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Structural Cycles in Food Webs

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Abstract

Traditionally, food webs have been constructed as structural directed graphs that describe "who eats whom," but it is common to interpret them directly as energy flow diagrams, where predations represent energy transfers from the prey to the predator. It is the aim of this work to point out that food webs are incomplete as energy flow diagrams if they ignore passive flows to detritus (dead organic material), a misconception that is common both in empirical data sets and in assembly models, where detritus often is either ignored or treated as an unlimited energy source. When individuals die, they contribute to the detritus pool, and might be an energy source for other species in the system. This feedback loop is of high importance, since it increases the number of pathways available for energy flow, revealing the significance of indirect effects, and making the functional role of the top predators less clear. These additional energy pathways increase the structural cyclicity of the system (measured in terms of the dominant eigenvalue λ of the adjacency matrix A). In this work we show the importance of the structural cyclicity by comparing empirical data sets to 5 different assembly models. Of these models: cascade (Cohen & Newman 1985), constant connectance (Martinez 1992), niche (Williams & Martinez 2000), modified niche (original in this work), and cyber-ecosystem (Fath, 2004), the two last include detritus feedback. We show that when passive flows to detritus are included, the structural cyclicity is increased both in models and empirical data sets. We also show that there is in an approximately linear relationship with the link density (L/N), defined as the number of links per specie.

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About the Author

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Introduction

An area of ecology concentrates on studying structural aspects of communities of species or food webs. The terms "community assemblies" and "food-webs" are used interchangeably, and both restrict the investigations to biotic interactions. The term food web refers to a conceptualization of a set of species and the connections between these, as opposed to the term ecosystem that normally is taken to refer to a broader picture, considering also inorganic material flows. Part of the difference arises from where the system boundaries are drawn. Food webs are often limited to active, macro-scale feeding interactions, whereas ecosystems comprise active and passive biotic and abiotic energy flow processes. Although many food webs include compartments such as "detritus" or "dead organic material", there is not a consistent approach for incorporating them, something that also shows the difficulties in defining clear system boundaries. The term "specie" is often used to mean "tropic specie", defined as the set of biological species that have the same level of predators and preys. There is also additional literature on how to lump species into conceptual species groups or compartments (Krause 2003), either strictly defined as "tropic species" or less strictly as "similar species" having more or less the same rolls in terms of predators and preys. It has been shown that species in real food webs are more "lumpable" than are species in model food webs (Solow & Beet 1998), suggesting that there are certain underlying structures that a good food web assembly model should be able to reproduce, and that networks that do not incorporate biologically relevant features in their structuring are not good approximations to the real food webs.

Although conclusions based on structural principles are limited and at best qualitative, they are valuable since structural knowledge about ecosystems is generally easier to acquire than quantitative flow data. A lot of focus has been put on the structure of food webs, and the simplest description of a food web is an adjacency matrix of binary elements that indicates whether two species are connected (1) or unconnected (0). In the typical food web scenario "connected" means that one of the species feeds on the other. The food web structures can be analyzed in terms of measures like maximum tropic position, degree of top-down control, number of species in each of the classes basal species, intermediate species, and top predators, lumpability (Solow & Beet 1998), or pathway proliferation (Borrett et al. 2005). These analyses are at best qualitative, and help to give a conceptualization of the food webs and an understanding of how their topologies may look. Since food webs are complex systems, many of these studies aim at revealing some simple universal features to grasp them with, such as global scaling relations (Ulanowicz & Wolff 1991; Garlaschelli et al. 2003) or general organizing

principles (Williams & Martinez 2000). The idea that there is an important connection between stability and diversity has been subject to many debates within the field (McCann 2000). The idea that food webs are scale invariant networks, was for a long time popular, and connected the field of research to fields like general network theory and graph theory. New empirical findings have however shown that the hypothesis of scale invariance does not seem to apply (Drossel & McKane 2002).

Since there is a significant lack of empirical data on food webs, topologies are often constructed using so called "assembly rules" that either set up a connectance matrix for a number of N species, or is generated step wise by successively adding species to a food web. Assembly rules are in general a set of rules that will generate a network based on a few parameters, such as the size of the food web, the number of species belonging in different groups, and the connectivity. The aim of these assembly rules is to produce a model-food web that can be tested against empirical data, and also can be an object for network analysis.

One early and simple assembly model was called the cascade model (Cohen & Newman 1985). In the cascade model, the n species are given a rank from 1 to n and all species predate on a random number of the species with lower rank than them self. The structure of this model is thus a set of food chains, in general branched, but in all cases originating with basal species (in-degree equal to zero) and terminating at top predators (out degree equal to zero). There are per definition no cycles in the system, and this is one of the main criticisms against it, since we know that examples of intraguild predation, longer cycles, and even cannibalism can be found in nature. The constant connectance model or random model (Martinez 1992) was developed to produce food webs that allowed for this kind of feedback from higher to lower species. In this model all the N species are connected randomly among each other, with each connection having the same probability of occurring, thus resulting in a system that is likely to have structural cycles. A criticism towards the random model is that it has no biological or ecological knowledge incorporated in the structural principles, and it has been shown that both the cascade model and the random model are incapable of reproducing many important features of real food webs. A later assembly model is called the niche model (Williams & Martinez 2000), and has become one of the most accepted models since it incorporates the probability of cycling and cannibalism in the generation of food webs, and since it is also based on some biological relevant parameters. It has been tested against both random and cascade models (Martinez et. al. – 2005, in press), and has been proven more successful in reproducing several empirically found food web properties, like the relative fractions of primary producers, intermediate species and top predators. These analyses were made, however, without recognizing the additional structural cycles due to decomposing and uptake of dead organic material. Also the empirical food webs that the model was tested against (Table 1) ignored the detritus feedback loop.

It is an important point of this work to stress that the detritus compartment should be included in a structural analysis of food webs or ecosystems. Both in models and in empirical studies, detritus is often ignored. Furthermore, when detritus is included as a compartment, it is often treated as an unlimited energy source that does not receive input from any of the species in the food web. Although traditional food webs strictly could be regarded as diagrams of who eats whom, they are frequently interpreted directly as energy flow diagrams, something that makes them more useful since they

then give a clue on where resource transactions occur in the system. However, the conception that energy flows in simple chains from the primary producers to the top predators, does not give a complete picture, for two reasons: First, energy is lost to the environment due to dissipation, but since this does not alter the internal structure of the systems, it is not relevant in a structural analysis. Second, individuals in all the compartments in the food web die, and may then contribute to a reservoir of detritus that works as an energy source for other species in the system. This does change the structure of the system in a significant way since the detritus compartment connects in a structurally different way than the "real" and more hierarchically structured species in the food web. Most importantly, the detritus compartment makes a pathway for energy to flow from the top predators and back to lower levels in the hierarchy, something that creates a feedback loop and increases the amount of structural cycling in the system. This also makes the functional role of the top predator less unique, and makes the distinction between top-down or bottom-up control ambiguous.

In this work we analyze and compare five different assembly models among each other and to empirical data, in order to investigate the importance of the detritus feedback loop. Three of the models are the cascade, constant connectance and niche model that have already been briefly described. We compare these to two models that include detritus in their structure. One of these is the cyber-ecosystem model (Fath, 2004), which is slightly more complex than three described models, since it operates with six different functional categories (primary producers, grazers, omnivores, carnivores, detrital feeders and detritus) linked in accordance with basic biological rules. The last model is original in this work, and is a modified version of the niche model. It is given a more detailed treatment in the Methods section below.

Methods

The Modified Niche model

The niche model (Williams & Martinez 2000) is an assembly model that generates food webs when the number of species N and the connectance C (defined as the fraction of the theoretical number of connections N^2 that actually are present) are specified as input parameters. The niche model, as well as the other models considered, use random distributions to assign connections, so that the input C actually represents the expected connectance, and not the connectance itself, of the resulting food web-structure. For simplicity we will throughout the Methods section refer to this input as the connectance. It should be noted that in the Results section we always use the real connectance when we compare assembled and empirical food webs.

The general idea of the niche model is that the N species each are assigned a random niche value n between zero and one, representing somewhat the species' positions in a food hierarchy. These N species are then allowed to predate on species within a range of niche values centered somewhere behind their own niche values. If the range of predation is called r, its center is placed randomly at in the interval [$r/2, n$], meaning that there also is a probability of predation on species with niche values higher than n. The niche model therefore allows for limited cycling and cannibalism in a more realistic way than the earlier models. The size of r is $x*n$, where x is a random number, drawn from a beta-distribution with expected value $2C$.

In the niche model, species are not preset to belong to subgroups of species, like basal, intermediate and top species. Properties like these are a byproduct of the niche-algorithm. The only exception to this is the demand that at least one species should be basal, that is: There should at least be one species that does not feed on any others but receives energy input external to the system, assumingly via solar radiation. This is included in the model by letting the species with the lowest niche value have $r=0$.

There is a possibility, especially for low N and C values, that the niche model generates a food web with one or several unconnected nodes. In this case, the unconnected nodes are replaced by new species (new niche values), and the algorithm is rerun. Another possibility, not considered in the original paper (Williams & Martinez 2000), also most likely to occur at low N and C-values, is the possibility of having isolated clusters, that is; a group of species that are connected amongst each other, but isolated from other groups. Certain global parameters of the N species food web would then in reality be measures only of the subsystem with less than N species. We traced the occurrence of these clusters, but did not reprogram the model in order to avoid them. For the N and C values relevant for data comparison, isolated clusters rarely occurred in our simulations, and the problem was negligible.

The algorithm we used for the Niche model returns an adjacency matrix A (matrix of zeros and ones) where the elements a_{ij} decide whether species i predates on species j (meaning the flow transaction is from j to i).

We propose a modified niche model, which expands the basic food web structure (of size N) that is generated by the original niche model. The modification is a detritus feedback loop that we add to the system by letting all species be connected to a detritus compartment (compartment $N+1$), meaning that death works as a predator on all living things. We also add an additional compartment of detrital feeders (compartment $N+2$), representing bacteria or other small organisms that feed on the detritus compartment, and that are were not represented in the initial structure (Figure 1). Through predation on these microorganisms by the species in the food web, energy can reenter the system. We let all species that are not primary producers have the same probability of feeding on the detrital feeders, and let this probability be equal to C.
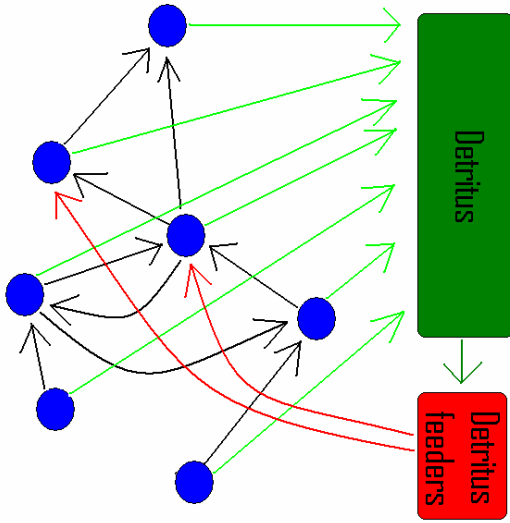
Figure 1: The structure of the modified niche model. The original niche model (blue) is used to construct the food web structure to the left. Detritus and detritus feeders are then added to this structure, creating an extra feedback loop that allows energy to flow from the top predators towards lower levels in the niche-hierarchy.

The modified niche model uses the original niche model to generate a structure with *N* compartments, and then adds two compartments, ending with an *N+2* compartment structure. In order to control the expected connectivity of the total structure, it is necessary to derive the relationship between the connectivity of the original substructure *C* and the connectivity of the modified structure $\tilde{C}$.

The standard niche model with input *C* and *N* constructs the *N* first species of the *N+2* species modified web. When the detritus feedback loop then is added to the system, the expected number of links (*E[L]*) should be:

$$E[L] = CN^2 + N + CN(1-b) + 1,$$

where the first term on the right is the number of expected links in the basic niche model structure. The second term is the *N* connections that make all species go to detritus. The third term is the expected number of connections back to a fraction *C* of all the species *(1-b)N* that are not basal species. The last term is due to the one connection between the detritus compartment and the detritus feeders. This total number of expected links should by definition equal

$$E[L] = \tilde{C}(N+2)^2,$$

where $\tilde{C}$ is the expected connectivity for the total *N+2* species modified niche model. The relation between *C* and $\tilde{C}$ is thus given by

$$C = \frac{\tilde{C}(N+2)^2 - (N+1)}{N^2 + (1-b)N},$$

Which means that a modified niche food web with *N+2* species and expected connectance $\tilde{C}$ is generated by adding the detritus loop to a standard niche food web with *N* species and connectance *C*.

As mentioned earlier, we use the "real" connectance of the assembled food web-structures (and not the input value *C*) for model comparison, so that the input parameters just serve to ensure that the models generate food webs in an appropriate range of connectance values. Since, in addition, the N^2-term dominates the denominator of the above equation, the rough approximation *b = 1/3* will work for our purpose, although *b* in general will be a complex function of *C* and *N*.

Empirical data

In a well-studied dataset of 17 food webs, we considered only the 10 (Table 1) that already included detritus. These ten data sets, however, only described which species fed on the detritus reservoir, and did not reflect the effect of individuals dying and contributing to this energy source. The detritus compartment was thus treated as some autonomous source of available energy, which is clearly not a realistic case. We therefore considered two cases, first the data as given, and second modifying the data set in the same way as we modified the niche model – by assuming that individuals from all species died and contributed to the detritus pool. The connections back to the systems were kept as in the original data sets, where only a subgroup of the species fed on detritus.

Table 1: Properties of 10 empirical food webs where flows to detritus originally were ignored. *N* is the size of the food web, while *C* is the connectance (L/N^2). Both the original connectance (without passive flows to detritus) and the modified connectance (when all species go to detritus) are shown.

Food Web	N	C (Orig.)	C (Mod.)	Reference
Coachella Valley	30	0.071	0.104	Polis 1991
St. Martin Island	44	0.068	0.090	Goldwasser & Roughgarden 1993
El Verde Rainforest	156	0.062	0.069	Waide & Reagen 1996
Skipworth Pond	37	0.070	0.098	Warren 1989
Bridge Brook Lake	220	0.011	0.016	Havens 1992
Canton Creek	109	0.060	0.069	Townsend et al. 1998
Stony Stream	113	0.065	0.074	Townsend et al. 1998
St. Marks Estuary (TRO)	48	0.096	0.117	Christian & Luczkovich 1999
Caribbean Reef, small	50	0.222	0.242	Opitz 1996
NE US Shelf	81	0.226	0.238	Link 2002

Also some data sets that consider both the flow of energy from species to detritus, and from detritus to detrital feeders can be found in the literature. These food webs are ecologically and thermodynamically more realistic than those which do not include this feedback loop. A goal of our research is to bring to light the discrepancies in how food webs are developed and encourage a consistent approach that includes detritus and detritus feeders. The ecosystems listed in Table 2 were included in our analysis in an unmodified form.

Table 2: Properties of 16 empirical food webs that considered flows to detritus. N is the size of the food web, while C is the connectance (L/N^2).

Ecosystems	N	C	Reference
Gramnoids (wet season)	66	0.182	Heymans et al. 2002
Gramnoids (dry season)	66	0.182	Heymans et al. 2002
Cypress (wet season)	68	0.118	Heymans et al. 2002
Cypress (wet season)	68	0.120	Heymans et al. 2002
Mangrove Estuary (wet season)	94	0.152	Heymans et al. 2002
Mangrove Estuary (dry season)	94	0.152	Heymans et al. 2002
Florida Bay (wet season)	125	0.124	Heymans et al. 2002
Florida Bay (dry season)	125	0.126	Heymans et al. 2002
Baltic Proper	12	0.250	Sandberg et al. 2000
Bothnian Sea	12	0.236	Sandberg et al. 2000
Bothnian Bay	12	0.222	Sandberg et al. 2000
Oyster Reef	6	0.333	Dame & Patten 1981
Okefenokee Swamp	24	0.201	Patten et al. 1989
Brouage	13	0.195	Leguerrier et al. 2003
Zostera meadows	28	0.220	Patricio et al. 2004.
Cedar Bog Lake	8	0.359	Lindeman 1942

Measures and simulations

Aiming to understand the importance of occurrence of structural cycles in food webs and ecosystems, we compare simulation results for 5 different assembly models (cascade, constant connectance, niche, modified niche and cyber ecosystem) among each other and also to empirical food web structures.

All the five models were programmed so that they could be run with *N* and *C* as input parameters. Note that the input parameter *C* represents the expected connectivity. A single simulation would then return the adjacency matrix *A* for the structure generated by the particular assembly model, and the actual value for the connectance was then used for the presentation of the simulation results. Our main measure was the dominant eigenvalue, λ, of the adjacency matrix *A*, which works as a measure of structural cycling (Fath 1998; Jain and Krishna 2003). If this eigenvalue is zero, then there is no cycling (or feedback) anywhere in the system. If the eigenvalue is unity, then there is weak cycling, which means that there is at least one simple cycle in the system, acknowledging the presence of a strongly connected component (it could be the whole network or a subset). A strongly connected component is a system in which all compartments are reachable to and from each other. If the eigenvalue exceeds unity, then the adjacency matrix has strong cycling. In the case discussed earlier, where *A* describes a system that consists of isolated clusters, the highest eigenvalue will be the same as the eigenvalue of the strongest cycling subsystem.

The number of indirect pathways (length *m>1*) between two nodes is found by raising the adjacency matrix to the *m*'th power (Ponstein, 1966). Pathway proliferation, developed as a measure on how the number of possible pathways between two nodes increases with path length, has been used as a good measure of the influence of indirect interaction in strongly connected networks (Fath 1998; Borrett et al. 2005 – in press). It is easy to show that the number of pathways of length *m* between two nodes increases with *m* in a system with strong cycling. The eigenvalue is thus a measure of how fast the number of pathways of length *m* increases with *m*. Much of this theory, that seems to be frequently reinvented in the field of theoretical ecology, relates strongly to the theory of Markov Chains (Kemeny & Snell 1960).

Results

We ran 400 independent simulations for each community assembly rule model. For each simulation we randomly drew input values from uniform distributions within the range of the empirical data set values (*6≤N≤220 & 0.016≤C≤0.359*). After each run, the dominant eigenvalue of the resulting adjacency matrix was plotted against the link density $L/N = NC$ of the resulting structures. We found that all models have a more or less linear relationship between λ and *NC* (Figure 2). Also, we see how the modified niche model (purple line) has a stronger structural cycling than the original one. It is also clear from the simulation data set that the variance in the original niche model is greater than in the modified one, since the detritus feedback loop is a more or less fixed structure. More generally, both versions of the niche model had a higher λ-variance than the other models. The constant connectance model (red) and the cyber ecosystem model (green) give the structures with the strongest cycling, following approximately the relation λ = *NC*. The cascade model (cyan) has by definition no cycling.
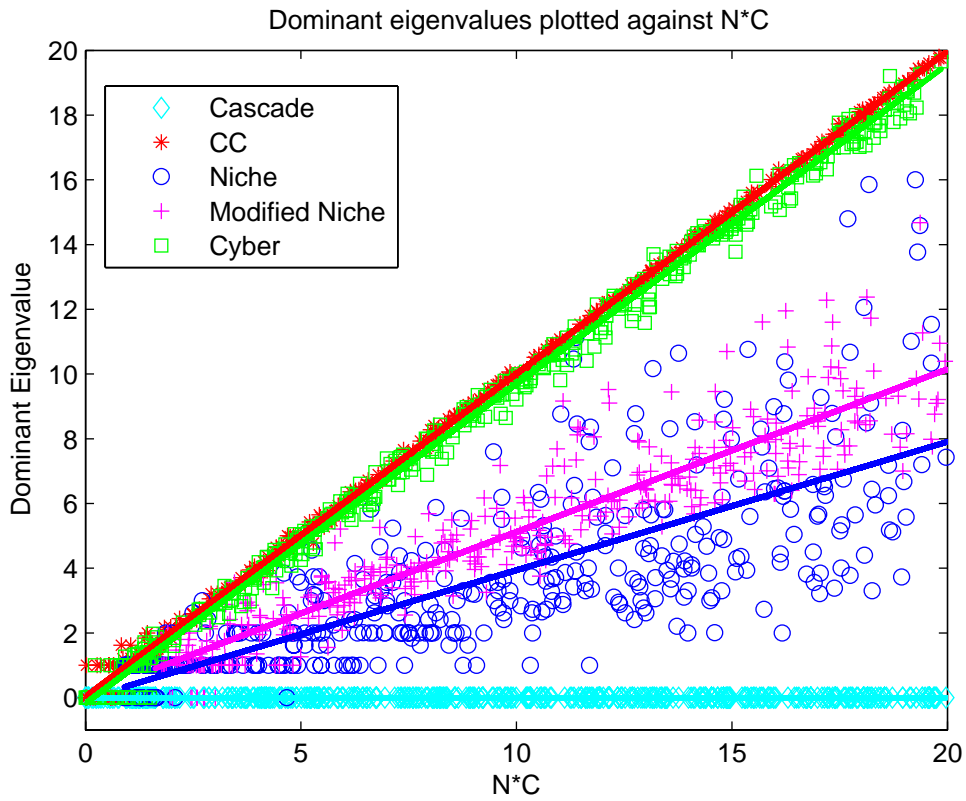
Figure 2: The dominant eigenvalue λ plotted against *NC* for 400 independent runs with each of the five assembly models. The regression lines show the approximately linear relationship between λ and *NC*.

When the data set from Table 1 was plotted in its original form (when detritus is treated as a primary producer or unlimited energy source), we could not see any clear trend in the relationship between the structural cycling and the *NC* product (Figure 3a). However, when we added connections from all species to the detritus compartment, the data set roughly followed the observed *NC* trend, apparent in Figure 3b, and the values of λ were close to the ones produced by the Constant Connectance and Cyber Ecosystem models for the same *N* and *C* values.
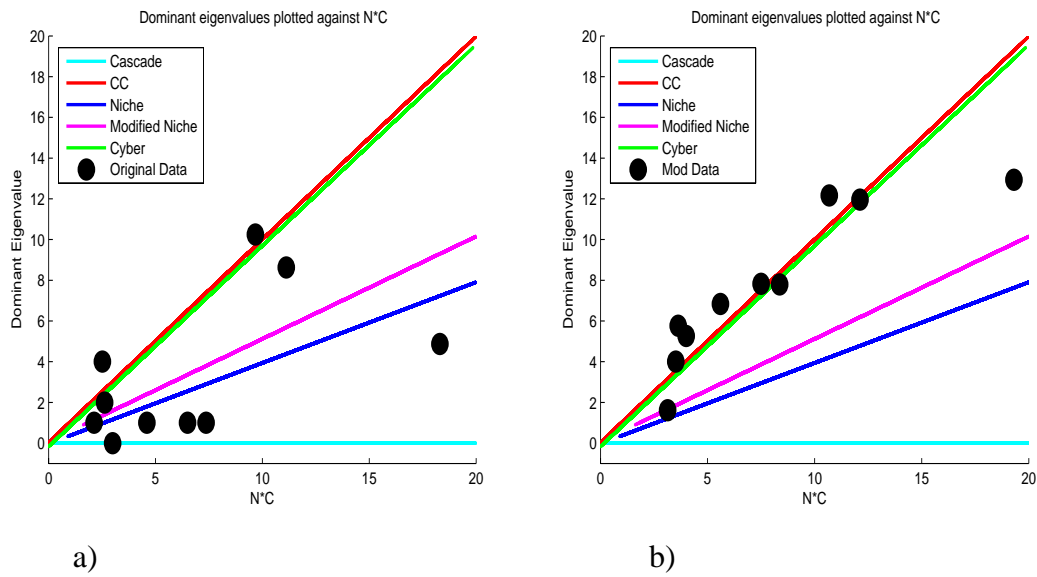
Figure 3: The regression lines, derived from the simulations in Figure 2, show the relationship between λ and *NC* for different models. The black dots show the dominant eigenvalues for the 10 different empirical datasets from Table 1. In a), the original data set is used, where all passive flows to detritus were ignored. In b), the data set was modified so that all species contribute to the detritus pool.

Finally, in Figure 4, the data from all the empirical food webs/ecosystems are presented. The dots mark the 10 modified systems as before, and the crosses mark the data from the empirical systems that originally included the detritus feedback loop. Three of the five assembly models underestimated the amount of structural cycling in the data sets. The two models that performed best were the Constant Connectance model and the Cyber Ecosystem model, whose clear linear trends fitted the data sets well. The modified Niche model were performing only slightly better than the original Niche model.
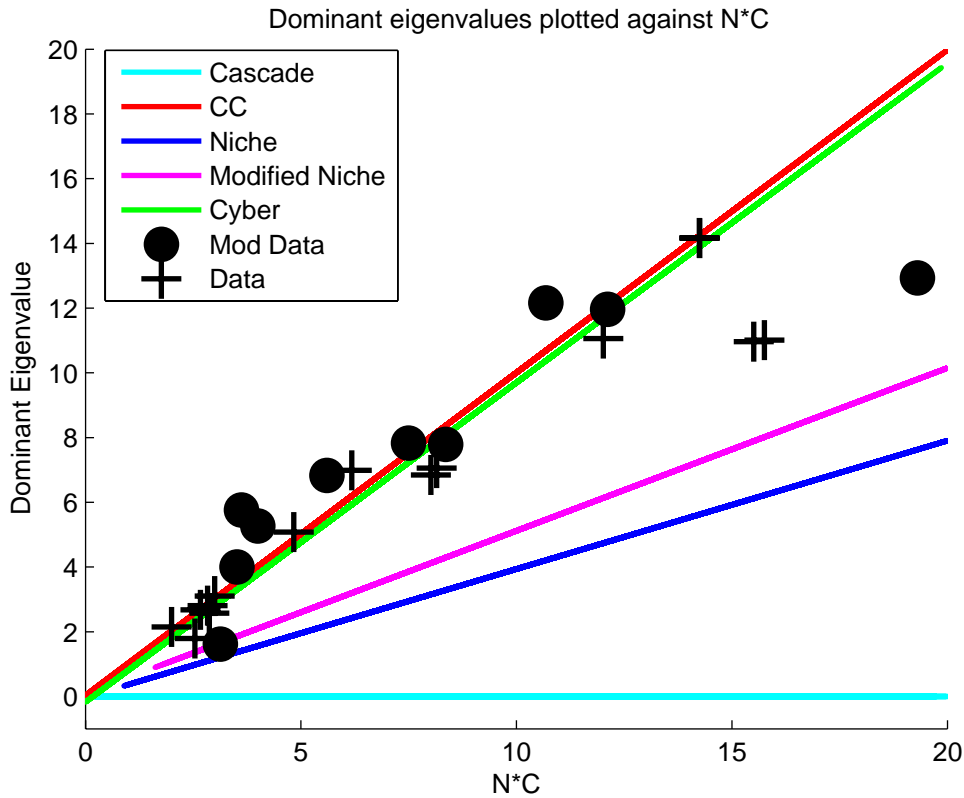
Figure 4: The regression lines, derived from the simulations in Figure 2, show the relationship between λ and *NC* for different models. The black dots show the dominant eigenvalues for the 10 different empirical datasets in Table 1, when the datasets were modified so that all species contributed to the detritus pool. The black crosses display the eigenvalues for the ecosystems in Table 2 that originally included a detritus feedback loop.

It should be noted that even though the constant connectance model performs well with respect to the empirical eigenvalues, it has been shown to give bad fits with respect to other important food web properties (Williams & Martinez 2000). Different behaviors of the cyber ecosystem model and constant connectance model with respect to some food web properties were also investigated when the cyber ecosystem model was first proposed (Fath 2004). Although the structures produced by the cyber ecosystem- and constant connectance models have roughly the same amount of structural cycling, the structures in themselves are not in any way similar. Figure 5 shows a graphical representation (Matlab spy-plots) of the typical adjacent matrices resulting from three of the models.
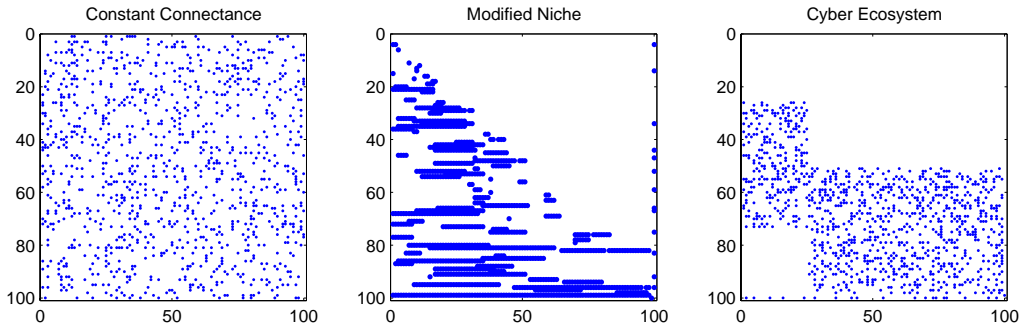
Figure 5: Graphical representation (Matlab Spy-plots) of the typical adjacent matrices produced by the three models Constant Connectance, Modified Niche and Cyber Ecosystem, for $N = 100$ and $C = 0.1$. The ones (connections) in the A-matrices are marked with blue dots.

The connections (row predates on column) are marked by blue dots, and with proper ordering blue dots above the main diagonal indicate a feedback connection (predation on species that are higher in the hierarchy). For the constant connectance model the dots are randomly distributed, and the feedback connections are equally many as the feed forward connections. A strong structural cycling is not unexpected in this case. For the cyber ecosystem model, the structural cycling is the same as for the constant connectance model, although the number of feedback connection is more restricted in this case. The modified niche has even fewer appearing over the main diagonal, but still a fairly high value for λ, even though it is lower than for the constant connectance- and cyber ecosystem models.

For comparison with the empirical data, the structural spy plots for 6 of the systems are presented in Figure 6. For the modified data set (Table 1), the three data sets with highest *NC* values were chosen. For the remaining data (Table 2) we chose from the two data sources from which we had more than one ecosystem, the system with highest *NC* value, and at last the system with the highest *NC* value that were not from these two sources. Also in the empirical data sets has a bias towards hierarchical connections, favoring the structures of the modified niche- and cyber ecosystem models.
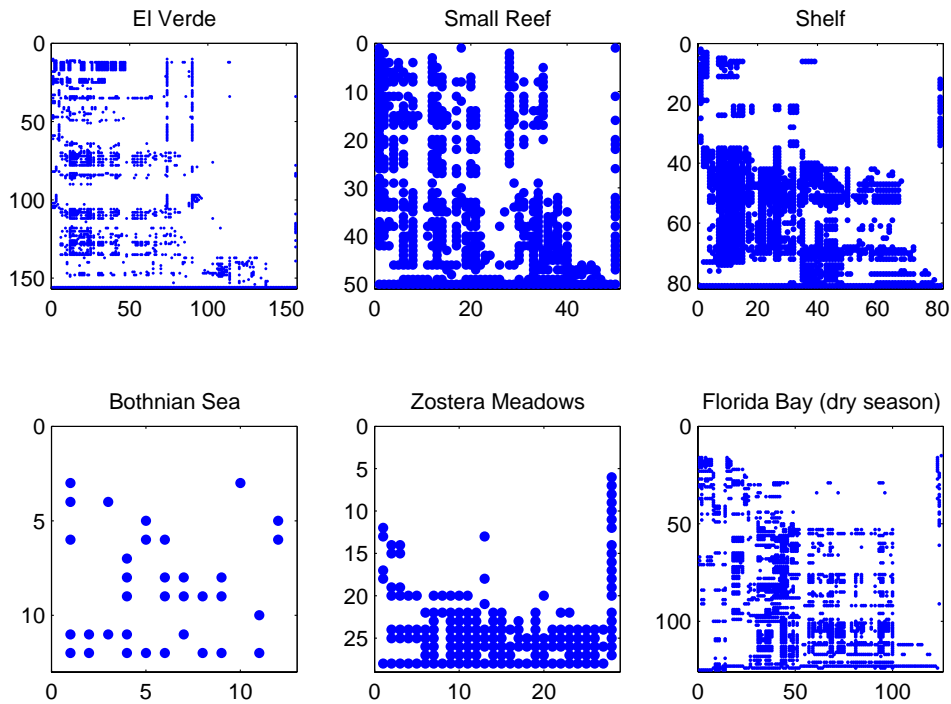
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Figure 6: Graphical representation (Matlab Spy-plots) of the typical adjacent matrices from 6 empirical data sets. The ones (connections) in the *A*-matrices are marked with blue dots.

Discussion

Assembly models like the modified niche model and the cyber ecosystem model produce webs that have both the bias towards hierarchically directed connections and a greater amount of structural cyclicity than was previously acknowledged. They are also more consistent with food webs that include detritus and detritus feeders. The detritus feedback loop consists of relatively few connections, but because it is structurally different than the conventional predations, it works as an important pathway for energy to flow from top predators and back to a lower level in the food hierarchy. In this way, the cyclicity in the system can be increased by just a few key connections.

Functionally, the existence of the detritus feedback cycle does also make the roll of top predators less clear, and the discussion around top-down vs. bottom-up control becomes rather ambiguous in the cyclic picture with continuous dissipative paths reaching also beyond the level of *N* trophic steps.

A possible criticism toward the detritus feedback loop is that the interactions along it are likely to happen at a different time scale than the conventional predation. At least some of the processes of breaking down detritus into the energetic forms that can reenter the system are expected to be slower than the conventional predations, although the existence of scavengers suggests that there also are ways for the detritus feeding to happen at the same time scale as conventional predations. A structural description could

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never reflect such differences, in the same way as a structural analysis does not reflect the differences in flow rates in a weighted ecosystem- description. In a dynamic description this problem could be overcome by describing interactions with time delayed differential equations.

While structural analysis is valuable because of data availability, it is our belief that a quantitative flow-based analysis is required in order to draw further conclusions about food web properties. In flow based analysis connections are weighted, and a greater variety of properties could be studied, such as the importance of weak vs. strong interactions (McCann et al. 1998). In a dynamical approach, the state of the nodes will represent populations whose sizes change over time. The possibility of species dying out, and the possibility of following real flows through the system open for a greater variety of measures, among which different stability measures (McCann, 2000) like for instance community persistence (Kondoh 2003) have gained much focus. Also other network properties, such as compartmentalization, require knowledge about interaction strength in order to be investigated (Pimm & Lawton 1980). A practical problem with such models is that flow quantities are expensive and difficult to acquire.

A flow analysis considers not only the presence of cycles, but also the weighted flow of energy or nutrients (normalized as a transfer efficiency) between compartments (Patten 1985). A high degree of cyclicity generally means that the number of pathways between two nodes of a given length m increases with m. The rate of increase is reflected in the eigenvalue of the adjacency matrix, and generally cycling increases the importance of indirect effects. Although energy is lost at each transfer due to dissipation, the diverging number of pathways may still ensure that indirect effects play an important role (Fath & Patten 1999). This is one of the reasons why cyclic structures should not be neglected.

By assuming that the system is in static steady state equilibrium with the environment, one can adapt to a flow picture without having to go to a framework of differential equations. Such an assumption could only be relevant on a non-evolutionary scale, and clearly limits the number possible scenarios that can be studied. However, the advantages of such a static treatment is that it allows for a rather simple analysis of how the network behaves with respect to certain thermodynamical goal functions (Fath et al. 2001; Fath et al. 2004). Also measures like network amplification, network homogenization, synergism and the ratio of indirect to direct effects have been studied in steady state ecosystems (Fath & Patten 1999), and also this work emphasizes the importance of including cyclic structures.

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