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

Jonathan J. Borrelli

Department of Ecology and Evolution

Stony Brook University

Stony Brook, NY 11794

[**jonathan.borrelli@stonybrook.edu**](mailto:jonathan.borrelli@stonybrook.edu)

**Abstract**

Food web structure can be characterized by the particular frequencies of subgraphs found within them. Although there are thirteen possible configurations of three species subgraphs, some are consistently over-represented in empirical food webs. This is a robust pattern that is found across marine, freshwater, or terrestrial environments. The preferential elimination of unstable subgraphs during the assembly of the food web can explain the observed pattern. It follows from this hypothesis 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 in empirical food webs.

**Introduction**

. Much of the past 40 years of food web ecology has focused on finding the “devious strategies which make for stability in enduring natural systems,” to quote Robert May (1973a). 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 of the species that make them up (Thébault and Fontaine 2010). While large scale emergent properites of networks (modularity, nestedness, connectance, etc.) has been the focus of much research in the past, there are many other ways to characterize the structure of an ecological network. Here I assess the substructural composition of food webs in light of the stability of their basic building blocks (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. Subgraphs that 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 of 16) 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 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). While these two hypotheses are not mutually exclusive, Camacho et al. (2007) and Prill et al. (2005) offer different perspectives on which is more important for generating the observed pattern. Camacho et al. (2007) find that because food web models are able to reproduce observed subgraph patterns constraints on food web generation are most important. Alternatively because structure is related to function, Prill et al. (2005) hypothesize that it is the properties of the subgraph that lead to its abundance in a network. I suggest that a combination of the two hypotheses in the form of selection against unstable structures offers the simplest explanation for the occurrence of particular motifs. Such a process would eliminate those subgraphs that are unstable with greater frequency than expected by chance, 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). Here 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 (evaluated at equilibrium) 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 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 1973b). In order for a food web to be qualitatively stable the Jacobian matrix must fulfill certain conditions, such as having at least one negative term along the diagonal. Most ecological communities do not fulfill the conditions for qualitative stability (May 1973b), 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 asked whether the commonly observed pattern of subgraph frequency results fits with what is expected based on the hypothesis of selection against unstable configurations. To answer this question I examined the 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 there should be 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, so to compare these webs to food webs without parasites only predator-prey links were considered. Fourteen webs were also 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. The frequency of each subgraph was then compared against a null distribution.

To create the null distribution each of the fifty adjacency matrices (each food web) was permuted using the recently described Curveball algorithm (Strona et al. 2014). This algorithm maintains both the number of predators of a species has and the number of prey a species has (maintaining row and column sums) and has been shown to be unbiased in the creation of null distributions (Strona et al. 2014). As a second null model additional constraints were added to the Curveball algorithm to maintain not only the row and column sums, but also the number of single, double, and self (cannibalistic) links in each web. This is similar to the null model used by Stouffer et al. (2007) but where they preserve the number of single, double, and cannibal links per species the modified Curveball algorithm I use preserves the number of each type of link per web.

The frequency of each subgraph was determined in each of thirty thousand permuted matrices that were generated for each food web using both null models. 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 Appendix 1.

**Subgraph Stability**

Using numerical simulations in R *version 3.0* (R Core Team 2014) I determined the probability that a given subgraph would be stable (quasi sign-stability, QSS). The adjacency matrix of each subgraph was translated into its corresponding sign-structured matrix. Only predator-prey interactions were considered, so if *aij = 1* then *aij* will be a positive while *aji* is negative. When interactions were bidirectional, both *aij* and *aji* were positive. Positive elements of the matrix were given a random value drawn independently from a uniform distribution between 0 and 10, while negative elements were given a value drawn independently 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). Asymmetry can be derived from a general predator-dependent functional response (a functional response that is dependent on both prey and predator densities) where the predator is not saturated (“hungry predators”). Note that the particular structure of the equations governing population dynamics was not defined. Instead, assumptions about the values of the Jacobian matrix were made based on what may be predicted from the general form of the function.

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. By including density dependence for each species I allow the greatest chance of stability.

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 Appendix 1 for details on the code used for simulations.

**Results**

Subgraphs differed in how frequently they were observed relative to permuted webs (Figure 1). Tritrophic chains (s1), apparent competition (s4), and direct competition (s5) all tended to be over-represented in food webs based on both null models. Intra-guild predation (s2) was typically under-represented, more so when compared to webs generated by the modified Curveball algorithm, but was over-represented in some webs. The three-species trophic loop (s3) was under-represented in all webs, as were most subgraphs that include bidirectional links (A eats B, B eats A). When the numbers of each link type were preserved the d1, d2, and d6 subgraphs were over-represented in the twelve webs that had double links.

There was also variation in the quasi sign-stability of each subgraph (Figure 2). The three subgraphs that tended to be over-represented were all very likely to be stable. Intra-guild predation was also moderately likely to be stable (approximately 0.5). The remaining subgraphs were all unlikely to be stable, with quasi sign-stability less than 0.2. Subgraphs with a higher quasi sign-stability occurred more frequently than expected by chance, while those with lower quasi sign-stability tend to occur less frequently than expected by chance.

**Discussion**

If there is a selection against unstable food web configurations, then those configurations that are most likely to be stable in a varying environment should be those that are most commonly observed in nature. In order for such a process to work, different food web configurations must be variable in their stability. A signature of this selection against instability should then be if variability in the stability of different food web configurations is correlated with their observed frequency.

The signature of selection against unstable configurations is clearly seen by comparing the observed frequencies of three-node subgraphs and their quasi sign-stability. Those subgraphs that are most quasi sign-stable are also those that are observed more frequently than expected by random chance. Subgraphs that are less quasi sign-stable are typically either under-represented (observed less frequently than expected by chance) or observed about as frequently as expected by random chance, although this depends on the null model to some extent. While this does not provide concrete proof that there is a selection against unstable subgraphs in nature, it does offer convincing evidence that such a process could affect the way food webs are structured.

The null model used to generate the subgraph frequencies does have an effect. In part this explains why the pattern of frequencies is different from those determined by Stouffer et al. (2007). Additional differences may also be the result of the larger sample of food webs, 50 compared to 16. The frequency of subgraphs that include double links is especially of interest when comparing the outcome from the two different null models used (Figure 1). In particular, the d1, d2, and d6 subgraphs occur more frequently than expected at random when the number of single, double, and self links are constrained. However, while this is true for those webs that have double links, the occurrence of double links is rare. In both null models the tritrophic chain, apparent competition, and direct competition are consistently over-represented.

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 be informative. Yet quasi sign-stability can reveal a considerable amount 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 an expectation of what should be observed in nature can be built. In their study introducing the concept of quasi sign-stability Allesina and Pascual (2008) found that when predator-prey links dominate the community, the community should be more stable. My results show that tritrophic chains, direct competition, and apparent competition should be expected more frequently; while Borrelli and Ginzburg (2014) demonstrated that short food chains should be more frequent than longer ones. The results of this study show that these expectations match what is actually observed in nature, as was shown for food chains by Borrelli and Ginzburg (2014).

If 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, the expectation is 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. An equilibrium point would be feasible if 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 on the magnitude of the elements of the Jacobian, and that region of “parameter space” could be smaller than the region that is considered stable.

Alternatively, constraints could be imposed at higher levels of organization. As 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 will be to learn how the stability properties of the three-node configurations scale up to larger networks. I 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 predict that when the addition of 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 extinctions would be more likely to occur.

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**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.

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. 1973a. Stability and Complexity in Model Ecosystems. - Princeton University Press.

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

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 (RDC Team, Ed.). - R Found. Stat. Comput. in press.

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. in press.

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.

Strona, G. et al. 2014. A fast and unbiased procedure to randomize ecological binary matrices with fixed row and column totals. - Nat. Commun. 5: 4114.

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.

**Figure Legends:**

**Figure 1: 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. Boxplots represent the median and interquartile range of the z-scores. Whiskers extend to the most extreme point within 1.5 times the interquartile range.**

**Figure 2: Quasi sign-stability for each subgraph, determined as the proportion of randomly parameterized sign matrices that were locally stable. Subgraphs have been ordered along the x-axis from greatest to least quasi sign-stability.**