**Selection against instability: stable subgraphs are most frequent in empirical food webs**

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**Abstract**

Food web structure can be characterized by the particular frequencies of subgraphs. Of the thirteen possible configurations of three species, some are consistently over-represented in empirical food webs. This is a robust pattern that spans multiple environments. Any potential explanation of this must therefore apply without respect to the particulars of marine, freshwater, or terrestrial environments. I argue that the elimination of unstable subgraphs during the development of the food web can explain the observed pattern. A clear prediction of this hypothesis is that there should be differences in the stability of different subgraphs, and that stability should be positively correlated to their frequency in food webs. Using 50 food webs collected from a variety of databases I determined the frequency of each of the thirteen possible subgraphs with respect to randomized webs. Then by numerical simulation I determined the quasi sign stability (QSS) of each subgraph. My results clearly show a positive correlation between QSS and over-representation of the different subgraphs. (162 words)

**Introduction**

The ecological networks that are observed in nature are those that are able to persist in a dynamically changing environment. Much of the past 40 years of food web ecology has focused on finding those “devious strategies which make for stability in enduring natural systems,” to quote Robert May (1974). There is a clear link between those structures observed in ecological networks (e.g., modularity in food webs and nestedness in mutualistic webs) and the population dynamics underlying the system (Thébault and Fontaine 2010). While large scale network architecture (modularity, nestedness, connectance, etc.) has been the focus in the past, there are many ways to characterize the structure of an ecological network. Here I assess the substructural composition of food webs in light of the stability of its components (three-node subgraphs).

Larger networks are made up of many smaller subnetworks (hereafter subgraphs) that are assembled together. Any large network with *N* nodes can be decomposed into smaller networks of size 1 to *N*-1. There are thirteen possible (connected, directed) configurations of three nodes, five of which require only single direction links and 8 which combine single and bi-directional links. Milo *et al.* (2002) showed that the observed frequency of these three node configurations varies in different types of networks (e.g., food webs, neural networks, electronic networks, etc.). For example, in food webs the tritrophic chain tends to be over-represented compared to random. Those subgraphs which tend to be over-represented are commonly termed *motifs*.

In a study of 16 food webs Stouffer et al.(2007) showed that there were two distinct patterns of the frequency of subgraphs in food webs. Most webs (10) were characterized by over-representation of intra-guild predation and under-representation of apparent and direct competition. The other 6 webs were characterized by the opposite pattern. Overall most webs tended to have similar relative frequencies of the different subgraphs.

The structure of a subgraph is related to its dynamic properties in the same way as the dynamics of a network is related to its structure. Because structure and dynamics are so closely related we may expect that the cause of the apparent pattern in subgraph frequencies in networks is related to the dynamic properties of the different subgraphs. The two prevailing hypothesis for the pattern of subgraph frequencies are (1) that there are constraints in the assembly of a network, and (2) that there is some advantage to motifs that make them more likely to become over-represented (Prill et al. 2005, Camacho et al. 2007). I suggest that a combination of the two hypotheses in the form of selection against unstable structures offers the simplest explanation. Such a process would systematically eliminate those subgraphs that are unstable, while increasing the relative abundance of those that are more likely to be stable.

Many definitions of stability have been used in the ecological literature (Pimm 1984, Donohue et al. 2013). In this paper I focus on the unity of two forms of mathematical stability; local (or eigenvalue) stability and qualitative stability. A system is locally stable if all of the eigenvalues of the Jacobian matrix have negative real parts. Functionally this means that following a small perturbation from equilibrium, the system will return to the original equilibrium state. Local stability has been very frequently used in the theoretical ecology literature to understand the relationship between structure and stability (May 1972, Pimm and Lawton 1977, Sterner et al. 1997, Allesina and Tang 2012). Determining local stability, however, requires knowledge of the magnitudes of the elements of the Jacobian matrix (where each element represents the impact that species *i* has on the *jth* species). A qualitatively stable system is one that is stable based only on the signs of the elements of the Jacobian matrix, rather than their magnitudes (May 1973). Most ecological communities do not fulfill the conditions for qualitative stability, for example many food webs contain trophic loops of three or more species.

Allesina and Pascual (2008) linked these two concepts with the development of quasi sign-stability (QSS). QSS is a measure of how robust a system is to changes in the magnitude of the elements of its corresponding Jacobian matrix. Thus the more quasi sign-stable a system is the closer it is to being qualitatively stable. If a number of matrices are created by sampling the values of the Jacobian from a distribution (preserving the sign structure) the proportion that are locally stable is the system’s QSS. Using this measure I can determine the tendency of a given sign structure, determined by the configuration of the subgraph, to be stable.

In this study I ask whether the commonly observed pattern of subgraph frequency results fits with what we would expect based on the hypothesis of selection against unstable configurations. To answer this question I will first demonstrate that there exists variation in both frequency and the QSS of the thirteen different three-node subgraphs. Where other studies comparing subgraph frequency to their dynamic properties have used absolute frequencies (Prill *et al.* 2005), I compute frequency relative to a null model. If there is a systemic selection against unstable subgraphs in nature, then we should expect to find a positive correlation between the frequency of a given subgraph and the probability that that subgraph will be stable.

**Methods**

**Data**

I used 50 food webs collected from a variety of sources. Three food webs were downloaded from the [Dryad Digital Repository](http://datadryad.org/resource/doi:10.5061/dryad.c213h) (Roopnarine and Hertog 2012a, b). Another seven were available from Ecological Archives (Hechinger et al. 2011, Thieltges et al. 2011, Zander et al. 2011, Mouritsen et al. 2011, Preston et al. 2012). These seven webs all included parasitic links, but for the purposes of comparing to food webs without parasites only predator-prey links were considered. Fourteen webs were provided by Jennifer Dunne of the PEaCE Lab (Baird and Ulanowicz 1989, Warren 1989, Polis 1991, Hall and Raffaelli 1991, Martinez 1991, Christensen and Pauly 1992, Havens 1992, Goldwasser and Roughgarden 1993, Opitz 1996, Waide and Reagan 1996, Yodzis 1998, 2000, Martinez et al. 1999, Christian and Luczkovich 1999, Memmott et al. 2000, Link 2002). The remaining 26 food webs were downloaded from the Interaction Web Database (Townsend et al. 1998, Jaarsma et al. 1998, Thompson and Townsend 1999, 2000, 2003, 2005, Thompson and Edwards 2001).

**Subgraph Frequency**

The frequency of each subgraph was found using the *triad.census* function from the *igraph*  package (Csárdi and Nepusz 2006) in R *version 3.0* (R Core Team 2014). Counts of each of the thirteen subgraphs were determined for each of the 50 food webs described above. Each frequency was then compared against a null distribution.

To create the null distribution each of the fifty adjacency matrices (each food web) was permuted, maintaining both the number of predators of a species and the number of prey a species has (maintaining row and column sums). One thousand permuted matrices were generated for each food web, and the frequency of each subgraph type was found. Z-scores were computed using the formula:

where is the frequency of the *ith* subgraphin each empirical food web, is the mean frequency of the *ith* subgraph in the permuted matrices, and σ*l* is the standard deviation . The z-scores were then normalized by dividing by the square root of the sum of the squared z-scores for that food web following previous studies of motifs by Milo et al. (2002) and Stouffer et al. (2007).

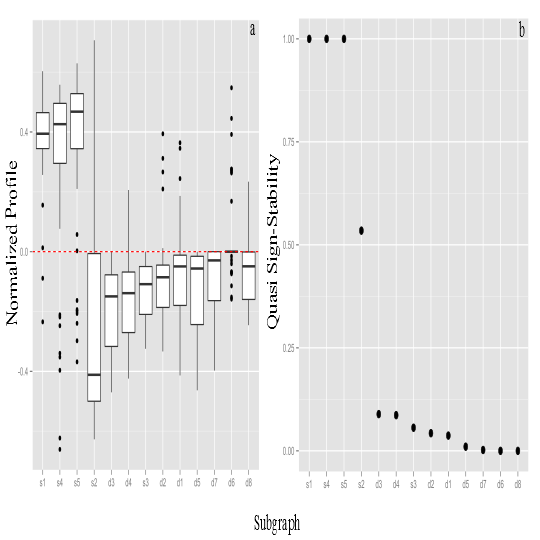
The code for determining subgraph frequency can be found in the Appendix.

**Subgraph Stability**

Using numerical simulations in R *version 3.0* (R Core Team 2014) I determined the probability of a given subgraph will be stable (quasi sign-stability, QSS), following the method of Borrelli and Ginzburg (2014). Each subgraph was translated into its corresponding sign-structured matrix. Positive elements of the matrix were given a random value drawn from a uniform distribution between 0 and 10, while negative elements were given a value drawn from a uniform between -1 and 0. These distributions were chosen to reflect asymmetry in the relative impact of the prey on the predator (positive) and the predator on the prey (negative). Such asymmetry can be derived from a general predator-dependent functional response where the predator is not saturated (“hungry predators”).

Diagonal elements have a large impact on the stability of the matrix (Sterner *et al.* 1997), so each diagonal element was assigned a random value drawn from a uniform distribution between -1 and 0. Thus the average intraspecific effect on population growth rate was approximately the same as the effect of predation. This process was repeated 10,000 times for each subgraph. Quasi sign stability was then calculated as the proportion of randomly sampled matrices whose eigenvalue with the largest real part (Max(Re(λ))) was negative (Allesina and Pascual 2008). See the Appendix for more details on the code used for simulations.

**Results**



**Figure 1: (a) The normalized profile of the 13 possible 3-node subgraphs in a set of 50 food webs arranged in order of decreasing quasi sign-stability. (b) Quasi sign-stability for each subgraph, determined as the proportion of randomly parameterized sign matrices that were locally stable.**

The different subgraphs are variable in how frequently they are observed relative to permuted webs (Figure 1a). Tritrophic chains, apparent competition, and direct competition all tend to be over-represented in food webs. Intra-guild predation is typically under-represented but is over-represented in some webs. The three-species trophic loop (s3) is under-represented in all webs, as are most subgraphs that include bidirectional links (A eats B, B eats A).

There is also variation in the quasi sign-stability of each subgraph (Figure 1b). The three subgraphs that tend to be over-represented are all very likely to be stable. Intra-guild predation is also moderately likely to be stable (approximately 0.5). The remaining subgraphs are all unlikely to be stable, with quasi sign-stability less than 0.2. Subgraphs with a higher quasi sign-stability occur more frequently than expected by random chance, while those with lower quasi sign-stability tend to occur less frequently than expected by chance.

**Discussion**

This study represents the third case in which quasi sign-stability has shown to be a useful measure to help explain observed food web patterns (Allesina and Pascual 2008, Borrelli and Ginzburg 2014). Quasi sign-stability is a simple yet powerful measure when considering stability in a stochastic environment. As a result of environmental and/or demographic stochasticity any given parameterization of the community matrix (to determine local stability) is not likely to tell you much. Yet quasi sign-stability can reveal quite a lot about the system, given just the sign-structure of the community.

The simplicity of the argument underlies its usefulness to ecologists. Given knowledge of the quasi sign-stability of community configurations we can build an expectation of what we should observe in nature. In the study introducing the concept of quasi sign-stability Allesina and Pascual (2008) found that when predator-prey links dominate the community, we should expect the community to be more stable. My results show that we should expect to observe tritrophic chains, direct competition, and apparent competition more frequently; while Borrelli and Ginzburg (2014) demonstrated that we should expect short food chains to be more frequent than longer ones. Comparing that expectation to what is actually observed in nature, my results show that what we expect is what is observed, and Borrelli and Ginzburg (2014) showed the same for food chains.

Alternatively when the observed pattern does not match our expectation based on quasi sign-stability, it may be an indication of some underlying biologically interesting phenomenon. For example, while the intra-guild predation subgraph (A eats B, A eats C, B eats C) is moderately quasi sign-stable, such that it should be somewhat over-represented in the data. Yet I found that intra-guild predation is mostly under-represented, albeit with a large variance. Likewise, in a few food webs apparent competition is under-represented yet is very likely to be stable.

One potential explanation for the lack of intra-guild predation subgraphs is one of feasibility. A system would be feasible if, at equilibrium, all species had positive densities. In the present study I have not considered feasibility constraints, as I chose not to impose any particular equation structure, rather relying on the general case of a predator dependent functional response. It is possible that for species to maintain positive densities in an intra-guild predation framework there are constraints for what the magnitude of the elements of the Jacobian could be, and that region of “parameter space” could arguably be smaller than the region that is considered stable.

Alternatively, constraints could be imposed at higher levels of organization. As these different subgraphs are assembled into larger networks, there could be interactions among them, which alter their probability of being stable. The next step in understanding the relationship between motifs and stability is to learn how the stability properties of the three-node configurations scale up to larger networks. I would expect that, in general, networks with subgraph patterns that show over-representation of subgraphs that are more quasi sign-stable should themselves be more stable.

An ideal test of the hypothesis of selection against unstable configurations would involve food web assembly data. During food web assembly, new species enter the food web and establish feeding links with the species that are present. This establishment alters the structure of the food web, and can be measured as changes in the relative frequency of the different three-node subgraphs. Following the introduction of the new species one of two events could occur; (1) the new species becomes integrated into the network and the food web grows (in terms of the number of species), or (2) the introduction of the new species leads to extinction events and the food web shrinks. The selection against instability hypothesis would thus predict that when the new species increases the relative frequency of more stable subgraphs compared to less stable ones, the web should grow. If the frequency of less stable subgraphs is increased more than the stable ones, then we should expect extinctions to occur.

**References**

Allesina, S. and Pascual, M. 2008. Network structure, predator–prey modules, and stability in large food webs. - Theor. Ecol. 1: 55–64.

Allesina, S. and Tang, S. 2012. Stability criteria for complex ecosystems. - Nature 483: 205–208.

Baird, D. and Ulanowicz, R. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. - Ecol. Monogr. 59: 329–364.

Borrelli, J. J. and Ginzburg, L. R. 2014. Why are there so few trophic levels: selection against instability explains the pattern. - Food Webs in press.

Camacho, J. et al. 2007. Quantitative analysis of the local structure of food webs. - J. Theor. Biol. 246: 260–268.

Christensen, V. and Pauly, D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. - Ecol. Modell. 61: 169–185.

Christian, R. R. and Luczkovich, J. J. 1999. Organizing and understanding a winter’s seagrass foodweb network through effective trophic levels. - Ecol. Modell. 117: 99–124.

Csárdi, G. and Nepusz, T. 2006. The igraph software package for complex network research. - InterJournal Complex Sy: 1695.http://igraph.org.

Donohue, I. et al. 2013. On the dimensionality of ecological stability. - Ecol. Lett. 16: 421–429.

Goldwasser, L. and Roughgarden, J. 1993. Construction and analysis of a large Carribean food web. - Ecology 74: 1216–1233.

Hall, S. and Raffaelli, D. 1991. Food-web patterns: lessons from a species-rich web. - J. Anim. Ecol. 60: 823–841.

Havens, K. 1992. Scale and structure in natural food webs. - Science 257: 1107–1109.

Hechinger, R. F. et al. 2011. Food webs including parasites, biomass, body sizes, and life stages for three California/Baja California estuaries. - Ecology 92: 791.

Jaarsma, N. G. et al. 1998. Characterising food‐webs in two New Zealand streams. - New Zeal. J. Mar. Freshw. Res. 32: 271–286.

Link, J. 2002. Does food web theory work for marine ecosystems? - Mar. Ecol. Prog. Ser. 230: 1–9.

Martinez, N. 1991. Artifacts or Attributes? Effects of Resolution on the Little Rock Lake Food Web. - Ecol. Monogr. 61: 367–392.

Martinez, N. et al. 1999. Effects of sampling effort on characterization of food-web structure. - Ecology 80: 1044–1055.

May, R. M. 1972. Will a large complex system be stable? - Nature 238: 413–414.

May, R. M. 1973. Qualitative stability in model ecosystems. - Ecology 54: 638–641.

May, R. M. 1974. Stability and Complexity in Model Ecosystems. - Princeton University Press.

Memmott, J. et al. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. - J. Anim. Ecol. 69: 1–15.

Milo, R. et al. 2002. Network motifs: simple building blocks of complex networks. - Science 298: 824–827.

Mouritsen, K. N. et al. 2011. Food web including metazoan parasites for an intertidal ecosystem in New Zealand. - Ecology 92: 2006.

Opitz, S. 1996. Trophic interactions in Caribbean coral reefs. - ICALRM Tech.

Pimm, S. L. 1984. The complexity and stability of ecosystems. - Nature 307: 321–326.

Pimm, S. L. and Lawton, J. H. 1977. Number of trophic levels in ecological communities. - Nature 268: 329–331.

Polis, G. 1991. Complex trophic interactions in deserts : an empirical critique of food-web theory. - Am. Nat. 138: 123–155.

Preston, D. L. et al. 2012. Food web including infectious agents for a California freshwater pond. - Ecology 93: 1760.

Prill, R. J. et al. 2005. Dynamic properties of network motifs contribute to biological network organization. - PLoS Biol. 3: 1881–1892.

R Core Team, R. 2014. R: A Language and Environment for Statistical Computing. - R Found. Stat. Comput. http://www.R-project.org.

Roopnarine, P. D. and Hertog, R. 2012a. Detailed food web networks of three Greater Antillean coral reef systems: the Cayman Islands, Cuba, and Jamaica. - Dataset Pap. Ecol. 2013: 857470.

Roopnarine, P. D. and Hertog, R. 2012b. Data from: Detailed food web networks of three Greater Antillean coral reef systems: the Cayman Islands, Cuba, and Jamaica.  Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.c213h>

Sterner, R. W. et al. 1997. The enigma of food chain length: absence of theoretical evidence for dynamic constraints. - Ecology 78: 2258–2262.

Stouffer, D. B. et al. 2007. Evidence for the existence of a robust pattern of prey selection in food webs. - Proc. R. Soc. B 274: 1931–1940.

Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. - Science 329: 853–856.

Thieltges, D. et al. 2011. Food web including metazoan parasites for a tidal basin in Germany and Denmark. - Ecology 92: 2005.

Thompson, R. and Townsend, C. 1999. The effect of seasonal variation on the community structure and food-web attributes of two streams: implications for food-web science. - Oikos 87: 75–88.

Thompson, R. M. and Townsend, C. R. 2000. Is resolution the solution?: the effect of taxonomic resolution on the calculated properties of three stream food webs. - Freshw. Biol. 44: 413–422.

Thompson, R. and Edwards, E. 2001. Allocation of effort in stream food-web studies: the best compromise? - Mar. Freshw. Res. 52: 339–345.

Thompson, R. and Townsend, C. 2003. Impacts on stream food webs of native and exotic forest: an intercontinental comparison. - Ecology 84: 145–161.

Thompson, R. and Townsend, C. 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. - Oikos 108: 137–148.

Townsend, C. R. et al. 1998. Disturbance, resource supply, and food-web architecture in streams. - Ecol. Lett. 1: 200–209.

Waide, R. and Reagan, W. 1996. The food web of a tropical rainforest. - University of Chicago Press.

Warren, P. 1989. Spatial and temporal variation in the structure of a freshwater food web. - Oikos 55: 299–311.

Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. - J. Anim. Ecol. 67: 635–658.

Yodzis, P. 2000. Diffuse Effects in Food Webs. - Ecology 81: 261–266.

Zander, C. D. et al. 2011. Food web including metazoan parasites for a brackish shallow water ecosystem in Germany and Denmark. - Ecology 92: 2007.