Diversification in Simulated Food Webs:
The Role of Closed Motifs

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Abstract

We allow a simulated food web to self-construct by repeated introduction of predators. Networks start with a source of biomass, and predators choose their prey according to a niche model. Species thrive or go extinct according to a standard predator-prey biomass model. We examine the correlation between structural motifs and the evolution of network architecture. We find two motifs that correlate strongly with network expansion, and we speculate casually but optimistically on implications and further research possibilities.

1 Introduction

Population dynamics on predation networks and the structural properties of such networks have separately received thorough scholarly attention since the first modeling attempts by Lotka and Volterra in the 20's. Most papers on network structure focus on the stability and invasibility of a priori networks, taken from real-world data or pre-fabricated using a niche model or similar device. While these methods can study networks at a fixed point in time, they ignore the process by which networks attain, fail to attain, maintain, and fail to maintain stable states. Such information would be invaluable in attempts to rebuilt destroyed ecosystems and avoid catastrophic crashes, and it might also offer historical explanations for the structure of extant food networks.

In order to explore this territory, we decided to create a food-web simulation with two overarching questions in mind. The first: how does network structure in food webs constrain biomass dynamics? In particular, what substructures promote dynamic stability? The second: how do biomass dynamics on food webs guide their structural growth? In particular, which patterns of growth are promoted and which are prevented by the requirement of some dynamic stability during growth?

In this paper, we draw on the existing literature on predator-prey population dynamics and niche-model construction of food webs in order to run a longitudinal computational study on the structural evolution of food webs. Webs begin with a single steady source of biomass. New species are periodically introduced to the web and choose their prey by a niche model. Between introductions, species interact by a type-3 predator-prey dynamic model, and species attaining negligible biomass go extinct and are eliminated from the web.

Casual observation of these simulations suggested that certain motifs correlate strongly with both network stability and network growth. In particular, two closed-loop motifs tended to precede growth: the three-species omnivory motif and the four-species diamond motif, described in the Methods section. We examined the correlation of the formation of these motifs with ensuing network growth, and we were pleasantly surprised.

2 Methods

In repeated simulations, an accumulating food web was periodically invaded with randomly generated species and allowed time to stabilize following each invasion. Each of 60 repetitions of the simulation began with a single source S of biomass. Every 10,000 time steps, a new species i was introduced to the food web with biomass $B_i = 1$. The simulations were run for 1,000 species introductions.

2.1 Food-web construction

Food webs were initialized with a single source species (producer) undergoing logistic growth. When an invading species i was introduced into the web, it was considered a consumer, and established predator-prey relationships to existing species in the web by a niche method (Williams and Martinez 2000). A single niche parameter representing the natural log of the species body mass was used as a reasonable first approximation of the many variables that determine predation. Upon the introduction of species i, its log-body size x_i was generated from a $unif(0, 6)$ distribution. The feeding niche of species i determined the range of body masses potentially edible to it; it was determined by generating a random niche centre, $c_i \sim unif(0, 6)$ and niche breadth with radius $r_i \sim unif(0, 3)$. This method of niche generation allowed for both very narrow and broad feeding niches. It also allowed the possibility for a species to consume species with larger body size (e.g. to represent parasitism), therefore removing some of the structural constraints associated with other niche models and rendering edible very large species that would otherwise be both metabolically superior and inaccessible to predators. Upon the introduction of species i, any other species j within i's niche would receive an incoming predation link L_{ij} with probability $p_i = 2/(r_i + 2)$. Similarly, predation links L_{ji} on species i were formed with probability p_j for those species j for which i lay within their niche. The decrease in p_i with increasing r_i was imposed in order to defray the obvious advantage of a large niche (i.e. reduce the chance that a new species would eat everything in the food web). Note that this food web construction method also differs from other implementations of the niche model in that there is no constraint placed on the average conductance of the food web (c.f. Stouffer and Bascompte 2010; Pascual and Dunne 2006), which instead emerges naturally over the course of simulation.

2.2 Biomass Dynamics

The biomass dynamics following species introduction are modeled by a multispecies consumer-resource model (Yodzis and Innes 1992; Williams and Brose 2007), also termed an Allometric-Trophic-Network (ATN) model (Berlow et al. 2009):

$$\frac{\mathrm{d}B_s}{\mathrm{d}t} = r_s B_s (1 - B_s/K_s) - \sum_{j=pred} m_j y B_j F_{js}/e \tag{1}$$

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = -m_i B_i - \sum_{j=pred} m_j y B_j F_{ji}/e + \sum_{j=prey} m_i y B_i F_{ij} \tag{2}$$

where equation 1 represents the dynamics of the source (primary producer) and equation 2 represents the dynamics of each consumer introduced. B_s is the biomass of the source species, r_s and K_s are the intrinsic rate of growth and carrying capacity of s, B_i is the biomass of species i, a is the scaling parameter, y is the maximum consumption rate, F_{ij} is the functional response of species i preying on species j, e is the assimilation efficiency (ecological efficiency) of predation, and m_i is the metabolic rate of species i, allometrically related to mass (e.g. Brown et al. 2004) by:

$$m_i = a\left(\frac{10^{x_i}}{10^{x_s}}\right)^{-0.25} \tag{3}$$

The functional response F_{ij} was modeled according to a type III (Real 1977) feeding relationship:

$$F_{ij} = \frac{\omega_{ij} B_j^2}{B_0^2 + \sum_{k=prey} \omega_{ik} B_k^2} \tag{4}$$

where B_0 is the half-saturation level and ω_{ij} is the preference predator i has for prey j, determined by

$$\omega_{ij} = 1/N_i \tag{5}$$

where N_i is the number of prey linked to predator i. Values of constants are given in Table 1.

Numerical integration was performed using a simple one-step Euler method with $dt = 1$. When a species' biomass dropped below .0001, it was considered extinct and eliminated from the food web.

2.3 Food-web Metrics

Before and after each species introduction and each extinction, web statistics were collected for analysis, including the number of species in the web, the number of predation links in the web, the number of triangular omnivory motifs (Figure 1), and the number of diamond motifs (Figure 2). To determine whether increases in the number of consumers in a web were associated with the addition of omnivory or diamond motifs, we compared the net increase in the number of consumer species over 10 consumer introductions (i.e. 1×10^5 time steps) in cases where the first introduction resulted in the addition of an omnivory or diamond motif, to cases where the first introduction did not add a motif. In the case of omnivory motifs, we analyzed only webs initially containing one consumer and the resource species. We used linear mixed-effects models (LMMs) to compare mean change in consumer species number between these two groups. We treated "simulation" as a random effect to account for the fact that multiple observations were taken from each of the 60 simulations. In the case of diamond motifs, we restricted the analysis to webs that initially contained two consumers and the resource species. To determine whether the addition of motifs early in food web development affected the change in the number of consumers over the long-term, we repeated the analysis, comparing the mean change in number of consumer species over 100 species introductions (i.e. 1×10^6 time steps) in webs that gained an omnivory or diamond motif in the first 10 of these introductions, to webs did not. To determine whether consumer additions tend to occur one after another (i.e. to confirm the apparent "boom-bust" pattern visible in the simulation data), we compared the change in number of consumers over 5 consecutive consumer introductions following (1) the gain of a consumer, (2) the loss of a consumer, and (3) no change in the number of consumers (i.e. one consumer introduced and one consumer lost). Again, we compared mean change in consumer number among these groups using a LMM with simulation as a random effect (Everitt 2005).

3 Results

Over the course of 1,000 species introductions, each web fluctuated widely in size and connectivity. Most experienced at least one extinction of all consumers, and most at some point exceeded ten surviving species, some reaching as many as twenty species. Casual observation of three web histories (Figure 3) suggested that fluctuations in N were characterized by fast climbs and even faster events of mass extinction.

Food webs showed significant bias towards growing more after a growth and collapsing more after a collapse (Figure 4). Mean change in number of consumers after an gaining a consumer was 0.92, whereas the change in consumer number was close to zero (0.04) or negative (-1.4), in the five steps following an introduction leading to no change, or loss of a consumer, respectively (difference among groups: $F = 4561$, $p < 1 \times 10^{-16}$). This trend was even more striking considering that a random walk with strict minimum of zero consumers and a weakly enforced maximal capacity around twenty consumers would have shown the opposite tendency.

As we had hypothesized, species introduction events that completed omnivory or diamond motifs preceded a markedly larger expected gain in number of species than introduction events that did not complete these motifs over the next 10 time steps (Figure 5, mean change in number of consumer spp.: no omnivory added = 1.8, omnivory added = 2.7, $t = 5.8$, $p = 2 \times 10^{-7}$; no diamond added = 1.3, diamond added = 2.5, $t = 13.1$, $p < 1 \times 10^{-16}$). The difference over 100 time steps looked less meaningful (Figure 6, mean change in number of consumer spp.: no omnivory added = 5.9, omnivory added = 5.6, $t = -1.6$, $p = 0.11$; no diamond added = 4.7, diamond added = 5.0, $t = 3.8$, $p = 1 \times 10^{-4}$). Perhaps there is too much fluctuation over this time scale to preserve much correlation.

4 Discussion

Most of the focus in the literature on the structure of food webs has been to compare motif prevalence in empirical food webs to that in algorithmically generated systems (*e.g.* Milo et al. 2002; Stouffer et al. 2007). In most cases, the conclusions of such studies (i.e. that certain motifs are over-represented in empirical food webs compared to random ones) appear to be related to the type of model tested against. Prill et al. (2005) emphasize the need to understand whether there is a dynamic association between stability and the presence of network motifs.

Our results indicate that episodes of diversification and growth in evolving food networks preferentially follow the creation of the omnivory and diamond motif. We hypothesize that closed motifs are fairly robust to invasion; thus, by persisting and simultaneously populating the food web with potential sources of biomass, these motifs are ideal seeds for large, robust networks. Furthermore, omnivory and diamond motifs are formed with high probability relative to other closed motifs during the process of sequential introduction of niche predators. Thus, we hypothesize that most events of explosive growth in food webs occurs following the formation of one of these two motifs.

The tendency of closed motifs to form a core for network growth is explored in Jain and Krishna (2002). In their simulations, they introduce mutually catalyzing chemical species and track the creation of autocatalytic sets, or sets in which each species receives an incoming edge from another in the set. In these simulation, every persistent network is founded upon an autocatalytic core, and major changes in the network correspond to core shifts or core destruction.

Unlike their chemical networks, our food networks are given a constant input of biomass, so autocatalytic sets are not necessary for persistence. However, it may be accurate to compare the role of our closed motifs to that of autocatalytic sets. Though the species in a closed motif do not neatly fill each others' needs like the species in an autocatalytic set, they may mutually provide each other with a robustness mechanism.

The analyses in this paper are not sufficient to prove beyond reasonable doubt that our motifs cause network growth. It could be the the two happenings are mutually caused; ruling out this possibility would require more controls. With sufficient control, it should be possible to address the question of how much these motifs really do promote growth with more certainty. Experiments should also be performed addressing the results of motif completion in larger networks.

Second, these experiments all made use of a type-3 predator response with a particular set of parameters. A more thorough exploration should be made of the parameter- and model-space in order to separate these results from our reasonable but arbitrary modeling choices.

Third, these experiments provide only empirical evidence that omnivore and diamond motifs are actually robust. We would like to see a mathematical description of their robustness properties as compared to the properties of similar but open motifs. Such a description would hopefully be qualitative enough to generalize across models.

Fourth, our experiments provided sufficient data to examine the role of motifs in extinction events. In order to complete the analogy to autocatalytic sets, it would be useful to show that the destruction of closed motifs tends to lead to a collapse of the network. This would indicate that closed motifs not only act as a seed for network growth but also as a legitimate core of a network without which it is unlikely for diversity to persist. Some work has been done on keystone species essential to maintaining food web diversity; this idea should be extended to a corresponding notion of keystone motifs, the members of which will likely function as keystone species.

Finally, it would be valuable to look at how our hypotheses are upheld or contradicted by the formation of real food networks. Food web history data is not common, but some is available and could be compared to our results.

Our experiments have pointed to a strong role of small, closed motifs in supporting the development of large food networks. If this trail is pursued further, it should begin to fill in the gap between population-dynamic models and robustness studies of food webs, a gap in which significant insight may be gained into the process by which ecosystems gain, lose, and regain species diversity.

References

Berlow, E. L., J. A. Dunne, N. D. Martinez, P. B. Stark, R. J. Williams, and U. Brose (2009). Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences of the United States of America 106*(1), 187–191.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West (2004). Toward a metabolic theory of ecology. *Ecology 85*, 1771–1789.

Everitt, B. (2005). *An R and S-plus Companion to Multivariate Analysis.* Springer-Verlag, London, UK.

Jain, S. and S. Krishna (2002). Large extinctions in an evolutionary model: The role of innovation and keystone species. *Proceedings of the National Academy of Sciences of the United States of America 99*(4), 2055–2060.

Milo, R., S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, and U. Alon (2002). Network motifs: Simple building blocks of complex networks. *Science 298*(5594), 824–827.

Pascual, M. and J. Dunne (2006). *Ecological Networks: Linking Structure to Dynamics in Food Webs.* Oxford University Press, Oxford, UK.

Prill, R. J., P. A. Iglesias, and A. Levchenko (2005). Dynamic properties of network motifs contribute to biological network organization. *Plos Biology 3*(11), e343.

Real, L. (1977). The kinetics of functional response. *American Naturalist 111*, 289–300.

Stouffer, D. B. and J. Bascompte (2010). Understanding food-web persistence from local to global scales. *Ecology Letters 13*(2), 154–161.

Stouffer, D. B., J. Camacho, W. Jiang, and L. A. N. Amaral (2007). Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B-biological Sciences 274*(1621), 1931–1940.

Williams, R. J. and U. Brose (2007). *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems*, Chapter 2, pp. 3752. Springer.

Williams, R. J. and N. D. Martinez (2000). Simple rules yield complex food webs. *Nature 404*(6774), 180–183.

Yodzis, P. and S. Innes (1992). Body size and consumer-resource dynamics. *American Naturalist 139*(6), 1151–1175.

Table 1: Values for the parameters of the predator-prey dynamcis model

Parameter	Value
r_s	2
K_s	10
x_s	0
a	0.3
B_0	10
y	8
e	.6

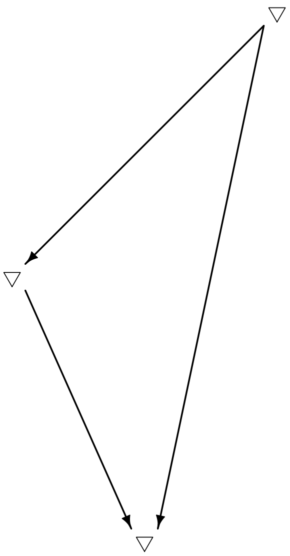

Figure 1: Network structure of triangular omnivory motif. Triangles denote species, arrows denote consumer links, direction of arrow indicates direction of predation.

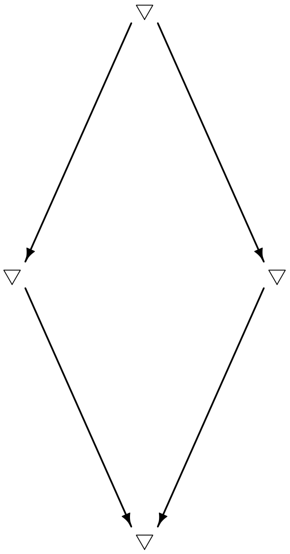

Figure 2: Network structure of diamond motif. Symbols as per Figure 1.

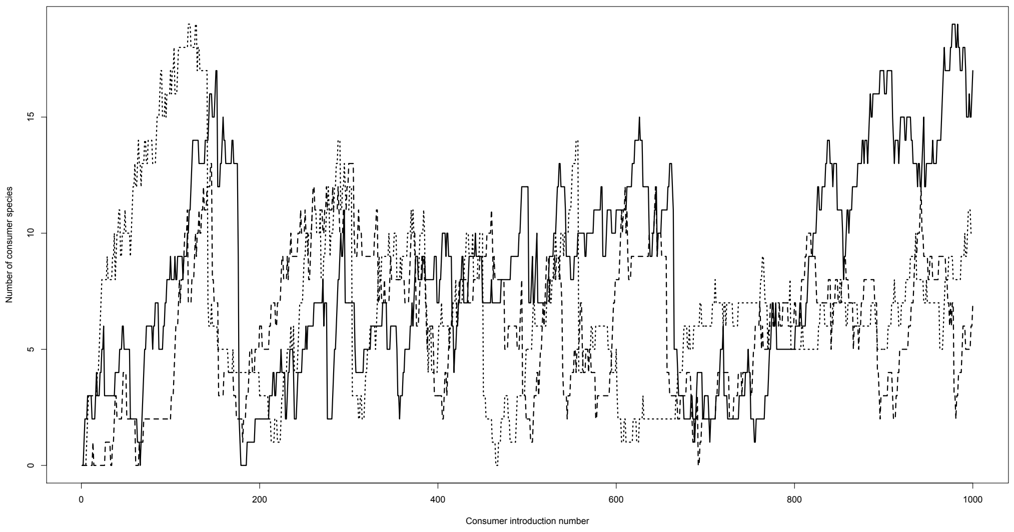

Figure 3: Time series of the number of species in the food web for three experiments.

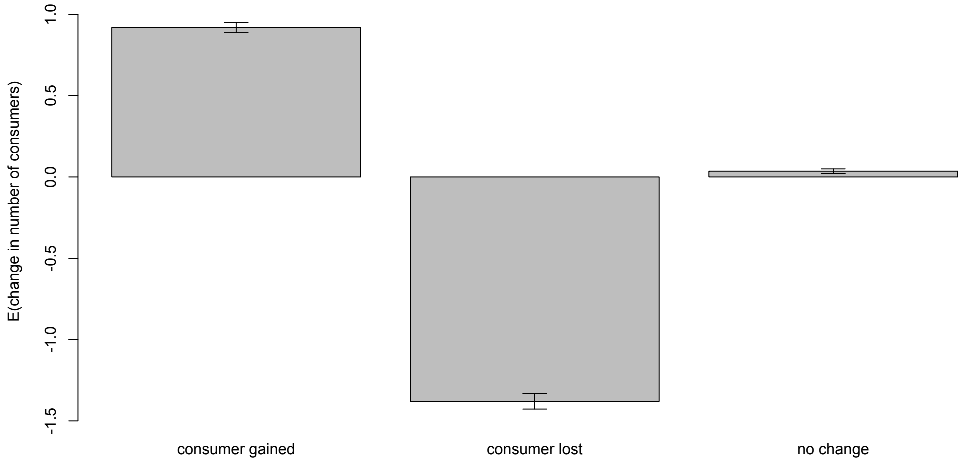

Figure 4: Expected change in the number of consumer species 5 time steps after introductions that lead to (1) the gain of a species, (2) loss of a species, (3) no change in species number.

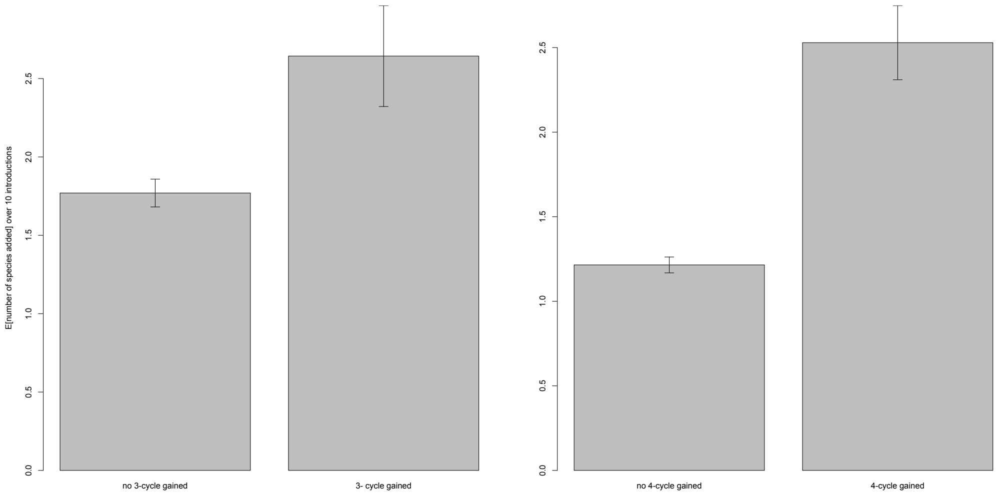

Figure 5: Expected increase in the number of consumers in the web after 10 introductions, depending on whether a 3-cycle or 4-cycle motif was completed or not.

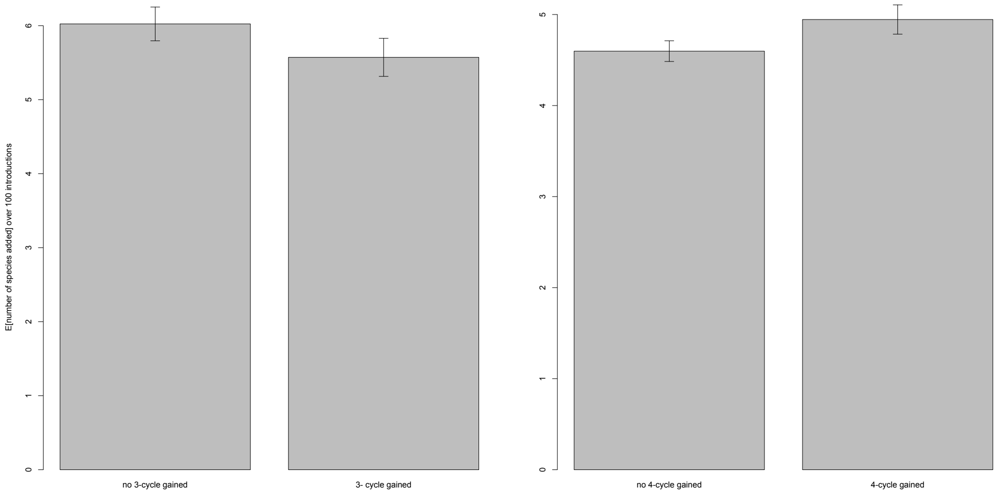

Figure 6: Expected increase in the number of consumers in the web after 10 introductions, depending on whether a 3-cycle or 4-cycle motif was completed or not.