**Predictions of selection against instability: does subgraph frequency relate to quasi sign-stability in food webs**

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**Abstract**

Food webs structure can be defined by the particular frequencies of three node subgraphs. Of the thirteen possible configurations of three species food webs, some are consistently over and underrepresented in larger (whole community) food webs. This is a robust pattern that spans multiple environments. Any potential explanation must also be able to 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 probability of stability in different subgraphs, and that this probability should be related 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 the relationship between QSS and over/under-representation of the different subgraphs.(172 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 (2001). Studies such as Thébault and Fontaine (2010) have demonstrated a link between those structures observed in ecological networks (e.g., modularity in food webs and nestedness in mutualistic webs) are also those that emerge from the population dynamics underlying the system. There are many ways to characterize the structure of an ecological network however. Here we discuss the relevance of dynamics to the substructural composition of food webs.

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 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 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.

There are many definitions of stability that 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 are negative. 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 (e.g., 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. 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), but most ecological communities do not fulfill the conditions for qualitative stability.

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 its elements. 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 QSS. Using this measure I can determine the tendency of a given sign structure (given 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, 2012b). Another seven were available from [Ecological Archives](http://esapubs.org/Archive/search.php) (Hechinger et al. 2011, Thieltges et al. 2011, Zander et al. 2011, Mouritsen et al. 2011, Preston et al. 2012). Fourteen webs were provided by Jennifer Dunne of the [PEaCE Lab](http://peacelab.net/) (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) that were analyzed in (Dunne et al. 2002, 2004). The remaining 26 food webs were downloaded from the [Interaction Web Database](http://www.nceas.ucsb.edu/interactionweb/html/thomps_towns.html) (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). 1000 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.

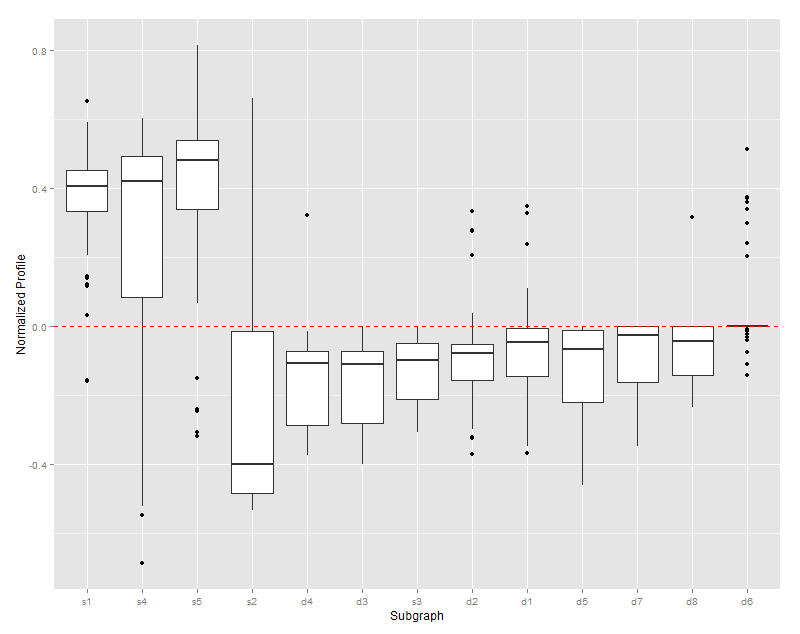
The code for determining subgraph frequency can be found in the Appendix and at <https://github.com/jjborrelli/Subgraph-Stability>.

**Subgraph Stability**

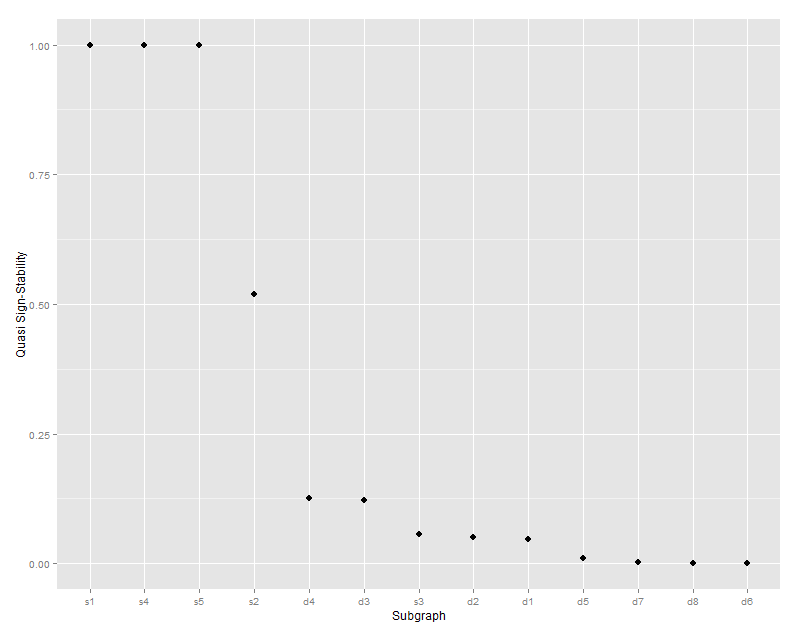
Using numerical simulations in R *version 3.0* (R Core Team 2014) I determined the probability of a given subgraph will be stable (quasi sign-stability, QSS), following the method of Borrelli and Ginzburg (in review). Each subgraph was translated into its corresponding sign-structured matrix. Positive 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). The code for these simulations is available in the Appendix and at <https://github.com/jjborrelli/Subgraph-Stability>.

**Results**

The different subgraphs are variable in how frequently they are observed relative to permuted webs. 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. 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.



Quasi sign-stability of a given subgraph is positively correlated (0.70; 95% CI: 0.25, 0.90; p-value = 0.007) with the frequency it is observed in empirical networks (relative to random). 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**

My results are similar to those found by other studies that have counted the frequency of different subgraphs in food webs (Milo et al. 2002, Bascompte and Melián 2005, Stouffer et al. 2007). In addition, these results closely match those of Prill et al. (2005), who found that the frequency of both three- and four-node subgraphs in transcription, signaling, and neuron networks was correlated with a measure of stability. The correlation between quasi-sign stability and the relative over- or under-representation of subgraphs is precisely what we would expect from selection against unstable configurations.

I do not make the claim that selection against instability is the causal mechanism of the observed pattern of subgraph frequencies. However, I would argue that what I have found is consistent with such an explanation.

Something about feasibility further constraining reality…

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