) is a *complete* graph. Any node to which another is linked is termed its *neighbor*. Note the alternative representation of a graph as an n by n binary *adjacency matrix*, where element v_iv_j equals one if an edge connects the two vertices, and zero otherwise.

The three graphs would obviously depict food webs with very different implications for the species involved. For example, the density of interactions increases as the number of edges, or |E|, increases (see Appendix 1 for an explanation of notation). This density is often described simply by the *connectance* (C) of the graph, standardized as the ratio of the number of edges to the maximum number of edges possible. Each node or species could hypothetically interact with every other species, therefore the number of possible interactions is n(n-1). Note, however, that links would be counted twice, for example {1,2} and {2,1}, so we halve this number. Then

$$C=\frac{2|E|}{n(n-1)}=\frac{2|E|}{n^2-n}$$

The connectances of Figures 1.1-1.3 are therefore zero, 0.333 and 1. We extend this by noting that species may sometimes interact with themselves trophically if individuals are true cannibals. The number of possible edges now increases by n. This situation is illustrated in figures as loops, or unit diagonal entries in the adjacency matrix (Fig. 1.4). We can now generalize by stating that the connectance of food webs expressed as graphs is measured as

$$C=|E|\left(n+\frac{n(n-1)}{2}\right)^{-1}=\frac{2|E|}{n^2+n}$$

and the connectance of the complete food web in Fig. 1.4 is therefore 1.

In addition to the overall link density of the graph, or the number of interactions in the food web, we are also interested in the number of interactions per species. This number indicates how trophically specialized or generalized a species is, and is interesting from both evolutionary and ecological perspectives. For example, very specialized species may have stronger ecological and coevolutionary interactions with the species to which they are linked, and specialization itself may require temporally extended intervals of stability or high productivity to evolve. Generalized species, on the other hand, might be less susceptible to major perturbations if the intensities of their interactions are distributed broadly among their neighbors. The number of edges or links attached to a node is termed the *degree* of the node. The simplest cases are those where all nodes are of the same degree, for example Figs. 1.1, 1.3 and 1.4. The distribution of links within the graph, or the link distribution, is then single-valued, and may be described as a Dirac delta function or Kronecker's delta. A slight probabilistic generalization, where nodes have the same number of links *on average*, instead of precisely the same degree, leads to the significant development of random graphs and the eventual study of real-world networks.

Random graphs.--Given a set of species V, let us construct a food web by assigning interactions (links) randomly to species (nodes), but with equal probability p. Species will therefore have equal numbers of interactions on average. The probability that a species can be found with r links, and therefore be of degree r, is given by the binomial probability

$$p(r)=\binom{|V|}{r}p^{r}(1-p)^{|V|-1-r}=\frac{|V|!}{r!(|V|-r)!}p^{r}(1-p)^{|V|-1-r}$$

If we assume that the number of species is far greater than the number of links per species, that is |V| >>r, then the above formula may be re-written as

$$p(r)\simeq \mathrm{e}^{-p|V|}\frac{(p|V|)^{r}}{r!}=\mathrm{e}^{-z}\frac{z^{r}}{r!} \quad ,$$

where z is the average number of links per species, or the *coordination number* of the graph. P(r) is the probability distribution function of a Poisson distribution with mean z. Such graphs are known as Erdös-Renyi graphs and possess many interesting properties. While Erdös-Renyi random graphs rarely describe real-world food webs (that is, species in a community do not have on average the same number of interactions), they prove useful in demonstrating certain concepts.

The link or degree distribution P(r) describes, for a set of nodes V, an entire ensemble of graphs. For example, the graphs illustrated in Figure 2.1 are both realizations of graphs with z = 2, and |E| = 5. No two realizations of graphs based on the same link distributions need be the same in detail, but they will have the same properties on average. The entire set of graphs based on a given set of parameters is the ensemble, and ensemble properties are usually written in angled brackets as <x>. The ensemble number of links per node in our two graphs is therefore <2>. It is also interesting to note that the two graphs are in fact identical if one ignores the labeling of the nodes. The vertex arrangements differ, but the graphs themselves are identical, bearing exactly the same information. Identical graphs are termed *isomorphic*. Recognizing graph isomorphism allows us to distinguish between the properties of a graph, and any particular depiction of that graph, whether by illustration or adjacency matrix. Determination, however, of whether two finite graph depictions are isomorphic becomes increasingly difficult as the size ($|V|$ and $|E|$) of the graph increases. In fact, no formulaic solution exists to the problem, it is believed to be NP-hard or NP-complete, and it is usually tackled with algorithmic computational approaches of varying efficiencies. Are the two graphs in Figure 2.2 isomorphic? The answer is yes, but I will leave that demonstration as an exercise for the reader!

NETWORKS

Perhaps the most obvious structural elements of real food webs that distinguishes them from the graphs presented earlier is directionality of the links. Links are trophic interactions, that is, predator-prey relationships, and they describe the passage of energy from prey species to predators. They can also be used to describe the impact of predation on a prey species, recognizing that the relationship is an asymmetrical one between nodes. The “traditional” manner in which to depict this graphically is with arrows between nodes (Fig. 3). Whereas the graphs illustrated so far have been *undirected* graphs, a food web is defined properly as a *directed* graph, or *digraph*. The asymmetry is also reflected by the adjacency matrix, which is no longer symmetric about the diagonal.

The most straightforward applications of graph theory to food web biology are analyses of the structure or topology of digraphs. Digraphs are often referred to as networks in modern usage, and the study of digraphs, especially those describing real-world networks such as the Internet or social networks, is termed network theory. The reader should be aware, however, that networks are technically graphs that are digraphs having weighted or parameterized links or nodes. A network therefore depicts a food web when it contains species interactions, the direction of those interactions, and some measure of the interactions, such as interaction strength. A digraph without measures or weights on the links is in reality a special case of a food web digraph, one in which all links are considered equivalent.

A very simple three species food web is illustrated in Fig. 3.1. Species 1 (S1) is prey only (perhaps a primary producer), S2 is both a predator or consumer of S1 while being prey to S3, and S3 is the top consumer in the network. Alternative arrangements for three species are illustrated in Fig. 3.2-3.4, including a simple food chain (Fig. 3.2), a web where the top consumer is also cannibalistic (Fig. 3.3), and a cycle among the three species (Fig. 3.4). These networks bear only information about the existence and direction of interactions among species, but this information is important because structure always affects function (Strogatz, 2001). The basic network approach has proven useful as a means of capturing the complexity of food webs, deriving basic comparative properties such as connectance and link (degree) distributions, and assessing one type of robustness against perturbation as discussed later.

System complexity.-- The complexity of a food web depends upon the taxon richness of the system, as well as the topology and dynamics of interspecific interactions. Although richness and topology are captured by graphic depictions, the utility of the depictions is often limited to impressing upon the viewer the overwhelming structural complexity of the systems. For example, Figure 4 is a Greater Antillean coral reef food web comprising 265 trophic guilds and 4,656 interactions (Roopnarine and Hertog, 2010), currently one of the most detailed food webs available. The system is definitely complicated, as expected of a coral reef community, but not much else can be concluded from the graph. In fact, it is in reality more complicated than illustrated, being based on a dataset comprising 750 species and 34,465 interspecific interactions. Many of the species have been aggregated into sets termed *trophic guilds*, where members of a guild share prey drawn from the same guild(s), and likewise for predators. Species aggregation is a common way in which to reduce food web network complexity, but there are few formulaic methods for aggregation. The most common method is based on the concept of *trophic species* (trophospecies), where aggregated species are assumed to have exactly the same prey and predators. The trophic guild concept on the other hand was formulated specifically for fossil taxa and assumes uncertainty in species interactions. It is very important to understand the impacts of aggregation on network structure and dynamics, and the implications for species' roles in the system. Whether different aggregation schemes yield similar insights into complex systems is currently poorly understood. I will return to this topic in a later section.

Connectance.-- A number of measures and summary statistics are used to describe and compare food webs, perhaps the most common one being connectance. Food web connectance differs from the graph connectance defined earlier, because the networks are now directional. Each node may link to every other node including itself, but a directional link from species A to B is no longer equivalent to a link from B to A. The maximum number of links possible is therefore now the square of the number of nodes. Using symbols common in the food web literature,

$$C=\frac{L}{S^2} \quad ,$$

where L is the number of directional links in the network, and S is the number of nodes. Connectance values are generally well below one, reflecting the relative sparsity of links in food webs (Dunne et al., 2002a, 2004), but it is difficult to compare connectances among food webs that use different aggregation schemes. Perhaps given this difficulty, it is quite surprising that there is a regular relationship between L and S spanning a large number of food webs (Martinez, 1992; Dunne et al., 2002b; Roopnarine et al., 2007; Hertog, 2009; Roopnarine and Hertog, 2010; see also Ings et al., 2009), compiled from a variety of sources, and using different aggregation methods (Fig. 5). The exponential nature of the relationship shows that link density, or connectance, increases with increasing node richness. It is possible that increasing taxon richness in a community demands greater connectivity in order to maintain efficient energy transfer and hence stability, or the relationship is spurious and any true relationship is obscured by the heterogeneity of food web metadata. This remains an open problem in food web theory.

Link or degree distributions.-- The other measure commonly taken of food web networks is the link or degree distribution. Real-world networks, unlike random graphs, rarely have Poisson or normal link distributions, having instead scale-free or power law distributions (Barabási and Jeong, 2000; Barabási et al., 2000). The terms scale-free and power law refer to the fact that these distributions lack characteristic scales (see below), and take the general form $P(X)=cX^{-\gamma}$, where the probability of a value is a power function of the value itself. Scale-free distributions have been found in networks as diverse as the Internet, transportation networks, anatomical circulatory networks, social networks and food webs (Strogatz, 2001). There are two features of these distributions that are of importance to food web theory. First, being scale-free means that the distribution has no characteristic scale. Many distributions have a characteristic scale, often captured by a peak (or high density region) and measured as a mean or mode, for example Poisson or normal distributions. The form of a sample drawn from one of those distributions depends on the range from which it is drawn, whereas the shape of a power law distribution is approximately invariant throughout its range. One part of the distribution may be used to predict another with a simple rescaling of the density (Fig. 6). Therefore, a partial sampling of the range yields an overall approximation.

Second, power law distributions are long-tailed decay distributions. The decay of the distribution's density with increasing X, dictated by the negative exponent γ, means that the distribution's density is concentrated at low values of X. Nevertheless, the long tail also means that there is measurable density high in the X range. Contrast this with the exponential distribution in Figure 6, which is also a decay distribution, but with a rapidly decaying short tail. A long tailed link distribution has nodes that are of considerably greater degree than others. These highly linked or hub nodes confer significant resistance to failure of network connectivity. The canonical example is the Internet. Random failure of any single server is unlikely to affect the network broadly because most servers are of low degree (drawn from the high density region of P(X), and hence of low degree), but there is a high probability that they are linked to high-degree hubs. The network is susceptible, however, to targeted attacks on hubs (Albert et al., 2000). It is not clear how long tailed distributions arise in networks, but models of preferential growth (Barabási et al., 2002; Yook et al., 2002), where new links have a greater probability of being added to already highly linked nodes (the "rich get richer" model) are reasonable hypotheses when applied to flow networks (for example, information, energy) or social networks (the blogosphere, personal relationships).

Food webs have been characterized most frequently by their in-link (or in-degree) distributions, which are the frequency distributions of the number of prey per consumer species (species in-degree). In-link distributions therefore describe patterns of energy flow in the system, as well as the trophic habits or dietary breadths of the species. Most documented food webs have decay in-link distributions and those are either scale-free, power law distributions, or they have properties of exponential decay, or seem to be a mixture of the two types of distributions (Camacho et al., 2002; Dunne et al., 2002b; Montoya and Sole, 2002). Exponentially decaying distributions have greater concentrations of density at low degree. The latter group of distributions, described as mixed exponential-power law distributions, are of the form

$$P(r) = \mathrm{e}^{-r/\varepsilon}$$

where

$$\varepsilon = \mathrm{e}^{(\gamma-1)\ln(M)/\gamma} \quad ,$$

r is species in-degree and M is the maximum number of prey species available (Fig. 6).

Dunne et al. (2002a) examined the link distributions of 16 published food webs, though the survey included both links to (in-links) and from (out-links) predators. They found significant variation among the networks, but distributions belonged mostly either to power law, exponential or uniform distributions. Camacho et al. (2002), in an analysis of six of those same food webs concluded that trophic in-link distributions in fact follow a universal functional form,

$$P(r) = e^{\frac{-r}{2\mathrm{z}}} - \frac{r}{2\mathrm{z}} E_1\left(\frac{r}{2\mathrm{z}}\right)$$

where z is the coordination number of the network and $E_1(x)$ is the exponential integral function. The above is also a decay function, significantly related to a scaled number of prey, r/2z. The authors derived a value of z=7.5 from the pooled data of the six networks. The distribution itself was derived analytically from an interpretation of the niche model of Williams and Martinez (2000), which has demonstrated some success in describing empirical trophic link distributions. The data are generally aggregated averages of species population distributions, however, and it is not clear to what extent, if any, the niche model actually predicts any underlying community mechanisms, rather than describing those specific parameterized and averaged representations.

The in-link distribution of the Greater Antillean coral reef raises again the issue of species aggregation. The distribution of the guild-level network, where 750 species are aggregated into 265 guilds on the basis of very precise trophic data, is a distinct power law distribution of the form

$$P(r) = 11196\,\mathrm{e}^{-1.98}$$

The high resolution of this dataset allows us, however, to also examine the species-level network, for which the distribution is certainly not a decay distribution, but instead has a distinct mode at 30 links (Fig. 7). The most precise trophic data are available for the vertebrate species in the network and the vertebrate-only distribution is similar to the overall species-level distribution, though with a mode at 76 links. Clearly the discrepancy between the guild- and species-level distributions is caused by the omission of species richnesses and accompanying degree variance from the aggregated guilds. Thus it remains to be resolved if communities in fact always have greater proportions of trophic specialists and hence decay-type in-link distributions, or if this pattern is restricted to guilds, and if the pattern occurs naturally at all or is in fact an artifact.

PALEO-FOOD WEB RECONSTRUCTION

Network treatments of food webs allow the application of graph theoretic concepts to the representation of food webs as complex systems. So far we have derived descriptive measures of food web networks, but the primary interest lies in using these networks to understand system dynamics. From a paleontological perspective, this means examining the behavior of communities and ecosystems on macroevolutionary and geological timescales, and the behaviors of those systems when they interact with large scale geophysical processes or other disruptions. The first area of inquiry has received little attention so far, but one opportunity there is to formalize food webs in frameworks such as Vermeij's Theory of Escalation (Vermeij, 1987), Bambach's “guilds through time” (Bambach, 1993), or Van Valen's Red Queen Hypothesis (Van Valen, 1973). Food webs, though not their representation as complex networks, have also been used in interesting models of recovery after mass extinction (Sole et al., 2002). Most recently, Angielczyk et al. (2008) have used food web networks to inquire into the macroevolutionary expansion of tetrapod herbivory during the Permian. The second area of inquiry has been the focus of the CEG model, which has been used most extensively to model a variety of paleocommunities, including Permian-Triassic terrestrial communities and Miocene-Pliocene marine communities, and their potential responses to different types of perturbation (Angielczyk et al., 2005; Roopnarine, 2006; Roopnarine et al., 2007; Hertog, 2009). Regardless of the question to which the network models are applied, there are several basic steps required for network construction and analysis. Many of these details are presented in Roopnarine (2009); here I will concentrate on the specific relationship to graph and network theories. Specifically, the remainder of the paper will cover the reconstruction of paleo-food web networks, dealing with uncertainty, calculating probabilities of extinction, and the analysis of community robustness.

Uncertainty.--Uncertainty is of paramount importance when dealing with paleo-food webs. There is uncertainty associated with and inherent to the structures of many modern food web models, but there is always the opportunity of reducing or even eliminating much of that through empirical observation. Opportunities are more limited in the fossil record. Two different approaches to the problem have developed, namely restricting reconstruction to exceptionally well-preserved portions of the record, and modeling uncertain data and the impact of uncertainty. Both approaches are discussed in the following section, but since the former approach differs little from the reconstruction of modern communities, emphasis is placed on the latter.

The first step in constructing a food web network model of a paleocommunity is the assembly of a comprehensive taxonomic database of species known to have been members of that particular community. I will not discuss definitions of paleocommunities here. There are two sources of uncertainty in this step: missing species and community averaging. There are many taxa that have never been preserved as fossils, or their preservation prevents proper enumeration for network purposes, for example many microbial taxa. Solutions to these problems include a restriction to lagerstattën, or restricting one's interpretations to comparative dynamics. The first option was adopted by Dunne et al. (2008) in their reconstruction of two Cambrian food webs. These marine food webs preserve several grades of organisms that are generally not present as fossils, namely soft-bodied organisms. The taxonomic completeness of the food webs are therefore expected to be greater than what is otherwise available for most of the fossil record. The other approach is suitable when two or more communities are being compared, for example the Permo-Triassic communities of the Karoo Basin compared in Angielczyk et al. (2006) and Roopnarine et al. (2007). This approach asserts that although the reconstructed food webs lack all the original species, consistent rules of reconstruction will result in comparable reconstructions. Any observed differences will therefore be the result of true ecological differences, and not be functions of the network model. The approach necessarily assumes reasonable taphonomic uniformity among the paleocommunities.

The impact of incompleteness has been investigated preliminarily by “fossilizing” two high quality modern marine food webs, the Greater Antillean coral reef discussed earlier, and the San Francisco Bay community (LaScala-Gruenewald et al., 2009). Fossilization was simulated by removing from the networks all genera that are not represented at the genus level in the Sepkoski genus-level database (Sepkoski, 2002). Comparing the perturbation dynamics (see below) of the modern and fossil networks shows that the fossilized and incomplete networks exhibit greater variance and lowered resistance to perturbation, but that the qualitative form of the results is unchanged.

Trophic parameterization and taxon aggregation.--The second step is the basic trophic parameterization of the species, that is, determining the prey and predators of each species. A key assertion of the CEG model is that a paleocommunity's trophic network can never be specified by a single topology (Roopnarine, 2006, 2009). There is uncertainty associated with the biotic interactions of a fossil species because no one was there to observe them. Preserved evidence of interactions such as bite marks, gut contents or leaf damage record a subset of the possible range of interactions. Moreover, the topology specified for a single community is expected to vary spatially and temporally (Eveleigh et al., 2007). The strength and direction of interspecific interactions of extant species are known to vary according to physical conditions, the presence or absence of other species in the community (Edeline et al., 2008; Petanidou et al., 2008), relative population sizes, and the incumbency of species when addition to the community is asynchronous (Edgell and Rochette, 2008). These uncertainties must be incorporated into any realistically complex model of a community food web. In the CEG model, species are therefore grouped into *trophic guilds* based on the most accurate trophic interpretations available. Trophic guilds are defined by the trophic habits and habitats of member species, for example, the "very small carnivorous amniotes" of a Late Permian terrestrial community.

The resulting guild structure represents a species aggregation scheme. The aggregation scheme used most commonly is the assembly of species into groups called "*trophic species*" (Cohen and Briand, 1984). Trophic species group species that are assumed to have the same prey and predators. The motivation for this grouping is unclear in cases where link data are available at the species level. One advantage, however, may be to avoid biases introduced by an undersampling of poorly resolved links. Patterns of connection among trophic species may also illuminate patterns of energy and nutrient flow among major species ecotypes in the community (Allesina et al., 2005). There is no guarantee, though, and in fact no expectation for the preservation of network topology in the conversion of species-level data to a trophic species network. It is always preferable to use species-level data to represent true community complexity. Furthermore, aggregation into trophic species is an inference the strength of which cannot be justified for fossil taxa, and the scheme should be avoided in paleo-food webs. Given that species-level data are rarely available for fossil species, however, and are basically never complete, aggregation is usually necessary. Dunne et al. (2008) therefore converted species-level data to trophic species in their study of the Cambrian food webs. The CEG model, as mentioned, aggregates species into trophic guilds, groups of species that cannot be distinguished trophically on the basis of available data. Another example would be “epifaunal, seagrass-dwelling suspension feeding bivalves”. Those species, in a particular community, potentially share the same predators and prey. Trophic guilds are similar but not equivalent to trophic species, yet it is clear that if a trophic species is an accurate representation of the species which it comprises, then the composition of a similar trophic guild will approach the composition of the trophic species as the species data become more precise. A network of trophic guilds is termed a *metanetwork* (Roopnarine, 2006) to distinguish it from a fully detailed food web, and is an hierarchically higher level representation of a species-level food web network (Fig. 8). Two trophic guilds linked in a metanetwork contain species that are potentially trophic interactors. A metanetwork therefore summarizes the most accurate and precise data available for a paleocommunity's food web.

The contrast between the two aggregation schemes is therefore reducible to one of accuracy and precision. The trophic species scheme assumes a high level of precision, thereby justifying an assumption of trophic neutrality among species within the trophic species. This level of precision is unlikely to be available for fossil taxa, and in any case can never be tested. The metanetwork and trophic guild scheme assumes that the understanding of a species trophic habit is accurate, even though its precise interspecific interactions may be unknown or known incompletely. These uncertainties, stemming from incomplete data and temporal-spatial variance of the data, are addressed in the next section by exploring the range of species-level food webs implied by the metanetwork.

Species-level networks.--The final step in network construction is the generation of species-level networks (SLNs). A SLN is considered a single potential pattern of food web interactions in any given place at an instant of time, and may be constructed in two distinctly different ways. First, using empirical observations, one could construct the SLN of a community. This is typically the fashion in which SLNs are reconstructed for modern communities; workers observe and record the community's trophic interactions. SLNs of this type are precise and without error, though usually taxonomically incomplete, and we cannot have similar confidence in their accuracies because of the sources of uncertainty and variability described above. Capturing their variability requires repeated observations, which is possible under some circumstances. Such repeated observations are impossible for paleo-food webs. The best that can be done is to measure spatial or temporal variation in taxonomic composition. The latter of course could describe variability on only the longest of ecological timescales. Dunne et al. (2008) compiled SLNs of the two Cambrian food webs derived from the Burgess Shale and Chenjiang lagerstatten, comprising 142 and 85 taxa respectively. The taxa in both these networks were subsequently aggregated into trophic species, 48 and 33 respectively, on the basis that species within the trophic species have identical consumers and resources. As argued above, it is impossible to validate this claim for fossil taxa. Trophic species-level links were ranked according to uncertainty in these networks, but there was no explicit attention paid to uncertainty at the level of species *within* the trophic species.

The CEG model takes an alternative approach to SLN reconstruction, generating multiple plausible SLNs from the metanetwork and hypothetical or underlying principles of food web networks as gleaned from modern food webs. This type of SLN generation requires a trophic in-link distribution for each guild. Recall that a trophic in-link distribution describes the number of prey per species within a guild. This number ranges from 1 (a heterotrophic species must prey upon at least 1 other species) up to the total species-richness of all guilds that are specified as prey of the guild in the metanetwork. SLN-generation requires initially that species within a guild be treated neutrally, that is, they have no distinguishing trophic properties. Stochastic draws from specific guild trophic in-link distributions then determine the number of prey to be assigned to each species. The prey species themselves are drawn randomly from the pool of prey guilds of the predatory species. The result is a directed graph or network in which each species in the community has been assigned prey, and many therefore also have predators (Fig. 9). SLNs capture the uncertainty associated with the reconstruction of fossil food webs, and in fact any food web, in a manner in which static or unvarying trophic link determinations cannot. Repeated stochastic generation of SLNs accounts for the sources of uncertainty discussed earlier, namely uncertainty of the particular interactions of a species, and the temporal and spatial variability of a community type. Also, even though any two SLNs derived from any moderately complex metanetwork are unlikely to share the same exact topology (isomorphic), they are drawn from the same ensemble, as discussed earlier for Erdös-Renyi random graphs. Whether the argument can then be extended to claim that they will also have the same behavior on average, as with random graphs, is an interesting question, because the ensemble is the range of variation possible for a paleocommunity's food web based on paleontological uncertainty. The remainder of the paper therefore deals with a description of the ensemble, and the ecological dynamics of the SLNs in an ensemble.

SLN SPACE

I begin the description of the ensemble space by recognizing that it is a probability space of all the species-level networks possible given a specific metanetwork. We will adopt a set of formal definitions of the space, namely as a probability space (S, *F*, P). The set S is the complete sample space of the metanetwork whose topology is U, *F* is the set of sets for which real-world SLNs exist (see below) and P is the probability of an element in *F*, that is, P(SLN). *F* is often taken to be the power set of S, or the set of all sets, but as shown below, many of those sets in S would contain SLNs that cannot exist in the real world.

Ensemble size.-- The number of *SLN*s that can be derived from a metanetwork ensemble is finite, because there is a finite number of arrangements or graphs of the species. The number or ensemble size also defines the maximum variation possible for a real community, unless the taxon composition itself changes. The number of SLNs (the number of elements in S, or the cardinality of S) is designated |S|. Examine the simple metanetwork in Figure 10. We will designate the metanetwork U, and the number of guilds as |U|. Guilds 1 and 2 (G1 and G2) comprise species that are preyed upon by species in G4. In order to construct a SLN, we must specify exactly which species in G1 and G2 are preyed upon by each species in G4. Let the presence of a metanetwork link be indicated by elements a_{ij} of the adjacency matrix, being one if a link exists, and zero otherwise. Then the maximum number of prey species (maximum in-degree) available to any species in G4, denoted r_{max} is

$$r_{max}(G_4)=a_{31}|G_1|+a_{32}|G_2|+a_{33}|G_3|+a_{34}|G_4|=a_{31}|G_1|+a_{32}|G_2|=5$$

since a_{33} and a_{34} equal zero. This can be generalized to a metanetwork of any complexity as

$$r_{max}(G_i)=\sum_{j=1}^{|U|} a_{ij}|G_j|$$

Since every species in G4 may have an in-degree range of one to r_{max}, and every one of these possibilities or predatory states could be combined with every other state of the remaining species in G4, the maximum number of possible networks is simply $r_{max}^{|G4|}$. Moreover, the in-degree or number of predatory states of every species in the network may be combined regardless of guild membership, allowing us to generalize to metanetworks of all sizes and complexity. By this argument, the number of possible SLNs, |S|, is the product of the number of predatory states of species in every guild, that is,

$$|S|=\prod_{i=1}^{|U|}\sum_{j=1}^{|U|}\left(a_{ij}|G_j|\right)^{|G_i|}$$

This formula overestimates |S| because prey species in a guild are treated neutrally from a consumer's point of view. Neutral is used here in the sense of ecological neutrality; the species are indistinguishable from each other on the basis of trophic properties. In other words, the above calculation of |S| does not specify *which* prey species are linked to when the predatory states of different predators are combined. Therefore, many of the combinations counted in the calculation will be isomorphic food webs, and they would not have unique ecological properties.

In order to resolve this problem, and gain a more accurate measure of |S|, we need to understand the number of different ways in which a consumer's links can be distributed among it's prey. This is a classic partitioning problem, where say we wish to determine the number of ways in which n fossils can be distributed among m museum drawers, with k_1 fossils in the first drawer, k_2 in the second, and so on. The fossils (links) are not distinct, and we do not care specifically to which drawer (prey species and guild) they are assigned. The trick is to first state the problem as: How many combinations of n fossils can I get if I have m drawers to select from? Or, how many combinations of r links can I get if there are g guilds to select from? We recognize that we are in fact permuting n fossils plus m-1 partitions among the drawers, yielding

$$\binom{n+m-1}{m}$$

Therefore in our sample food web (Fig. 10), if a species in G4 has three in-links, then the problem is

$$\binom{3+2-1}{3}=\binom{4}{3}=4$$

The links can be partitioned between guilds G1 and G2 as {3,0}, {2,1}, {1,2} or {0,3}. None of these are isomorphic topologies.

The calculation of |S| can now be refined, where the topologies obtained for a particular in-degree are combined with those of other species, rather than simply combining the number of in-degrees possible. We proceed in several steps. First, determine the maximum number of in-links possible for a species in guild G_i. Next, determine the number of in-link topologies possible for each in-degree (1 to r_{max}), given the set of prey guilds,

$$t_i^x = \sum_{r_x=1}^{r_{max}} \binom{r_i^x + a_i - 1}{a_i}$$

where t_i^x is the number of topologies possible for species x_i, which is a member of guild G_i ($x_i \in G_i$), r_i^x is the in-degree of x_i, and a_i is the number of guilds upon which G_i preys (sum of the G_i^{th} row of the adjacency matrix). Note that this is calculated and summed over all possible in-degree values, one to r_{max}. Following from the earlier calculation of |S|, the number of topological combinations among species in G_i is $\left(t_i^x\right)^{|G_i|}$. We therefore re-calculate |S| as

$$|S| = \prod_{i=1}^{|U|} \left(t_i^x\right)^{|G_i|}$$

This calculation is still an overestimate, however, because the number of links between a consumer species and any prey guild is unconstrained. It represents all elements in the power set of S. In terms of the museum fossils analogy, we have assumed that the cabinet drawers are of infinite capacity (sadly, a curatorial fantasy). A more accurate measure of |S| is possible if we limit drawer capacity to some finite number of fossils, thereby limiting ourselves to the set *F* of real possibilities. The food web situation is more complicated because different prey guilds will most likely have different species-richnesses, and hence differing capacities for links. The situations would be analogous if drawers in the collection were of different sizes, indeed a curatorial nightmare! The solution would be to modify the above formula for t_i^x, using only topologies where the number of links from a prey guild to x_i is less than or equal to the species-richness of the prey guild. That is, the capacity of the prey guild is not exhausted. This solution, however, requires partitioning r_x appropriately among the prey guilds so that this condition is met. The set of all such partitions that match the constraints of prey guild species-richnesses can be determined, but the solution is not straightforward and requires application of a partition function and partition theory. Both those topics are, unfortunately, beyond the scope of the current paper. Therefore, the given calculation of |S| remains an overestimate at this point. It is possible, however, to determine the probability of any particular SLN being found in a metanetwork's ensemble.

SLN probability.--There are elements or SLNs in S that cannot exist because they possess topologies inconsistent with observed guild species richnesses. We define those SLNs as having probabilities equal to zero, and are therefore interested in the subsets of *F*, which are those comprising SLNs of probability greater than zero. The above arguments on ensemble composition conclude that the members of *F* cannot be easily enumerated, but the probability of any specific SLN can be determined and if exceeding zero, could therefore have been an actual food web of the paleocommunity. Let species x_i ($x_i \in G_i$) have r_i^x in-links, or prey, and topology t_i^x. The probability of t_i^x, constrained by the metanetwork topology and guild species-richnesses, is given by the multinomial probability

$$p(t_i^x)=\frac{r_i^x!}{a_{i1}k_1!a_{i2}k_2!\ldots a_{i|U|}k_{|U|}!}p_1^{a_{i1}k_1}p_2^{a_{i2}k_2}\ldots p_{|U|}^{a_{i|U|}k_{|U|}}$$

where k_n is the number of links from species in guild G_n to x_i, $\sum_{n=1}^{|U|} k_n = r_i^x$, and p_n is the probability that a link, drawn randomly between x_i and any other species, will connect to a species in G_n. Factorial zero is defined conventionally as equal to one. p_n is estimated empirically from the data as

$$p_n=\frac{a_{in}|G_n|}{\sum_{j=1}^{|U|} a_{ij}|G_j|}$$

The multinomial formula calculates the number of ways in which r links can be arranged among the guilds with k_1 assigned to G_1, k_2 to G_2, and so on, and then multiplies this number by the product of the probabilities, which is equal to the probability of drawing $k_1$links between x_i and G_1, *and* k_2 links between x_i and G_2, and so on. In order for $p(t_i^x)$ to be greater than zero, no k_n can exceed the number of species in G_n. The probability of any SLN may now be defined formally as

$$p(t_i^x)=\begin{cases} \dfrac{r_i^x!}{a_{i1}k_1!\,a_{i2}k_2!\ldots a_{i|U|}k_{|U|}!}\,p_1^{a_{i1}k_1}\,p_2^{a_{i2}k_2}\ldots p_{|U|}^{a_{i|U|}k_{|U|}} & \mathit{if}\ 0\leq k_n\leq G_n\ \forall n, \\ 0 & \mathit{otherwise} \end{cases}$$

It now becomes immediately obvious that among SLNs of probability greater than zero, some are of greater probability than others. Examine the SLNs in Figure 11, arranged in order of descending probability. p_1 is 0.36, p_2 is 0.16 and p_3 is zero. The most probable food web is therefore one where the predatory species, with two in-links, preys exclusively on species in G_2. The third SLN is of probability zero since the metanetwork (Fig. 10) forbids links between G_3 and G_4. Most food webs are of course significantly more complicated than the example used here, but the probability of a SLN is simply the product of the topological probabilities of all species in the food web given the metanetwork,

$$p(SLN)=\prod_{i=1}^{|U|}\prod_{n=1}^{|G_n|}p(t_i^n)$$

Finally, although the set of possible SLNs cannot be delimited analytically, the preceding formula may be used as the basis of a likelihood model, facilitating Markov Chain Monte Carlo exploration of (S,*F*,P) (see Wang, this volume).

EXTINCTION DYNAMICS

The CEG model asserts that food web structure plays a role in extinction. The intricate patterns of relationships among species in a community distribute the effects of changes in one species to others in its community. Therefore, while the ultimate causes of increased extinction in an interval of time may be abiotic, and might affect only some species directly, the effects could be felt more broadly. Another way of viewing this is to realize that there is not necessarily a one to one relationship between ultimate cause and extinction; many species extinctions could be biotically-driven collateral damage. A recent claim of this sort is the effects of nannoplankton extinction after the K-T impact (Jiang et al., 2010). The CEG model, then, hypothesizes about the minimum direct effect of a perturbation required to explain an observed magnitude of extinction.

The role of food web structure in modern extinctions has been studied extensively, and mostly theoretically, leading to the concept of secondary extinction. Secondary extinction is often defined as the extinction of a species when it has lost all its resources. In a food web network, a species therefore becomes secondarily extinct when it loses all its in-links. Here I will use a broader definition, stating that a species becomes secondarily extinct when extinction is the result of changes to the demographics of at least one other species in its community. The various ways in which network structure might drive secondary extinction is unclear, mostly because of a lack of direct observations (experiments on natural communities is out of the question!), and the limitations of network models. A useful measure of the effect, however, is resistance, or the number of species which survive a perturbative event.

Topographic secondary extinction.--The narrow definition of secondary extinction, where a species becomes extinct because it has lost all its resources, is termed topological secondary extinction (Roopnarine, 2009). Topological refers to the dependence of extinction solely upon the topology (pattern) of the network. Note that topological secondary extinction affects the network only in a bottom-up fashion, that is, in the direction of energy flow from producers to consumers of increasing trophic level. It is impossible for a species to suffer topological secondary extinction as the result of a loss of any of its consumers (Allesina and Bodini, 2005; Roopnarine, 2006, 2009; Dunne and Williams, 2009) . The losses of higher trophic level predators can certainly result in local extinctions, for example the well known keystone predator effect, but resolving those top-down processes requires more information than is present in network topology alone.

Topological secondary extinction is a direct function of the in-degree of a species, and its relationship to the perturbed species. A species is immune to this extinction if its in-degree exceeds the magnitude of the perturbation, or the magnitude of the perturbation that has percolated to it through the network (Roopnarine, 2006). In general, higher connectance, which implies on average higher in-degrees or coordination number, lowers the probability of a topological species extinction because perturbations of greater magnitude are required.

Measuring or estimating topological secondary extinction in a food web, in response to a particular perturbation, can be approached in three ways, again depending on whether one assumes accuracy of a higher-level representation of the food web (e.g. a metanetwork) or precision of a species-level network. I will first outline a probabilistic approach, using metanetworks, that incorporates network uncertainty. I will then describe a straightforward method for measurement in precise SLNs, and finally mention an interesting new approach for estimating the potential for topological secondary extinction in networks.

Probabilistic approach.--Let a perturbation of magnitude ω be equal to the number of species removed randomly from the network. The probability that a species x_i will become secondarily extinct is the probability that all its links are to species that are a subset of the ω set. This is determined from a hypergeometric distribution, where we can first ask: Given an in-degree of r_i^x, what is the probability that n_i^x of them will be lost?

$$p(n_i^x|\omega)=\binom{r_i^x}{n_i^x}\binom{S-1-r_i^x}{\omega-n_i^x}\binom{S-1}{\omega}^{-1}$$

where there are S-1 other species in the network and $0\leqslant\omega\leqslant S-1$. The probability of x_i becoming extinct occurs when $n_i^x=r_i^x$,

$$p(e_i^x|\omega)=\binom{r_i^x}{r_i^x}\binom{S-1-r_i^x}{\omega-r_i^x}\binom{S-1}{\omega}^{-1}=\frac{(S-1-r_i^x)!}{(\omega-r_i^x)!(S-1-r_i^x-\omega+r_i^x)!}\frac{\omega!(S-1-\omega)!}{(S-1)!}$$

$$=\frac{\omega!(S-1-r_i^x)!}{(S-1)!(\omega-r_i^x)!}$$

The formula can be re-stated interestingly as

$$p(\text{extinction of species } x_i) = \frac{(\text{perturbation magnitude})!(\text{species richness} - \text{trophic breadth})!}{\text{species richness}!(\text{perturbation magnitude} - \text{trophic breadth})!}$$

where trophic breadth is the number of species consumed by species x_i, out of a pool of potential prey (species richness). For example, in a network of 10 species, $1 \leqslant r_i^x \leqslant 9$ and $0 \leqslant \omega \leqslant 9$, and the probability of extinction increases as $\omega \rightarrow S-1$, and decreases as $r_i^x \rightarrow S-1$ (Fig. 12). Species with more resources are thus more resistant to topological secondary extinction. This is the same as saying that the more trophically generalized a species, the greater its resistance to extinction.

This explains in part the suggestion that food webs of greater connectance (C) are more resistant to topological secondary extinction (Dunne et al., 2002a). Overall food web or network resistance to this type of extinction has been termed structural robustness (Dunne and Williams, 2009). Food web connectance does not increase, however, because of uniform increases in the in-degrees of all species in the network, but increases instead because of the presence of highly linked species. The skewed, long-tailed in-link distributions discussed earlier indicate the non-uniformity of in-degrees within real food webs. The above formula for extinction shows that $p(e_i^x) < p(e_i^y)$ for two species x_i and y_i if $r_i^x > r_i^y$, that is, x_i is of greater in-degree than y_i. This will also be the case if the species on which x_i preys are more resistant to extinction, even if $r_i^x = r_i^y$. The presence of generalist consumers therefore enhances robustness both because of their own greater resistance, and the resistance which they confer upon their consumers.

Propagation.--Understanding the dual role of in-degree on resistance makes it possible to examine the structural robustness of an entire metanetwork in response to a specific perturbation. First, the network is perturbed by the removal (extinction) of several species from one or more guild. If enough species, or the “right” ones are removed, this could in turn cause topological secondary extinctions of species that consume the extinct ones. Whether that actually happens or not depends on the probabilities of extinction. Therefore, to estimate topological secondary extinction in our network, after perturbing it, we have to follow the paths of propagation and estimate the levels of resulting secondary extinction from the probabilities of extinction.

Let guild G_j comprises species of different in-degrees, y_j, and hence probabilities of secondary extinction. If x_i ($x_i \in G_i$) is a species that potentially preys upon species in G_j, then its probability of extinction, given a measured level of extinction of y_j, denoted ψ_j^y , is

$$p(e_i^x|\psi_j^y)=\frac{\psi_j^y!(|y_j|-r_{ij}^x)!}{|y_j|!(\psi_j^y-r_{ij}^x)!}$$

Note that this is a simple re-statement of the earlier formula given for the probability of topological secondary extinction, with two differences. First, r_{ij}^x is the expected number of x_i's links that come from y_j-type species. It is estimated simply as the proportion of y_j-type species out of the total number of species available as prey to x_i:

$$E(r_{ij}^x)=a_{ij}\frac{|y_j|}{b_i}r_i^x$$

$|y_j|$ itself can be estimated from the trophic in-link distribution of guild G_j as

$$|y_j|\approx\left\lfloor\frac{\int_{r_j^y-1}^{r_j^y}P(r_j)}{\int_{0}^{|G_j|}P(r_j)}\right\rfloor$$

Second, ψ_j^y is substituted for ω as a generalization. Whereas ω referred specifically to the primary perturbation of the network, ψ_j^y refers to any species removal, including secondary extinction in guild G_j caused by perturbation elsewhere in the network.

The total expected level of secondary extinction of species of in-degree x_i can now be estimated by applying the above formula to all types of prey species in all guilds with in-links leading to G_i.

$$E(\psi_i^x) = |x_i| \prod_{j=1}^{|U|} \prod_{r_j^y=1}^{b_j} p(e_i^x | \psi_j^y)$$

Incorporating the estimates of secondary extinction, ψ for each class (in-degree) of species in each guild, we can see how an iterative estimate of secondary extinction can be made for the entire network. Say that the perturbation was a disruption of primary productivity and that guild G_j is a guild of primary consumers. Then ψ_j^y is an estimate of the level of topological secondary extinction of y_j species. If guild G_i is a guild of secondary consumers, carnivores, with species that prey on those in G_j, then we see why topological secondary extinction of species in G_i, x_i, is a function of ψ_j^y. The actual order in which the calculations is made is important, because the perturbation will propagate along paths in an order defined and constrained by the metanetwork and food web topologies.

The formulas for $p(e_i^x | \psi_j^y)$ and $E(\psi_i^x)$ are significant, because they enable the estimation of the magnitude of extinction in a paleocommunity in response to the extinction of any single species or guild.

Exact approach.--Topological secondary extinction can be calculated precisely in response to any perturbation to the network when species-level food webs (SLNs) are available. The SLNs can be the result of empirically-based assumptions (e.g. Dunne et al., 2008) or of stochastic draws from CEG-type metanetworks, uncertainty being kept in mind in both cases. Calculating topological secondary extinction is simply a matter of removing the targeted node(s) or species, and subsequently following all paths leading away from the perturbation. The perturbation propagates only in the direction of the links, those being the direction of prey to predator, and of energy transfer. A species anywhere in the metanetwork becomes secondarily extinct if all its prey nodes become extinct as a result of either the initial perturbation or of its propagation. The most comprehensive study to-date based on this approach is that of Dunne et. al (2002b), who examined 16 food webs of varying resolutions and extents of aggregation. The authors concluded that broadly, structural robustness increases with increasing connectance, regardless of whether the perturbation comprised the most connected nodes (usually aggregations of species) or were random. An explicit description of the methodology is not given, but one can presume that any method of manual tracking could be applied directly to small webs, or translated into a computer program for larger webs.

Roopnarine (2009) presented a simple algorithm that can be applied to the adjacency matrix of any graph or network. Let A0 be the binary asymmetric adjacency matrix of the species-level network. A row represents a species' incoming links, that is, the ijth element, or a_{ij} is one if species i consumes species j, and zero otherwise. The initial perturbation to the network is implemented by replacing all elements of the ith row and column with zeros, if the removal of species i constitutes part of the perturbation. An examination of the matrix will reveal if, as a consequence, the row elements of any other species now consists entirely of zeros. If this is the case, then that species has become topologically extinct because it has lost all incoming links or resources. Its own corresponding column elements are now also replaced with zeros. These steps are iterated until no more changes occur in the matrix, at which point propagation of the perturbation, and topological extinction, have ceased. A worked example is given in Roopnarine (2009).

This method was applied to a Late Miocene shallow coastal marine community from the Dominican Republic (Hertog, 2009). The metanetwork is illustrated in Roopnarine (2009), and only results of the perturbations are presented here. The paleocommunity has 29 guilds and 139 guild-level links. The guilds range from phytoplankton to epifaunal benthic carnivores to pelagic carnivorous fish. There are 130 species in the community. One hundred SLNs were drawn stochastically from the metanetwork and subjected to two types of perturbation. The first perturbation is a progressive bottom-up reduction of primary productivity, implemented as a progressive reduction in the size of all four primary production guilds. Primary production is represented as units of productivity in the SLNs, and not producer species since none of those have been preserved. The second perturbation is a top-down removal of apex fish guilds (16 species). Topological extinction caused by the bottom-up perturbation follows an “exponential-type” of increase (Fig. 13.1). This exponential increase is caused by the rapid extinction of highly-linked consumer species at increasing levels of perturbation, corresponding to the long-tails of the underlying in-link distributions. Notice also that the pattern takes a little “hop” at an approximate perturbation magnitude ω=0.67. The hop is due to the complete extinction, at that point, of two guilds: epifaunal herbivores, and shallow infaunal herbivores. These two guilds consume the macroalgae/seagrass guild exclusively.

The top-down perturbation generates noticeably lower levels of secondary extinction (Fig. 13.2). Secondary extinction increases approximately linearly in simple response to the removal of the high trophic level consumers. Those species represent 12.3% of the consumer diversity in the community. Maximum levels of secondary extinction of all the SLNs ranges between 15% and 25%. The additional species are invertebrate taxa that are dependent on the vertebrate consumers, either as predators or in a few cases, ectoparasites.

These results highlight a significant limitation of the use of topological secondary extinction to assess the robustness or resistance of food webs: Secondary extinction results solely from the removal and cascading loss of links in the network without any regard for the demographic or population dynamics of species in the community. Topological analyses of network vulnerabilities are minimal estimates of the severity of link losses when those links have variable interaction strengths, and the nodes cannot be treated neutrally (species differ in their properties). For example, species could and are likely to alter interaction strengths to compensate for lost resources. Topological vulnerability analyses may be well suited for networks with equivalent links and nodes with static properties, perhaps such as actor networks and the Internet, but are ill-suited for networks such as ecologic systems where links and nodes are dynamic. Reductions of primary productivity have been implicated in many intervals of increased extinction in the fossil record (Vermeij, 1995; Martin, 1996; Allmon, 2001), but it is difficult to conceive of reductions greater than 80% as being required to explain observed levels of extinction 60-70% if one simply imagines the consequences of perturbations of that scale in a modern ecosystem. Furthermore, perturbation of top-level consumers are observed in nature to often result in top-down cascading effects, compatible with notions such as keystone predators. These processes are simply not captured by the topological approach. Given these limitations, it is therefore unclear whether greater connectance does indeed promote greater robustness in food webs. That conclusion can only be valid if greater connectance has no effect on, or dampens the negative effect of the omitted demographic processes.

Dominators.--Allesina and Bodini (2004) suggested that food web robustness could be summarized by two metrics, error sensitivity and attack sensitivity. Error sensitivity (ES) measures robustness to random perturbations as

$$ES = \frac{\sum_{i \neq r} |dom(i)| - 1}{(N-1)^2}$$

which is the average number of dominators of every species in the network. A species dominates another if its extinction ensures the topological secondary extinction of the other. Attack sensitivity, AS, is the maximum level of secondary extinction that can be caused by the perturbation of a single species,

$$AS = max\left\{\frac{|dom(i) - 1|}{(N-1)}\right\}$$

On this basis, Allesina et al. (2006) introduced two interesting extension of the topological model. First, food web network links were weighted, that is, not all links are equivalent. The authors relied upon energy flow networks, where link weights are estimates of the energetic, or carbon transfer, dependency of consumers on their prey species. Second, they identified species that dominate other species energetically, in that extinction of the dominator ensures extinction of the dominated even in the absence of topological secondary extinction because of the dominator's significance in maintaining the energy supply chain of the consumer (dominated species). Such key species in a network are bottlenecks to energy flow.

Although the dominator model represents an advancement beyond the strict topological model because links are no longer treated uniformly, it is still limited to understanding perturbations from a bottom-up perspective only. Nevertheless, it is also important for recognizing that interspecific interactions vary in strength. Describing demographic interactions in food web networks requires parameterization beyond network topology and poses significant empirical challenges. A great deal of effort is focused on understanding the role of interaction strength variance, the distribution of interaction strengths, and how to measure them in modern food webs (Paine, 1992; Wootton, 1997; McCann et al., 1998; Neutel et al., 2002; Peacor and Werner, 2004; Navarette and Berlow, 2006; Novak and Wootton, 2008). Again, opportunities are more limited for paleo-food web analysis. The final section of the paper describes a modeling approach to these challenges.

Beyond pattern.--Moving beyond considerations of network topology alone is motivated by the knowledge that many additional parameters are important factors in food web dynamics. For example, there are both theoretical and empirical reasons to justify the importance of relative population sizes and interaction or link strengths. Furthermore, there are processes important to the extinction or survival of species in a community that are not captured by topology, such as top-down effects. A now standard framework incorporating many of those features are the numerous derivatives of the Lotka-

Volterra concept of coupled descriptions of species' population dynamics. Obtaining the parameters required to apply such descriptions to an entire real-world food web is generally not feasible, and essentially impossible for paleo-food webs. The CEG model addresses this problem, specifically to gain a more complete understanding of secondary extinction, by modeling the parameters based on network topology. CEG networks are dynamically weighted, in that links are no longer uniform but instead vary among species, and weights change in response to the demographic properties of neighboring species (prey and predators). Those demographic properties, most significantly relative population size, are also dynamic; an initial perturbation to the network is represented both as the removal of one of more species, as above, and also by the reduction of their relative population sizes to zero. The weighting of links and node (species) parameterization allows bi-directional effects and propagation in CEG networks, meaning that there are both bottom-up and top-down interactions.

The first major postulate of the CEG model is that at any given instant in time, species populations in a food web network will be in equilibrium between energy gained from the consumption of other species and energy lost to predation (Roopnarine, 2006). The second major postulate is that species will compensate for the extinction of a resource species by increasing the strengths of their interactions with any remaining resources. These postulates are combined into a discrete dynamic equation,

$$N_i^x(t) = \frac{1}{N_i^x(0)} \left[\sum_{j=1}^{r_i^x} s_x N_j^y(t) - \sum_{k=1}^{p_i^x} s_k N_k^z(t) \right]$$

where $N_i^x(t)$ is the relative (standardized) population size of species x_i at step t, s_x is the interaction strength with prey species y_j, s_k is the interaction strength with predator z_k, and there are p_i^x predators of x_i (that is, x_i is of out-degree p_i^x). Analysis proceeds by constructing a metanetwork of the target community, including parameterization of guild trophic in-link distributions, construction of one or more SLNs from the metanetwork, and then perturbation of the SLN. The model is implemented numerically with the dynamic equations of all species being updated iteratively after a perturbation until all species have attained steady states of either survival or extinction.

We have no precise knowledge of the guild or network parameters for paleo-food webs, and insufficient knowledge for most modern food webs. Uniform parameterization of multiple community networks, however, allows us to compare dynamics across multiple communities, and this is illuminating when examining communities throughout an interval of time, or distributed in space, both instances in which community and population compositions are expected to vary. The utility of this approach is demonstrated with an analysis of three stratigraphically successive paleocommunities from the late Permian through Early Triassic of the Karoo Basin of South Africa, representing the late Permian *Dicynodon* Assemblage Zone (DAZ), early Early Triassic *Lystrosaurus* Assemblage Zone (CAZ) and the late Early Triassic *Cynognathus* Assemblage Zone (CAZ). The DAZ would have been the community subjected to the end Permian upheaval, and LAZ represents the aftermath and earliest phases of recovery. Details of how these communities were reconstructed may be found in Angielczyk et al. (2005) and Roopnarine et al. (2007). One hundred SLNs were generated stochastically from each of the three metanetworks and subjected to bottom-up perturbations of primary productivity similar to the topological analysis of the Dominican Republic Miocene community presented earlier (Fig. 14).

The results show clearly that the dynamics of the aftermath community, LAZ, differs substantially from the pre-extinction DAZ and the perhaps more fully recovered CAZ (Fig. 14). The dynamics also differ significantly from the expectations of topological secondary extinction only (see also Roopnarine, 2009) in that secondary extinction is no longer a linearly smooth response to perturbation. Secondary extinction now includes both topological secondary extinction, and extinction driven by further demographic interactions (including top-down processes) among species. Both DAZ and CAZ exhibit uniform responses over a broad range of perturbation magnitudes up to a critical point where the level of secondary extinction increases rapidly in response to increasing perturbation. Beyond that, secondary extinction is catastrophically high. The nonlinearity of the full CEG model is even more extreme in the LAZ results, where some SLNs "conform" to the results of the other two communities, but others display extremely high levels of secondary extinction at even low levels of perturbation (Roopnarine et al., 2007).

The results bear implications for both food web network analysis and the comparative analysis of paleo-food webs. The implementation of weighted networks and top-down effects generally increases levels of secondary extinction compared to topological-only models. Moreover, it is no longer clear whether conclusions derived from the topological models are valid, such as the hypothesis that increasing connectance increases robustness. The LAZ community is more connected than either DAZ or CAZ (Roopnarine et al., 2007), and it is entirely possible that greater connectance among or generated by certain functional groups would in fact decrease resistance or robustness by generating greater feedback among species and perpetuating perturbation propagation. The greater variance of the LAZ results is also surprising given the multinomial probability model for SLNs outlined earlier. The non-uniform (decay) shape of the guild trophic in-link distributions used to model the Karoo communities, mixed exponential-power law distributions, should dictate a smooth probability space (S,F,P), meaning that there should be a class of topologically closely related SLNs that are more probable than other SLNs in the space. Imagine a landscape, where distance is measured discretely by the topological differences between networks (a simple differencing of adjacency matrices) and topographic height is a measure of resistance to secondary extinction. The expectation of drawing stochastically from (S,F,P) is that the SLNs will be of high probability and topologically similar, as dictated by the multinomial distribution. The CEG results demonstrate that those SLNs also possess similar dynamics, and we therefore depict the DAZ and CAZ landscapes as having a defined region of high probability SLNs of uniform resistance (Fig. 15.1). The LAZ results, on the other hand, comprise SLNs of very different resistances and clearly hail from a different landscape. Characterizing the landscape remains an outstanding problem, but could be performed using exploratory MCMC-based methods as suggested earlier. A conjecture at this point, however, is that the LAZ landscape is in fact rugged, with network resistance being highly sensitive to minor differences in food web topology (Fig. 15.2).

A comparison of the three communities also suggests that ecologically, the LAZ community was quite different. The apparent instability of LAZ networks can be interpreted as either real ecological vulnerability to secondary extinction, or an indication that in order for the LAZ community to have been as resistant to secondary extinction, it would have to have functioned very differently. Real vulnerability would have imposed harsh conditions on the long-term ecology of LAZ species and increased intensities of natural selection. Species would have responded with increased rates of evolution, possibly manifested as a high rate of species turnover because of either resultant speciation or extinction. The particular outcome would depend specifically on the biology and the network position of the species. The vulnerability, on the other hand, could be confined to the CEG model and the LAZ community was in reality as resistant to secondary extinction as the preceding and successive communities. The community after all was real enough to actually be preserved and reconstructed from the fossil record. In that case, the dynamics required for resistance would be quite different from those envisioned in the CEG model for the other communities, and would perhaps be informative of the nature of communities and recovery in the aftermath of mass extinctions.

FURTHER READING

Comprehensive but accessible treatments of counting, combinatorics and probability may be found in Goldberg (1960) and Riordan (1958). The topics of networks, network theory and complex systems are currently very popular and there are a large number of popular treatments. Several which I recommend are Barabási (2003), Watts (2003) and Mitchell (2009).

SUMMARY

1. Food webs can be represented as mathematical graphs, specifically weighted digraphs and networks. As such, they are amenable to many of the analytic tools and measures available in graph and network theory.
2. Paleo-food webs present unique challenges stemming from uncertainty in the data. The approach advocated here is a probabilistic one, incorporating uncertainty in taxon aggregration and species-level food webs.
3. Fossil taxa can be aggregated into trophic guilds if knowledge of their trophic habits is accurate. Guilds are further assembled into higher-level food webs called metanetworks.
4. Species-level food web networks are generated from metanetworks on the basis of current understanding of the link distributions underlying modern food webs.
5. Secondary extinction, the extinction of species in trophic response to the extinction of other species, can be explored probabilistically using the metanetwork, or precisely using derived species-level networks. Those calculations of secondary extinction are limited to bottom-up perturbations of the networks.
6. A more complete measure of secondary extinction, incorporating top-down and other demographic processes, requires modeling of demographic parameters in the metanetwork. Even though such parameters are rarely available for fossil taxa, uniform approaches to parameterization allow the comparison of different paleocommunities. The CEG model detailed in this paper is currently the only approach available for such analyses.

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APPENDIX

List of mathematical symbols and notation used in text.

$\in$ - a member of a set, for example, $x \in G$ reads as “x is a member or element in the set G”.

$|X|$ - the size or cardinality of a set X, that is, the number of members of X.

$\binom{x}{y}$ - the binomial coefficient, expanded as $\frac{x!}{y!(x-y)!}$

a_i^x - a parameter of a species x in guild i.

$\forall$ - for all.

FIGURE 1.--Simple graphs and corresponding adjacency matrices. Links, or edges, between nodes indicate a relationship between those nodes. Adjacency matrices are node by node matrices. An entry of one indicates the presence of an edge between the row and column nodes, and zero otherwise. Hence, the unconnected graph (Fig. 1.1) has all zero entries, while the complete graph (Fig. 1.4) has entries all equal to one.

FIGURE 2.--Isomorphic graphs. The pairs of graphs in Figures 2.1 and 2.2 are isomorphic, differing only in the graphic arrangements. The isomorphism is easily recognized in the first pair (Fig. 2.1) because the nodes are labeled. Simply equating numbered and lettered nodes between the graphs reveals the isomorphism. The second pair is more challenging.

FIGURE 3.--Simple food web networks. Species are labeled S1, S2 and S3. S1 is autotrophic, while S2 and S3 are consumers.

FIGURE 4.--Guild-level network of a Greater Antillean Caribbean coral reef food web. Circles on the periphery are guilds and links are trophic interactions. There are a total of 265 guilds and 4,656 links in the system.

FIGURE 5.--Link density, or numbers of links and nodes in published food webs. Open circles – modern terrestrial and aquatic food webs, closed circle – modern Greater Antillean coral reef food web, open triangles – Permo-Triassic terrestrial paleo-food webs from the Karoo Basin, South Africa (Roopnarine et al., 2007), and open square – Miocene marine paleo-food web from the Dominican Republic.

FIGURE 6.--Types of in-link or in-degree distributions underlying various networks and food webs. Solid line – exponential distribution, broken line – power law distribution, broken-dotted line – mixed exponential-power law distribution, and solid line with circles – Poisson distribution with a mean of 4. The inset focuses on the tails of the distributions, showing the more significant densities of the power law and mixed distributions.

FIGURE 7.--Trophic in-link distributions of the Greater Antillean coral reef species-level network. The upper plot includes all consumer species (unicellular and multicellular, invertebrate and vertebrate), while the lower plot includes vertebrate species only. Note that both distributions have distinct peaks (modes), but are also very right-skewed.

FIGURE 8.--Guild-level food web, or metanetwork, of a Late Miocene shallow coastal marine community from the Dominican Republic. A detailed description is given in Roopnarine (2009).

FIGURE 9.--A single species-level network (SLN) drawn stochastically from the metanetwork illustrated in Fig. 7. The lines represent trophic interactions, and points of convergence are species.

FIGURE 10.--Simple three-guild metanetwork. Guilds 1 and 2 (G1 and G2) comprise species that are potentially preyed upon by species in G4. Circles and rectangles within the guilds represent actual guild species-richnesses and individual species.

FIGURE 11.--Species-level networks (SLNs) derived from the model metanetwork (Fig. 10). SLN

probability depends upon the likelihood of links being drawn between guilds, and are dictated by metanetwork topology and guild richnesses. Probabilities of the SLNs are: 1 – p = 0.36, 2 – p = 0.16, and 3 – p = 0.

FIGURE 12.--Probability of extinction as a function of species in-degree (number of in-links) and magnitude of the perturbation. The relationship between in-degree and the probability of extinction is nonlinear, with species resistance to extinction increasing rapidly as in-degree increases incrementally. Also note that this is a stepped surface, because degrees and perturbation magnitudes occur as integer values only.

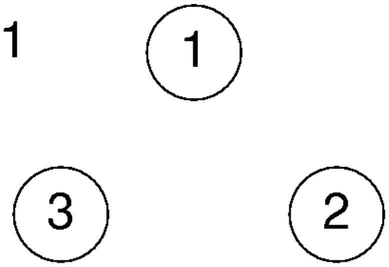
FIGURE 13.--Topological secondary extinction in the Dominican Republic metanetwork. Simulations were carried out on 100 SLNs. The upper figure plots extinction in response to an increasing shutdown of primary productivity (Perturbation magnitude), while the lower figure plots extinction in response to the removal of high trophic level fish.

FIGURE 14.--CEG simulations of secondary extinction in three paleocommunities of the Karoo Basin, South Africa, in stratigraphic order. Lower plot – Food web of the Late Permian *Dicynodon* Assemblage Zone, middle – food web of the early Early Triassic *Lystrosaurus* Assemblage Zone, and upper – food web of the late Early Triassic *Cynognathus* Assemblage Zone. Perturbation is a progressive shutdown of primary productivity in each system. Simulations were performed on 100 SLNs per paleocommunity.

FIGURE 15.--Heuristic landscapes as potential explanations of difference between the *Lystrosaurus*

Assemblage Zone and the other Karoo communities. The first figure illustrates a community represented by high probability SLNs with uniform dynamics, while the landscape on the right suggests a community with diverse, yet high probability SLNs with contrasting dynamics. The surface of the landscape is populated by SLN topologies, with a metric defined by topological differences. Topographic elevation is measured by extinction resistance of corresponding SLNs.

1



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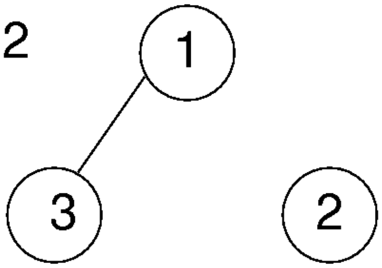

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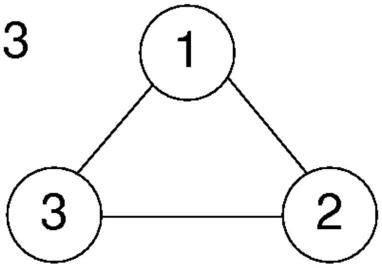

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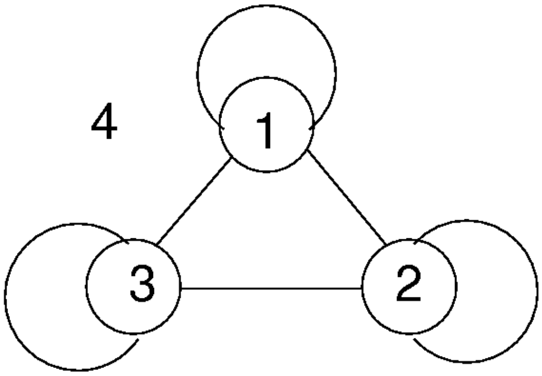

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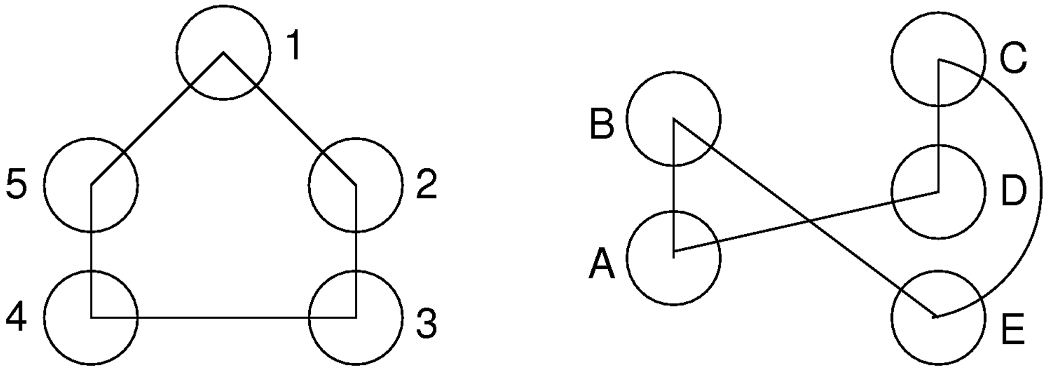

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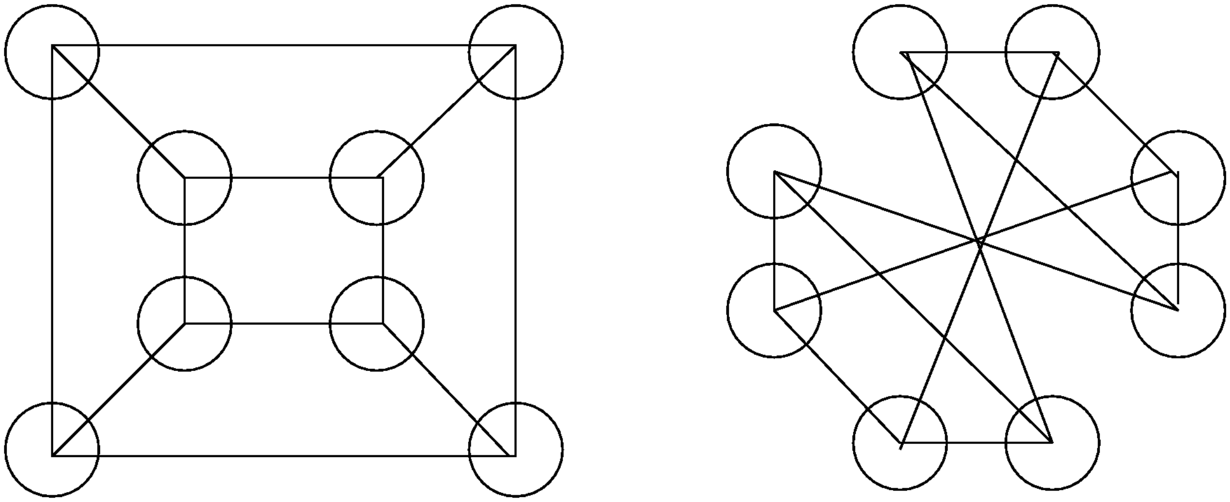

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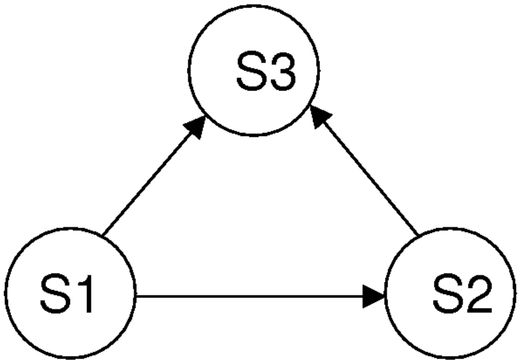

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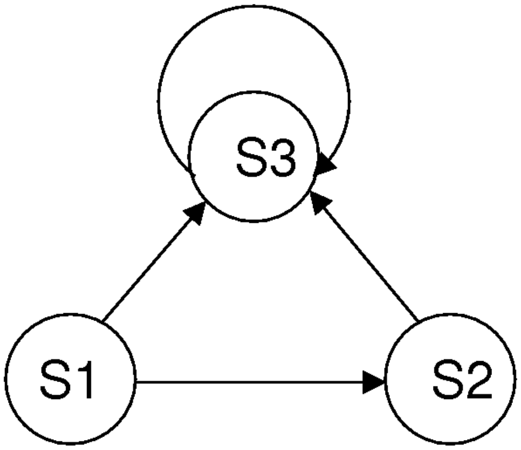

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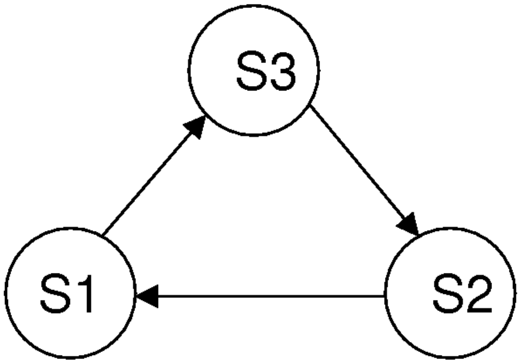

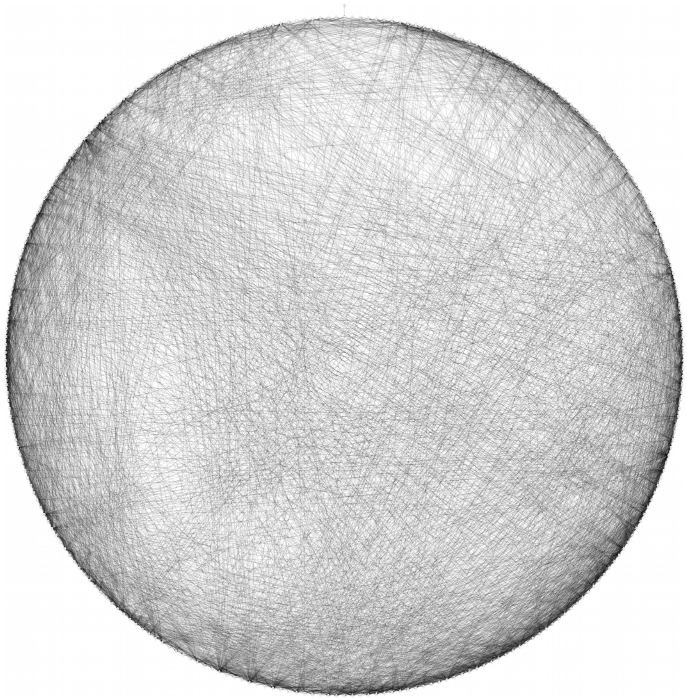

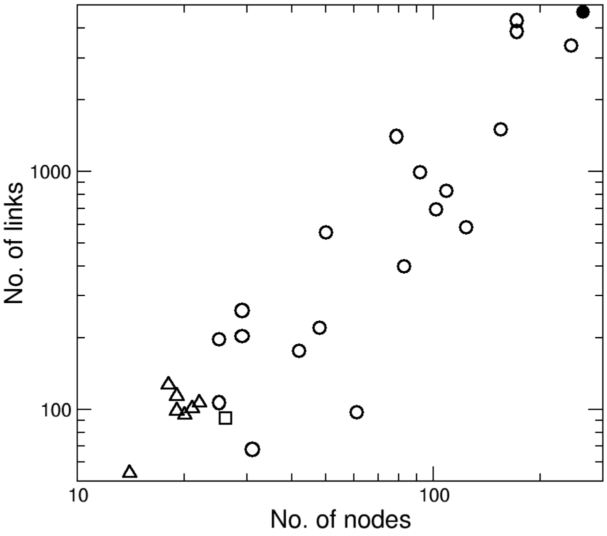
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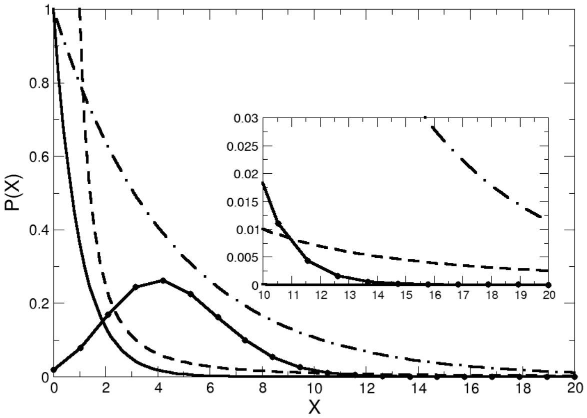
100
10
100
No. of nodes


P(X)
X
0
0.2
0.4
0.6
0.8
1
0
2
4
6
8
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12
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16
18
20
0
0.005
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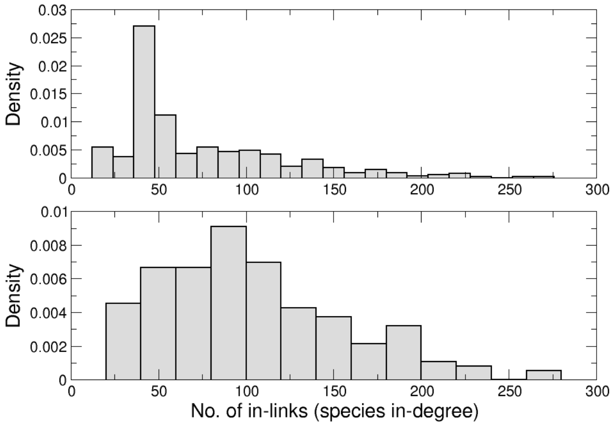
0.03
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Density
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250
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0.01
0.008
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Density
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50
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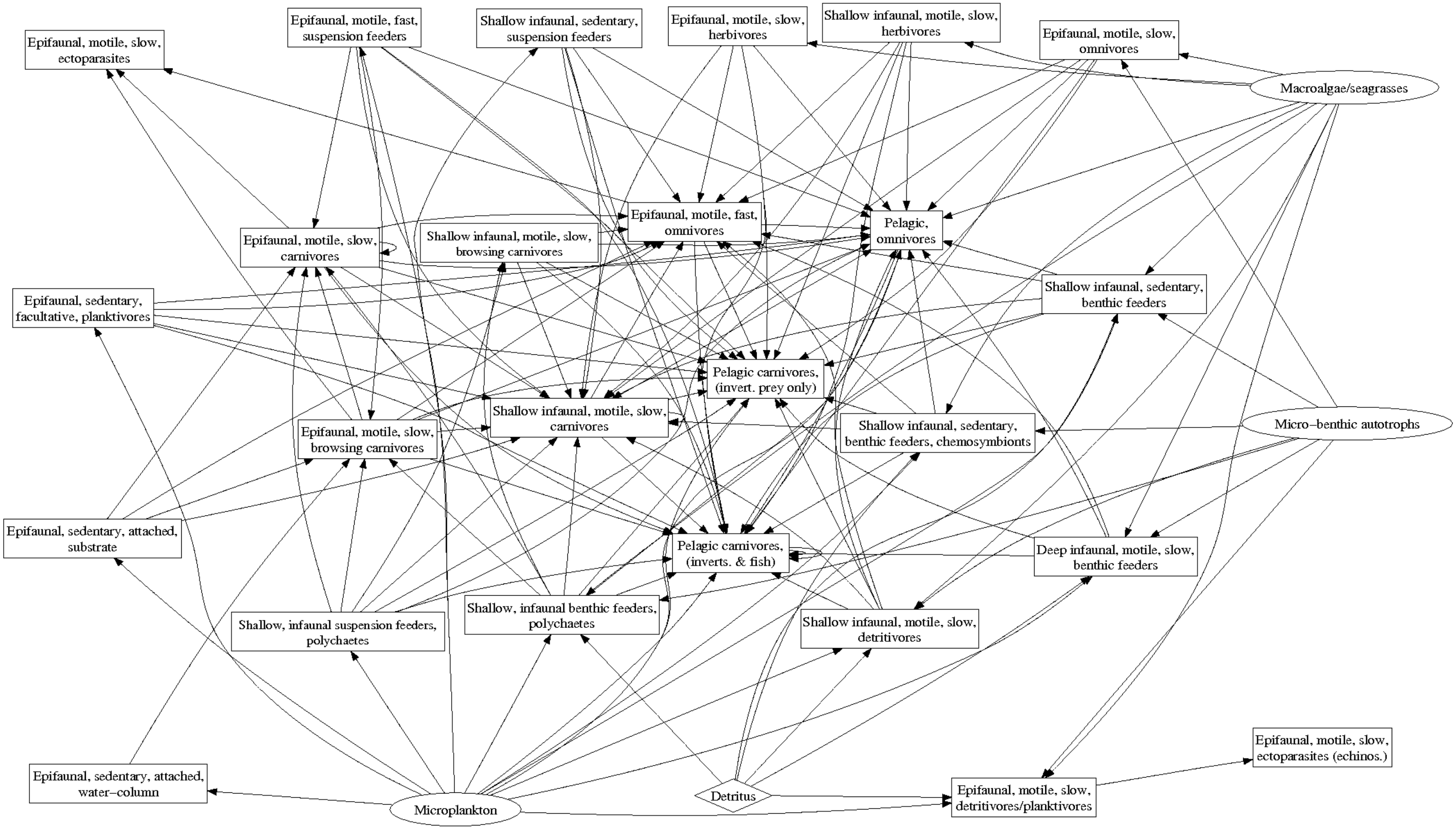
200
250
300
No. of in-links (species in-degree)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Epifaunal, motile, fast, suspension feeders
Shallow infaunal, sedentary, suspension feeders
Epifaunal, motile, slow, herbivores
Shallow infaunal, motile, slow, herbivores
Epifaunal, motile, slow, omnivores
Macroalgae/seagrasses
Epifaunal, motile, fast, omnivores
Pelagic, omnivores
Epifaunal, motile, slow, carnivores
Shallow infaunal, motile, slow, browsing carnivores
Epifaunal, sedentary, facultative, planktivores
Shallow infaunal, sedentary, benthic feeders
Pelagic carnivores, (invert. prey only)
Shallow infaunal, motile, slow, carnivores
Epifaunal, motile, slow, browsing carnivores
Shallow infaunal, sedentary, benthic feeders, chemosymbionts
Micro–benthic autotrophs
Epifaunal, sedentary, attached, substrate
Pelagic carnivores, (inverts. & fish)
Deep infaunal, motile, slow, benthic feeders
Shallow, infaunal benthic feeders, polychaetes
Shallow, infaunal suspension feeders, polychaetes
Shallow infaunal, motile, slow, detritivores
Epifaunal, motile, slow, ectoparasites (echinos.)
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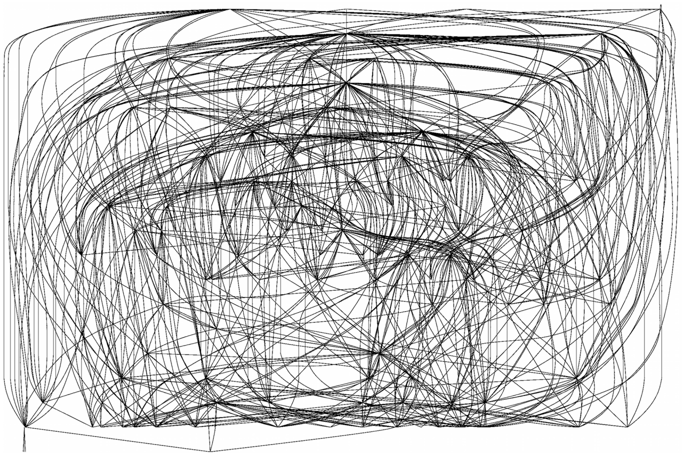
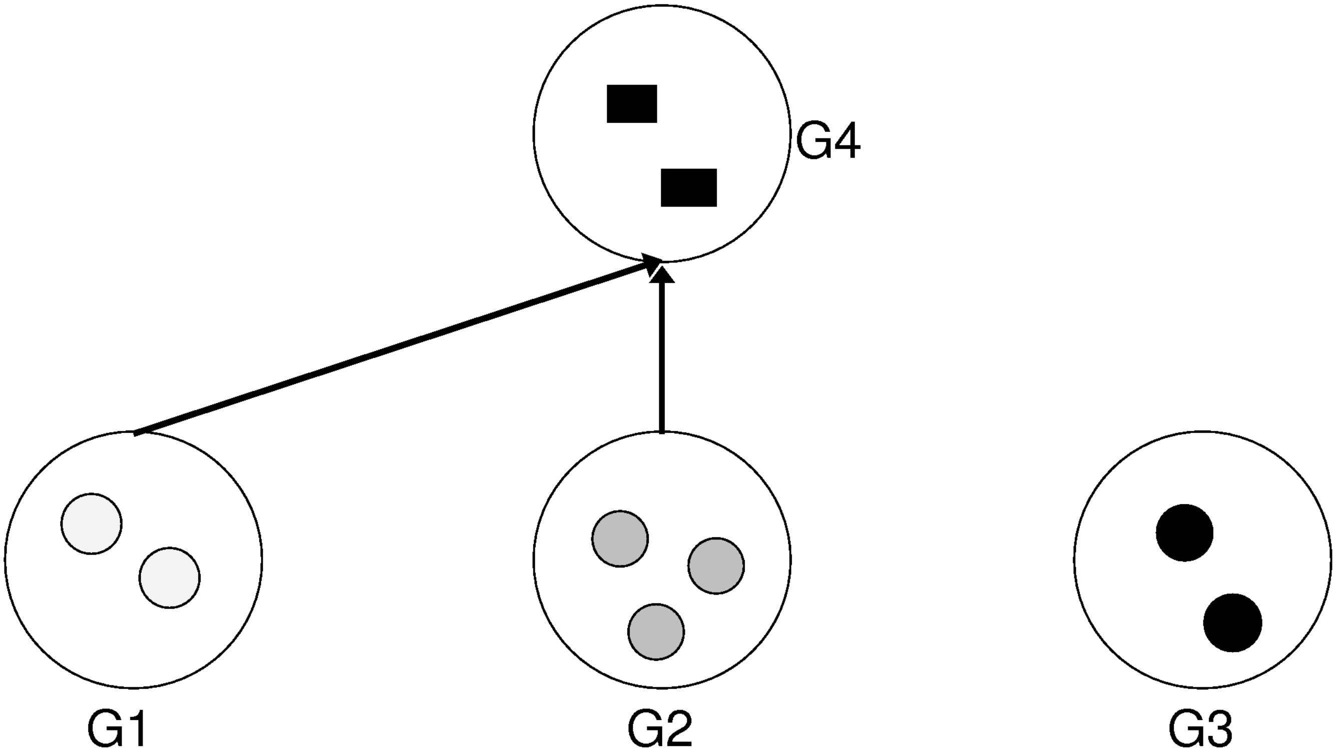
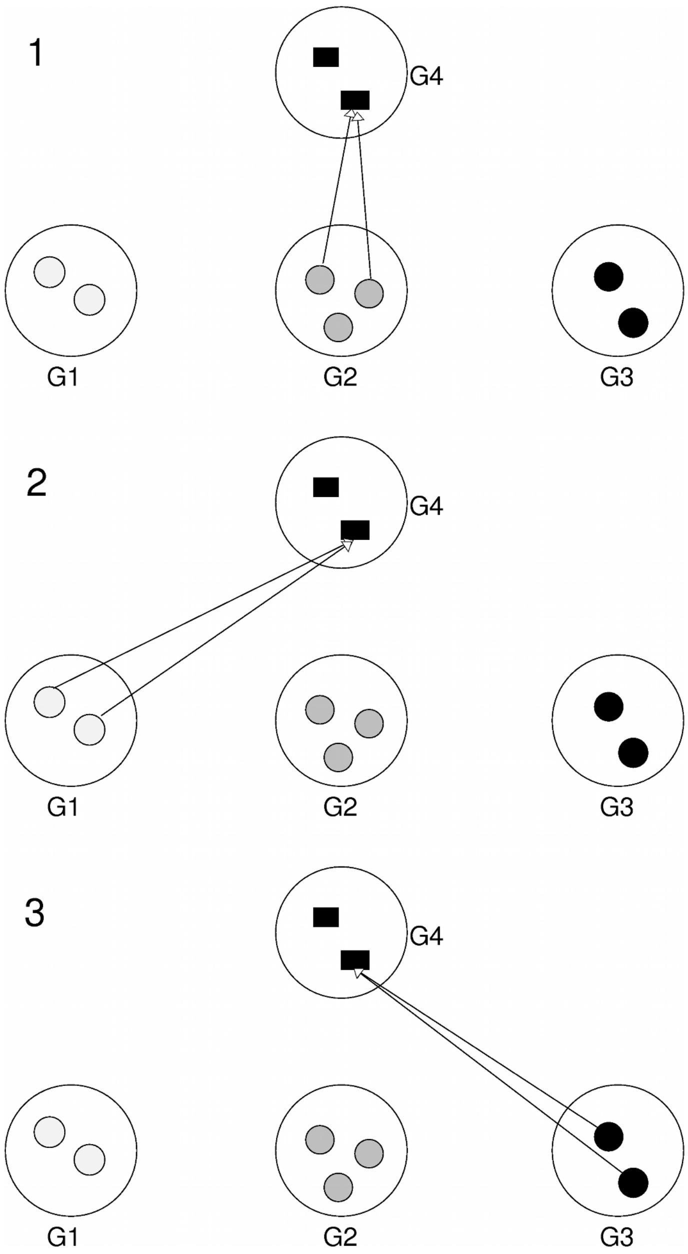
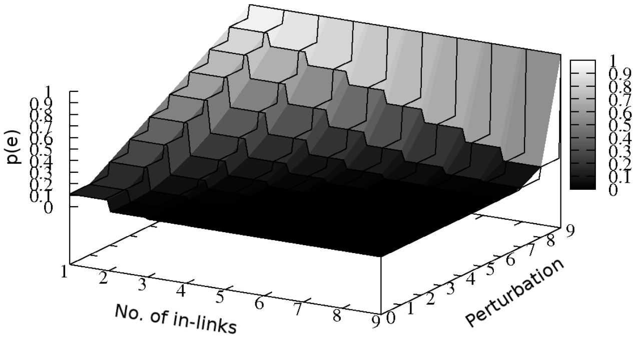
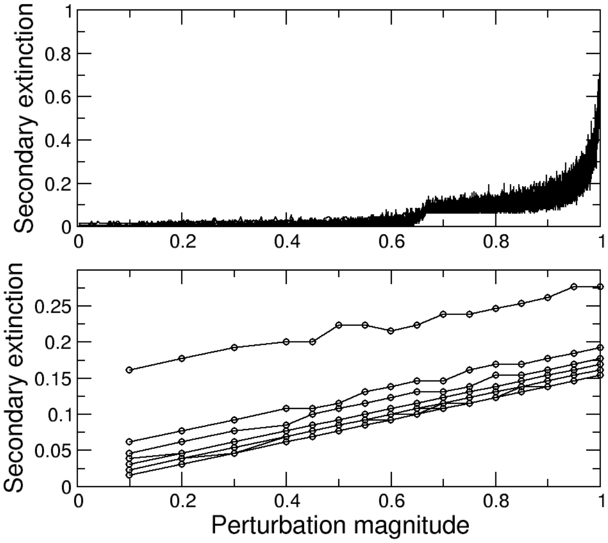
Detritus
Epifaunal, motile, slow, detritivores/planktivores

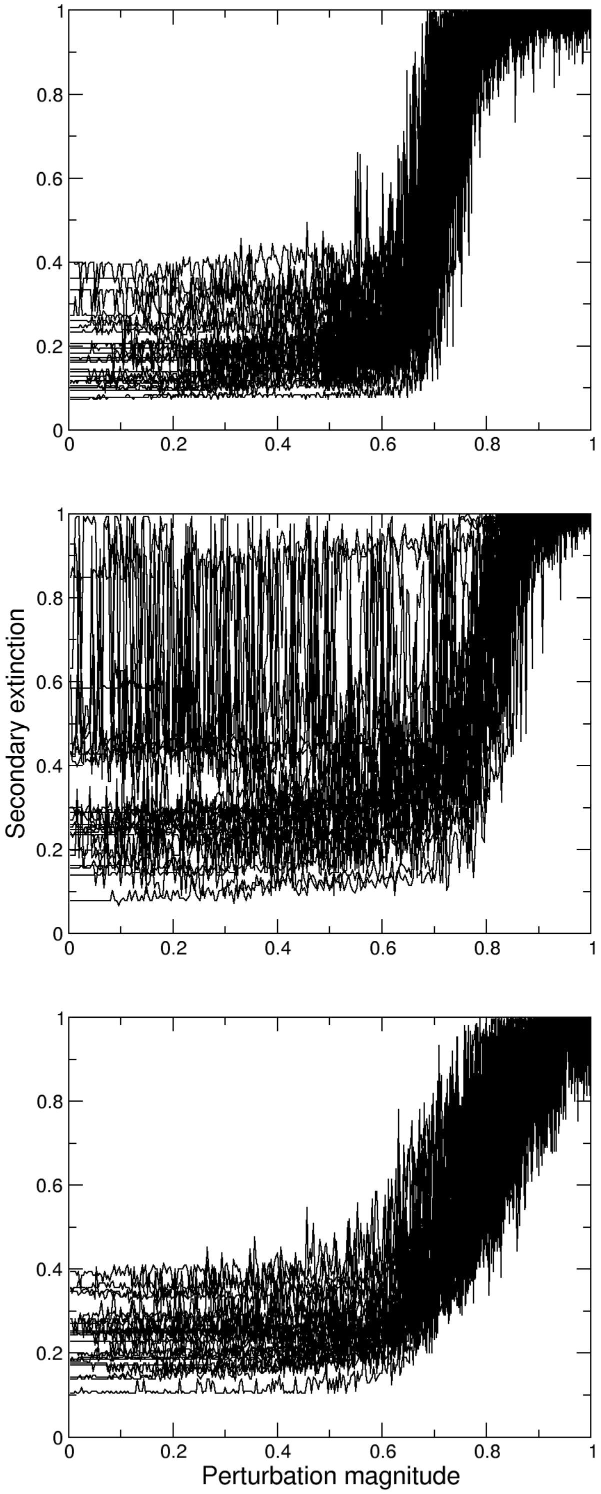


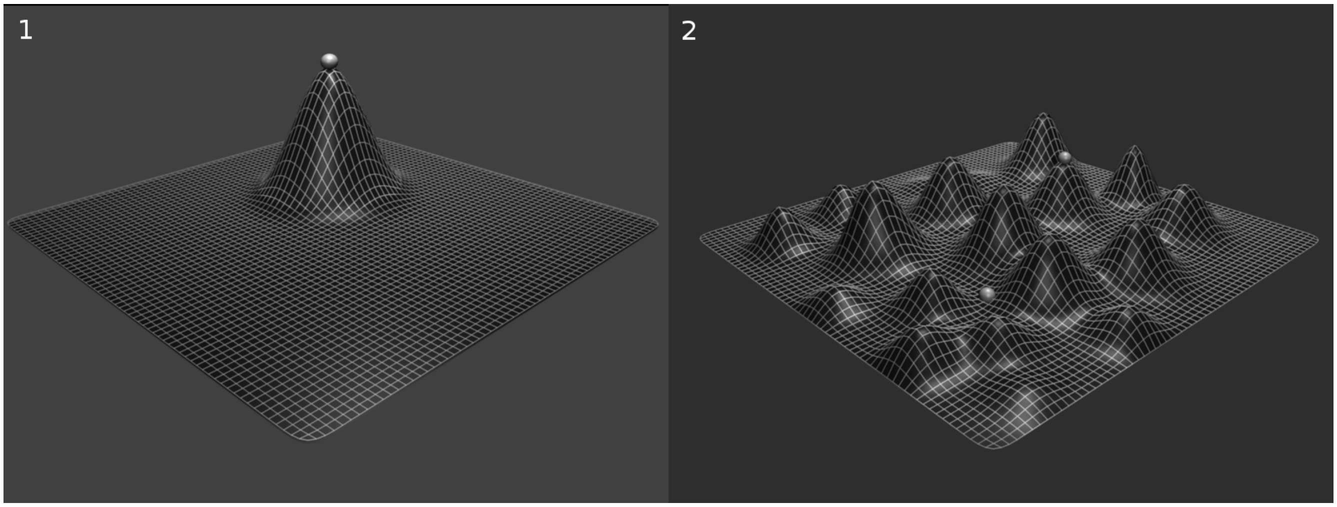

G4
G1
G2
G3


1
G4
G1
G2
G3
2
G4
G1
G2
G3
3
G4
G1
G2
G3


p(e)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
No. of in-links
1
2
3
4
5
6
7
8
9
Perturbation
0
1
2
3
4
5
6
7
8
9


Secondary extinction
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
Secondary extinction
0.25
0.2
0.15
0.1
0.05
0
0
0.2
0.4
0.6
0.8
1
Perturbation magnitude


1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
Secondary extinction
Perturbation magnitude


1
2