Stability and feedback levels in food web models

Matthew J. Smith[*], Elizabeth Sander, György Barabás & Stefano Allesina

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Abstract

Neutel & Thorne (Ecology Letters, 17:651-661, June 2014) provide an approximation for the leading eigenvalue of a food web community matrix involving coefficients of its characteristic polynomial. Though valuably incorporating three-way species interactions, two critical problems emerge when one considers the dimensions of the system, calling the approach's accuracy and precision into question.

Neutel and Thorne (2014) (hereafter NT) analyze the relationship between short feedback loops and the stability of ecological networks. The sign of the leading eigenvalue of the community matrix determines the stability of the steady-state, and its estimation has been researched for over 40 years (May 1971, 1973, 2001, Allesina and Tang 2012, Tang et al. 2014, Neutel and Thorne 2014). NT present a new approximation of the leading eigenvalue of an $N \times N$ community matrix $\mathbf{M}$:

$$\mathrm{Re}(\lambda_1) \approx \sqrt[3]{\frac{|a_3|}{|a_2|}}, \tag{1}$$

where a_k is the k^{th} coefficient of the characteristic polynomial $\mathrm{Det}(\lambda \mathbf{I} - \mathbf{M}) = \sum_{k=0}^{N} a_k \lambda^{N-k}$. Interestingly, a_3 embeds information about all three-way species interactions in the system—an important extension to previous approaches based on pairwise interactions (May 1973, Allesina and Pascual 2008, Tang et al. 2014), as well as a step toward understanding the effect of network structure on food web stability. Linking the correlation structure of three-link motifs to stability would be a valuable contribution to community ecology.

Dimensional Analysis

Despite this promise, two distinct problems emerge from the approach proposed by NT, limiting the scope of their findings. A food web can be modeled using a system of differential equations of the form $\mathrm{d}X_i/\mathrm{d}t$ in units of, for example, [biomass]/[time], yielding a community matrix $\mathbf{M}$ whose entries

$$m_{ij} = \left. \frac{\partial(\mathrm{d}X_i/\mathrm{d}t)}{\partial X_j} \right|_{X^*} \tag{2}$$

are measured in $[\mathrm{time}]^{-1}$. NT construct a "normalized" matrix by dividing each row of the community matrix by the absolute value of the corresponding diagonal element (i.e. $m'_{ij} = m_{ij}/|m_{ii}|$). They claim that this is a form of nondimensionalization, but in fact the units of measure still influence the properties of the new matrix since each row is scaled independently.

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Consider the following simple "omnivory module" **M** (with all coefficients measured in $[\text{days}]^{-1}$) and the corresponding **M'**:

$$\mathbf{M} = \begin{bmatrix} -\frac{1}{30.44} & -840 & -700 \\ 80 & -\frac{1}{7} & -280 \\ 20 & 140 & -24 \end{bmatrix} \quad \mathbf{M'} = \begin{bmatrix} -1 & -25567.5 & -21306.25 \\ 560 & -1 & -1960 \\ 0.83 & 5.83 & -1 \end{bmatrix}. \tag{3}$$

The NT procedure results in each row of **M'** having different units: the top row being essentially measured in $[\text{months}]^{-1}$, the second in $[\text{weeks}]^{-1}$, and the third in $[\text{hours}]^{-1}$. To truly nondimensionalize the system, one would have to apply the same transformation to the entire system by systematically changing the differential equations through substitution.

The operation performed by NT can alter fundamental properties of the matrix, including its stability. In the case above, the matrix **M'** is stable ($\text{Re}(\lambda_1) \approx -0.03$), while **M** is not ($\text{Re}(\lambda_1) \approx 7.55$) (the converse is also possible), which cannot occur in a true nondimensionalization (Chicone 2006). Though NT reference this in passing, they do not seem to consider it a detractor from their approach.

Finally, regardless of the normalization, the units of their approximation do not match those of the leading eigenvalue (measured in $[\text{time}]^{-1}$):

$$\sqrt[3]{\frac{|a_3|}{|a_2|}} = \sqrt[3]{\frac{\left|\sum_{i<j<k} \lambda_i \lambda_j \lambda_k\right|}{\left|\sum_{i<j} \lambda_i \lambda_j\right|}} \quad \text{in units of} \quad \sqrt[3]{\frac{[\text{time}]^{-3}}{[\text{time}]^{-2}}} = [\text{time}]^{-1/3}. \tag{4}$$

Estimated value for random matrices

It is nevertheless possible to accidentally obtain a numerically close approximation for particular parameterizations. This can be further explored by applying the approximation to random matrices (a case for which pairwise interactions are sufficient; Tang et al. 2014). Below, we calculate an analytic solution for NT's estimate in the case of a random matrix based on the distribution of matrix element coefficients. For these calculations, we will consider a random matrix **M** with diagonal elements $m_{ii} = 0$ and off-diagonal elements being $[m_{ij}, m_{ji}] = [0, 0]$ with probability $1 - C$, $[x, y]$ w.p. $C/2$, and $[y, x]$ w.p. $C/2$, where x, y are random variables with means $\mathbb{E}[x] = p > 0$ and $\mathbb{E}[y] = n < 0$ (i.e. consumer-resource interactions). In their asymmetric simulations, NT sample matrix coefficients from uniform distributions: positive from $\mathcal{U}[0, 0.1]$ and negative from $\mathcal{U}[0, -10]$, making $p = 1/20$ and $n = -5$.

We begin our calculation by noting that a_2 can be written as the sum of all second-order diagonal minors of **M**:

$$a_2 = \sum_{i<j} \text{Det}\begin{pmatrix} m_{ii} & m_{ij} \\ m_{ji} & m_{jj} \end{pmatrix} = \sum_{i<j} \text{Det}(M_{ij}), \tag{5}$$

which can be simplified for sufficiently large and connected matrices via the Central Limit Theorem:

$$\begin{aligned} a_2 \approx \mathbb{E}[a_2] &= \binom{S}{2} \mathbb{E}[\text{Det}(M_{ij})] \quad \text{where} \quad \begin{cases} \text{Det}(M_{ij}) = 0 & \text{w.p.} \quad 1 - C \\ \mathbb{E}[\text{Det}(M_{ij})] = -np & \text{w.p.} \quad C \end{cases} \\ &= -\binom{S}{2} Cnp. \end{aligned} \tag{6}$$

Because n is negative and p positive by definition, this value is positive and $\mathbb{E}[|a_2|] = \mathbb{E}[a_2]$.

We can perform a similar calculation for a_3:

$$a_3 = \sum_{i<j<k} \text{Det}\big(M_{ijk}\big) \approx \mathbb{E}[a_3] = \binom{S}{3} \mathbb{E}\big[\text{Det}\big(M_{ijk}\big)\big] = \binom{S}{3} C^3 \frac{(n+p)^3}{4}. \tag{7}$$

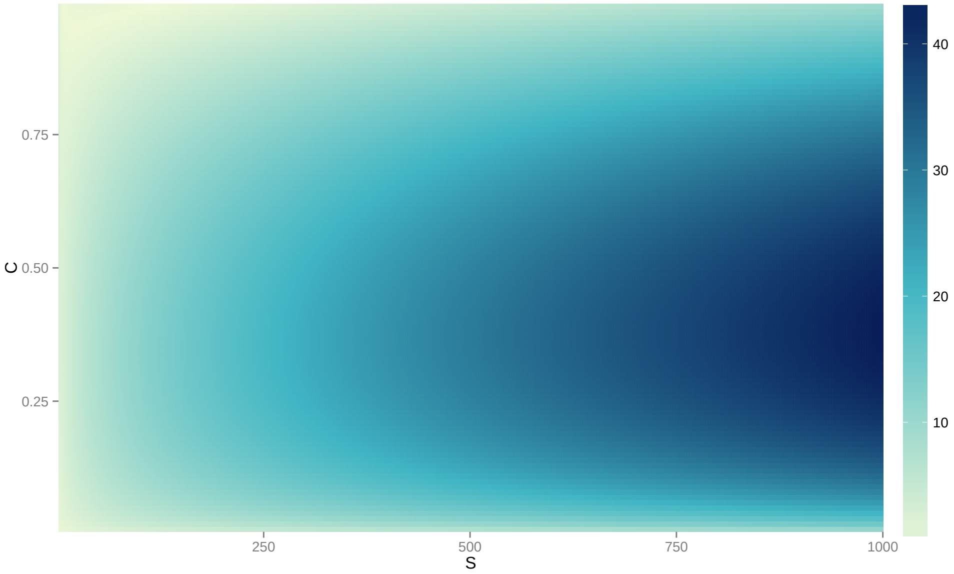

Figure 1: Heatmap of absolute difference between Neutel & Thorne's (2014) predicted $\mathrm{Re}(\lambda_1)$ (Eqn. 9) and the pairwise prediction of Tang et al. (2014) (Eqn. 12), given the asymmetric parameterization of Neutel & Thorne. Areas of lighter color show similarity between the predictions while the predictions diverge in darker areas. Though there is significant congruence at low size S or extreme values of connectance C, most ecological networks published today are large (>100 species) and moderately connected ($0.1 < C < 0.2$, Tang et al. 2014).

If $|n| \gg |p|$ (as in NT's asymmetric case), we can approximate $\mathbb{E}[|a_3|] \approx -\mathbb{E}[a_3]$. Substituting these into NT's approximation yields

$$\mathbb{E}\left[\sqrt[3]{\frac{|a_3|}{|a_2|}}\right] \approx \sqrt[3]{\frac{-\binom{S}{3}C^3(n+p)^3/4}{-\binom{S}{2}Cnp}} = \sqrt[3]{\frac{(S-2)C^2(n+p)^3}{12np}}, \tag{8}$$

which for $n=-5$ and $p=1/20$ becomes

$$\mathbb{E}\left[\sqrt[3]{\frac{|a_3|}{|a_2|}}\right] \approx 3.43\sqrt[3]{(S-2)C^2}. \tag{9}$$

If $\mathbf{M}$ is a random matrix, it has been shown (Tang et al. 2014) that

$$\mathrm{Re}(\lambda_1) \approx \sqrt{SV}(1+\rho) - E, \tag{10}$$

where E is the mean of the off diagonal coefficients of $\mathbf{M}$, V is their variance, and ρ is the correlation between elements m_{ij} and m_{ji}. Recasting in terms of n, p, S and C, this becomes

$$\mathrm{Re}(\lambda_1) \approx \frac{1}{6}\left(\left(\frac{3\left(C(n+p)^2-4np\right)}{(3C-8)\left(n^2+p^2\right)+6Cnp}+1\right)\sqrt{3CS\left(8\left(n^2+p^2\right)-3C(n+p)^2\right)}-3C(n+p)\right), \tag{11}$$

which for $n=-5$ and $p=1/20$ is

$$\mathrm{Re}(\lambda_1) \approx 0.17\left(\frac{3.46(C-1.34)\sqrt{SC(200.02-73.51C)}}{C-2.72}+14.85C\right). \tag{12}$$

While Eqn. 9 scales with $\sqrt[3]{SC^2}$, Eqn. 12 scales with $\sqrt{SC}$. Even though these functions differ, particular values of S and C give the illusion of accuracy (Figure 1). Using NT's asymmetric parameterization, we expect similar results at small matrix sizes or extreme connectances.

This finding can be further explored by considering a given connectance and simulating random matrices of increasing size, allowing the predictions to be compared to the actual $\mathrm{Re}(\lambda_1)$ of each matrix (Figure 2). Again, we see that NT's prediction appears to be accurate (relative error less than 10%) for small matrices (e.g., $S < 27$ for $C \approx 0.2$) but is not generally accurate. This region of accuracy is at odds with the hundreds of interconnected species we observe in nature, which are only simplified into "trophic groups" (as in NT) as a computational convenience.

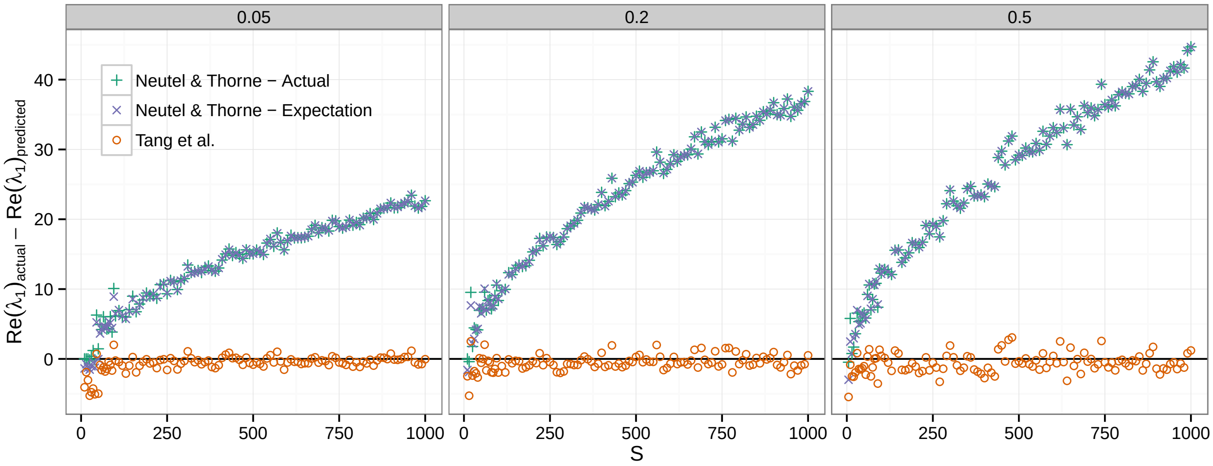

Figure 2: Absolute error of predicted $\mathrm{Re}(\lambda_1)$ by three methods for connectance $C = 0.05,\ 0.2,\ 0.5$. For matrix size S ranging from 5 to 1000, each approximation's absolute deviation $\mathrm{Re}(\lambda_1)_{\mathrm{actual}} - \mathrm{Re}(\lambda_1)_{\mathrm{predicted}}$ is plotted. Orange, the prediction based on pairwise interaction strengths (Tang et al. 2014) (Eqn. 12). Green, the prediction proposed by Neutel and Thorne (2014) (Eqn. 1). And Purple, the estimated value of NT's approximation for random matrices as described in main text (Eqn. 9), and parameterized following the asymmetric parameterization used by Neutel and Thorne (2014)).

Although NT provide an insightful consideration of network structures beyond the common focus on pairwise interactions, their approximation suffers from critical problems. The dimensional incongruity and the alteration of qualitative system properties such as stability raise concerns regarding the precision and accuracy of this prediction except for a particular (and unrealistic) range of parameter values. Though mathematical in nature, these problems have important and relevant biological consequences through the mis-approximation of the leading eigenvalue—an important indicator of the stability and reactivity of ecological systems.

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