Matrix Scaling and Tipping Points[*]

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Abstract. To assess which ecosystems are most vulnerable it is necessary to compare the resilience of complex interaction networks in a meaningful way. A fundamental problem for the comparative analysis of ecological stability is that the organisms in ecological networks operate on different time scales. A conventional solution to this problem has been to assume the intraspecific interaction strengths in the dynamical system (and diagonal elements in the community matrix) have the same value, ignoring the time scale differences, and therefore disregarding vital ecological information. In this paper, we consider two methods that have previously been developed to deal with community matrices arising from populations with widely different time scales and which contain differing self-regulation terms (diagonal entries). One approach considers the critical self-regulation in a system by proportionally adjusting the diagonal entries until the tipping point is found. The other is a scaling procedure that translates the intraspecific information on the diagonal on to the off-diagonal entries. We show the relation between the leading eigenvalue of the latter, and the numerical diagonal parameter of the former, which in many ecologically relevant networks is exact. In addition, we show for 3×3 scaled competitive systems how the feedback determines whether the leading eigenvalue is real- or complex-valued, which is important for knowing when the scaling procedure remains ecologically sensible. While arising from an ecological setting, this work has wider implications in network theory and linear algebra.

Key words. ecology, food webs, stability, networks, feedback

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1. Introduction. The development of ecological food web theory in the 20th century grew from the diagrammatic relationships between species elaborated by Elton [4] and the information-theoretic approach put forward by MacArthur [19]. MacArthur's work drew on Lindeman's [17] efficiency of trophic energy transfer and Odum's [30] criterion that increasing the channels that energy has in rising to higher trophic levels provides stability to a system. In so doing, MacArthur solidified the widely held view that increased diversity leads to increased stability [5], [11]. Following Levins' [15] construction of the community matrix based on Lotka–Volterra [18] equations at equilibrium, Gardner and Ashby [6], subsequently extended analytically by May [21], [22], [23], upended this assumption and set in train the complexity-stability debate [24]. But Gardner and Ashby's [6] and May's [22] inverse relationship result

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was arrived at through the removal of ecologically relevant energy transfer [17] and flow direction [30] information. This information is vital to the structure of an ecosystem, thus leaving their complexity begets instability result as an artifact of their structural choices and insistence on the significance of the pairwise interactions alone [2], [14], [32], [35], [8], [26], [27], [12].

However, within May's approach was the first analytic statement of the stabilizing role of self-regulation [22], [23], [7]. Yet long before May [19], [5], [11], [20] the stabilizing role of self-regulation was well understood (and see [2], [14], [35]). Still, in his analyses, May assumed that these terms could be normalized, and a uniform value was set for all the diagonal elements of his community matrices [22] just as, previously, Gardner and Ashby had set the self-regulation terms to uniformly random values within a small range [6]. But it has been argued that normalization in the way proposed by Gardner and Ashby or May is not possible when the components within a network operate on different time scales [8], [13]. When considered with more ecological relevance, the question often came down to the proportion of species requiring a uniformly applied self-regulation for the system to be stable [35]. Incorporation of varied, observation-based intraspecific terms came with de Ruiter, Neutel, and Moore [3], who derived upper limits for each population from nonpredatory loss rates [10]. In addition to these empirically derived rates, this study also incorporated, following Gardner and Ashby [6] and Yodzis [35], a discrete, proportional variable which was uniformly multiplied by the differing intraspecific values. This variable provided an assessment of how the stability changes as the proportion of the species' intraspecific interaction terms, which might operate on very different time scales from each other, was altered. Neutel, Heesterbeek, and de Ruiter [25] introduced the concept of critical self-regulation, using this same variable as a continuous control parameter, adjusted freely to find the proportional amount of the empirically derived terms on the diagonal needed to arrive at the tipping point between stability and instability of the system. This proportional amount, or critical self-regulation, can be seen as a stability measure: if it is less than one, the system is stable; if it is more than one, it is unstable. Critical self-regulation not only informs one about the vulnerability of the current system, but it also allows one to make comparisons across systems. Those systems that need relatively more self-regulatory input are more fragile than those that require less. In this sense, it is a metric much like the more generally recognized real part of the leading (maximal real part) eigenvalue that determines the stability in systems theory.

Neutel and Thorne [27] equated this numerical multiplier at the critical value, indicating the tipping point of the system, with the leading eigenvalue of a matrix obtained by scaling the off-diagonal interaction strengths by the self-regulating terms, followed by a linear shift. This scaling operation not only enabled the stability of disparate food webs to be compared, but it also simplified their feedback structure, which made it possible to correlate the stability in terms of the strength of key feedbacks.

In this paper, we analyze the relation between the two stability metrics, showing that the leading eigenvalue of a scaled matrix, when placed back as the diagonal multiplier, is either equal to the critical value that makes the original system stable or produces a subcritical zero. For mathematical closure, it is necessary to consider multipliers that are complex, yet this raises difficulties for ecological interpretation. In attempting to understand when scaled matrices have leading complex-valued eigenvalues, we compare the simplest matrix forms,

that of mutualistic and competitive systems. Through this comparison, we are able to show that when a 3×3 competitive system has a leading eigenvalue that is complex, it is due to an increase in negative feedback.

2. Scaling a community matrix by its diagonal elements can preserve essential stability information. Community matrices are made up of interaction strengths, representing the size of the effects of species on each other's dynamics near equilibrium, and are traditionally based on linearizations of sets of growth equations of ecological populations [15].

The classic predator-prey food web model uses growth equations of the Lotka–Volterra type [18] where the off-diagonal entries are the effects of one trophic group on another: the feeding rates relative to predator population size (negative effects) and growth rates relative to prey population size (positive effects). The diagonal entries are the intraspecific losses of a given group relative to the population size [31]. All the entries have the dimension "per time." Appendix A details the mathematical construction of a community matrix.

In general, community matrices can be constructed depicting many different relations among the groups. These systems can include predator-prey, mutualistic, commensalistic, competitive, and amensalistic, as well as any number of purely synthetic and random constructions, as was first explored by Gardner and Ashby [6].

Neutel, Heesterbeek, and de Ruiter [25] introduced a continuous, positive, real-valued variable s that was uniformly multiplied by the self-regulation terms on the diagonal from populations with widely differing time scales in empirically observed food webs. This variable enabled one to find the proportion of the upper-bound self-regulation required to be altered in the system (the critical self-regulation, $s*$) to find the stability tipping point, which could then be used to compare the vulnerability of different systems. An example of this approach can be seen with the following small 3×3 predator-prey community matrix:

$$(2.1) \qquad \boldsymbol{A} = \begin{bmatrix} -a & b & c \\ -d & -e & f \\ -g & -h & -k \end{bmatrix},$$

where the lower diagonal entries are negative or zero, the upper diagonal entries are positive or zero, and the diagonal entries are negative. Then, multiplying the diagonal elements of $\boldsymbol{A}$ by a variable s leads to the matrix

$$(2.2) \qquad \boldsymbol{A}_s = \begin{bmatrix} -sa & b & c \\ -d & -se & f \\ -g & -h & -sk \end{bmatrix}.$$

The variable s is then continuously shifted from 0 to a point designated as s^* at which the real part of the resulting maximal, or leading, eigenvalue (the eigenvalue with the largest real part) of $\boldsymbol{A}_s$ is just zero (or as close as possible within numerical precision). Any further increase in s should result in all eigenvalues having negative real parts.

Neutel and Thorne [27] subsequently applied a scaling method in which each row of the community matrix is divided by the absolute value of its diagonal entry and then the entire matrix translated by adding the identity matrix so that the diagonal entries all become zero.

Using the same example as above, we start with

$$\bar{A} = \left[\begin{array}{ccc} -1 & b/a & c/a \\ -d/e & -1 & f/e \\ -g/k & -h/k & -1 \end{array} \right],$$

which after adding the identity matrix $\boldsymbol{I}$ to $\bar{\boldsymbol{A}}$, effecting a linear shift, results in the matrix

$$(2.3) \qquad \bar{A}_0 = \left[\begin{array}{ccc} 0 & b/a & c/a \\ -d/e & 0 & f/e \\ -g/k & -h/k & 0 \end{array} \right].$$

In many cases, the resulting leading eigenvalue of such a scaled matrix is very close to, and sometimes exactly the same as, the critical self-regulation s^* of $\boldsymbol{A}_s$. If the leading eigenvalue of $\bar{\boldsymbol{A}}_0$ is real-valued with no imaginary part, then the relation to s^* can be exact. However, if the leading eigenvalue of $\bar{\boldsymbol{A}}_0$ consists of a complex pair, then we need to redefine the real-valued s in (2.2) to be a complex-valued variable, which we shall call σ. But allowing the diagonal variable to be complex-valued is a significant shift. While enabling mathematical closure, it opens up difficulties for ecological interpretation. We return to this issue in section 3.

With $\sigma \in \mathbb{C}$, (2.2) now becomes

$$(2.4) \qquad \boldsymbol{A}_\sigma = \left[\begin{array}{ccc} -\sigma a & b & c \\ -d & -\sigma e & f \\ -g & -h & -\sigma k \end{array} \right].$$

That is, the leading eigenvalue of (2.3), when placed back as σ in (2.4), often results in (2.4) having a leading eigenvalue of zero. To understand this statement more clearly, we first state a simple condition on the original matrix $\boldsymbol{A}$.

Let $\boldsymbol{A}$ be an $n \times n$ matrix comprised of elements a_{ij} with the condition that the diagonal elements are all negative, $a_{ii} < 0$. Even this condition may be relaxed, but ecological relevance to date has dictated that the diagonal elements are all negative.

To determine the relationship between the self-regulation term σ and the leading eigenvalue of the scaled matrix $\bar{\boldsymbol{A}}_0$, we rewrite the two matrices in terms of the original community matrix $\boldsymbol{A}$ as

$$(2.5) \qquad \boldsymbol{A}_\sigma = \boldsymbol{A} - (1 - \sigma) \cdot \mathrm{diag}(\boldsymbol{A})$$

and

$$(2.6) \qquad \bar{\boldsymbol{A}}_0 = -(\mathrm{diag}(\boldsymbol{A}))^{-1}\boldsymbol{A} + \boldsymbol{I},$$

where the role of the variable σ has been described, $\boldsymbol{I}$ is the $n \times n$ identity matrix, $\mathrm{diag}(\boldsymbol{A})$ is the matrix of diagonal elements a_{ii} of $\boldsymbol{A}$, and the superscript -1 denotes the inverse matrix operation.

We are interested in determining the values of σ such that $\boldsymbol{A}_\sigma$ has a zero eigenvalue. The criterion for this is given by

$$\det(\boldsymbol{A}_\sigma - (0)\boldsymbol{I}) = 0,$$

which can be rewritten using (2.5) as

$$(2.7) \qquad \det(\boldsymbol{A} - (1 - \sigma) \cdot \mathrm{diag}(\boldsymbol{A})) = 0.$$

We now consider $\bar{\boldsymbol{A}}_0$. Let λ be an eigenvalue of $\bar{\boldsymbol{A}}_0$ so that

$$\det(\bar{\boldsymbol{A}}_0 - \lambda\boldsymbol{I}) = 0.$$

Using (2.6), this can be rewritten as

$$\det((-(\mathrm{diag}(\boldsymbol{A}))^{-1}\boldsymbol{A} + \boldsymbol{I}) - \lambda\boldsymbol{I}) = 0.$$

Multiplying both sides by $\det(-\mathrm{diag}(\boldsymbol{A}))$ and using properties of determinants, one has

$$\det(-\mathrm{diag}(\boldsymbol{A})(-(\mathrm{diag}(\boldsymbol{A}))^{-1}\boldsymbol{A} + \boldsymbol{I} - \lambda\boldsymbol{I})) = 0,$$

which can be simplified to

$$(2.8) \qquad \det(\boldsymbol{A} - (1 - \lambda) \cdot \mathrm{diag}(\boldsymbol{A})) = 0.$$

While the relation between (2.7) and (2.8) assures us that there is a zero eigenvalue of $\boldsymbol{A}_\sigma$ when $\sigma = \lambda_{\max}$ of $\bar{\boldsymbol{A}}_0$ ($\lambda_{\max(\bar{A}_0)}$), it is not necessarily the leading eigenvalue of $\boldsymbol{A}_\sigma$. Rather, it may be submaximal (i.e., $\lambda_{\max(\bar{A}_0)} > 0$). If the leading eigenvalue of $\boldsymbol{A}_\sigma$ is zero when $\sigma = \lambda_{\max(\bar{A}_0)}$, then for convenience we designate σ as σ^*, analogous to s^*. In the majority of observed cases using empirical or ecologically considered community matrices, $\sigma^* = \lambda_{\max(\bar{A}_0)}$ and is therefore the tipping point of $\boldsymbol{A}_\sigma$.

The images in Figure 1 depict the σ landscape of a 22-species Antarctic predator-prey food web, SIRS1 (described in [27], [28], but without the last detrital row and column), and a number of randomized predator-prey variants of SIRS1 (where the nonzero elements of the matrices are assigned random values while keeping their sign intact). The coloring shows for a given value of σ ($\in \mathbb{C}$) in $\boldsymbol{A}_\sigma$ how many eigenvalues with positive real part would result. The black areas indicate the regions of stability, where the real part of all the eigenvalues would be negative (or zero if on the boundary). In the darker blue region bounding the black, there would be one positive (real part) eigenvalue, in the lighter blue there would be two positive eigenvalues, and so on. The yellow asterisks (if $\lambda_{\max(\bar{A}_0)} = \sigma^*$) or red asterisks (if $\lambda_{\max(\bar{A}_0)} \neq \sigma^*$) in each figure indicate where $\lambda_{\max(\bar{A}_0)}$ lies in the landscape. In Figure (1a), the empirical Antarctic web has a real-valued leading eigenvalue when scaled and $\lambda_{\max(\bar{A}_0)} = \sigma^*$, and so the yellow asterisk is therefore shown on the real axis just at the boundary between the black, stable region and the region where there would be one positive eigenvalue.

Figures (1b), (1d), and (1e) also depict the σ landscape for community matrices where $\lambda_{\max(\bar{A}_0)} = \sigma^*$. Note that Figure (1b) shows a small island of stability to the left in a larger unstable region. Figures (1c) and (1f) show a real-valued and complex-valued case, respectively, where $\lambda_{\max(\bar{A}_0)} \neq \sigma^*$. In both cases, the $\lambda_{\max(\bar{A}_0)}$ values can be seen to lie within the region of instability, indicating that for these values of σ, there are one (1f) or more (two in (1c)) eigenvalues with positive real part.
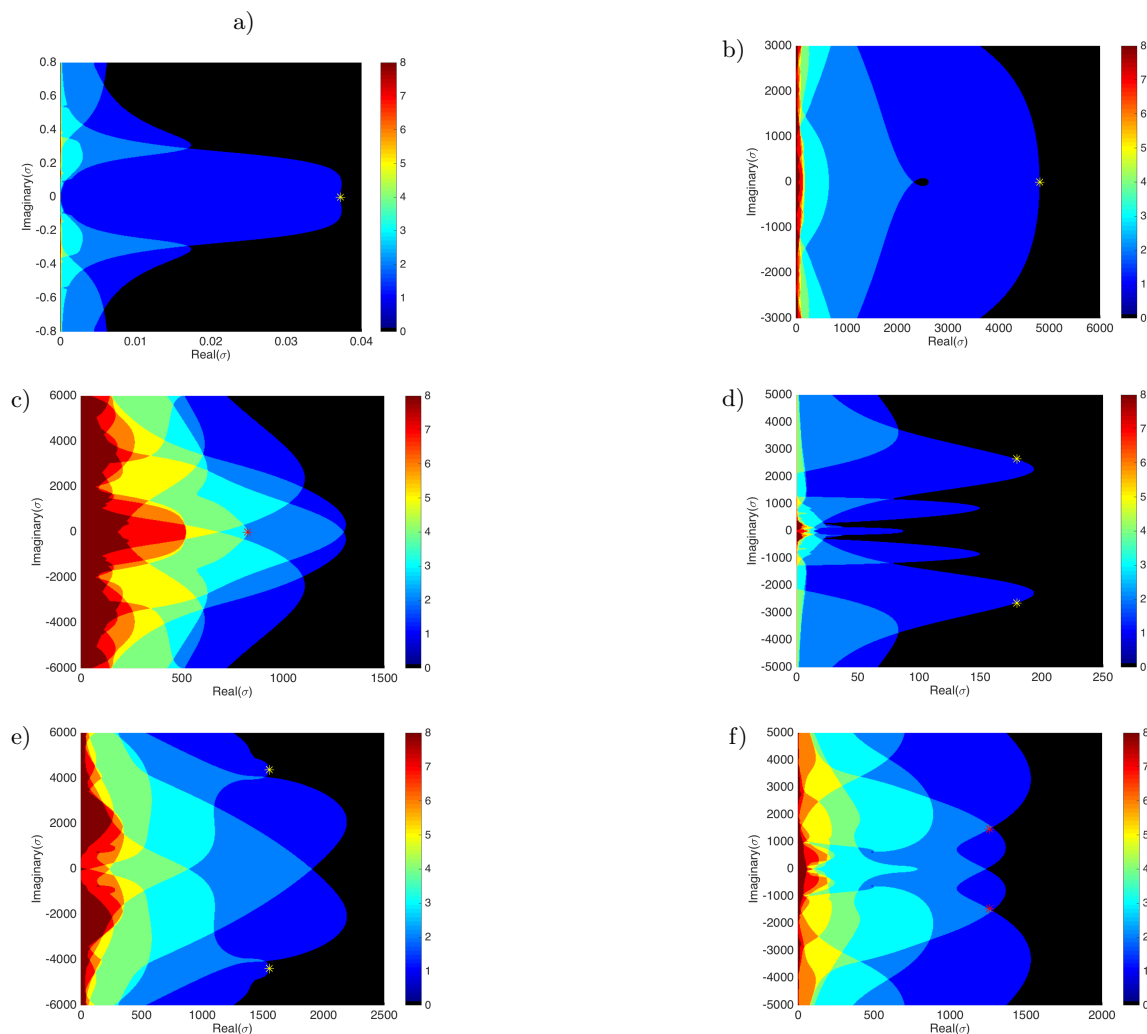
Figure 1. *In all subfigures, the coloring indicates the number of eigenvalues with positive real part in the spectrum of $\boldsymbol{A}_\sigma$ as σ is varied. The black region has none and is therefore the region of stability for $\boldsymbol{A}_\sigma$. Red is six or more. The boundary between the black and the darker blue regions (indicating one eigenvalue with positive real part) are tipping points where a σ produces a leading eigenvalue with real part zero. When $\lambda_{\max(\bar{\mathrm{A}}_0)} = \sigma^*$, then $\lambda_{\max(\bar{\mathrm{A}}_0)}$ lies on this boundary and is shown as a yellow asterisk (or two if complex). If $\lambda_{\max(\bar{\mathrm{A}}_0)} \neq \sigma^*$, then $\lambda_{\max(\bar{\mathrm{A}}_0)}$ (and its complement if complex) is shown as a red asterisk. (a) A 22-species Antarctic food web, SIRS1, whose leading scaled eigenvalue is real-valued and $\lambda_{\max(\bar{\mathrm{A}}_0)} = \sigma^*$. All other examples are predator-prey randomized variants of SIRS1. (b) An example for which $\lambda_{\max(\bar{\mathrm{A}}_0)} = \sigma^*$, yet which has a small stable island (the small black region between the two blue regions centered along the x axis) in the region of instability. (c) An example of a real-valued $\lambda_{\max(\bar{\mathrm{A}}_0)} \neq \sigma^*$, with $\lambda_{\max(\bar{\mathrm{A}}_0)}$ far to the left of the stable region. (d) and (e) Two examples with complex-valued $\lambda_{\max(\bar{\mathrm{A}}_0)} = \sigma^*$. (f) An example with a complex-valued $\lambda_{\max(\bar{\mathrm{A}}_0)} \neq \sigma^*$ pair which lies in the region of instability.*

3. The relation between paired mutualistic and competitive scaled community matrices highlights the role of feedback in determining the field of the leading eigenvalue. In order for the leading eigenvalue of a scaled matrix to be used as σ in $\boldsymbol{A}_\sigma$ and to make sense

in an ecological setting, it is ideal for σ to be real-valued. This is not to say, however, that a complex σ is any less likely to result in a tipping point of $\boldsymbol{A}_\sigma$ through the scaling relation or that one could not approximate σ as a real value. But there is no clear interpretation for a complex σ.

For understanding just when a community matrix has a real- rather than a complex-valued leading eigenvalue after scaling, it is useful to compare mutualistic and competitive systems, the two structurally simpler matrix forms. Scaled mutualistic matrices are assured, by the Perron–Frobenius theorem, to have a leading real-valued eigenvalue (even unscaled mutualistic matrices with negative diagonal elements have real leading eigenvalues, as shown in Appendix B). Competitive systems, however, do not in general have real-valued leading eigenvalues. Rather, like predator-prey systems (and more complicated sign structured matrices), the leading eigenvalue can be real or complex (see Appendix C for a combinatorial argument of the potential number of real to complex leading eigenvalues for competitive systems). The relevance of comparing paired, or companion, scaled mutualistic ($\boldsymbol{M}$) and competitive ($\boldsymbol{C}$) matrices (one formed by reversing the sign of the elements of the other) rests on the relation of their eigenvalue ordering, which in turn can help to understand how matrix structure determines when there is a complex-valued leading eigenvalue. This is best explored through the characteristic polynomial, $p(x)$. For a scaled mutualistic system,

$$p_{\boldsymbol{M}}(x) = \sum_{i=0}^{n} a_i x^{n-i},$$

where the eigenvalues ($\lambda_{\boldsymbol{M}_i}$), or roots, are the negative of those from its companion competitive system, $p_{\boldsymbol{C}}(x)$,

$$\{\lambda_{\boldsymbol{M}_1}, \ldots, \lambda_{\boldsymbol{M}_n}\} = -\{\lambda_{\boldsymbol{C}_1}, \ldots, \lambda_{\boldsymbol{C}_n}\},$$

so that

$$|\max\{\lambda_{\boldsymbol{M}_1}, \ldots, \lambda_{\boldsymbol{M}_n}\}| = |\min\{\lambda_{\boldsymbol{C}_1}, \ldots, \lambda_{\boldsymbol{C}_n}\}|.$$

Therefore,

$$p_{\boldsymbol{M}}(\lambda_{M_i}) = 0 \iff p_{\boldsymbol{C}}(-\lambda_{M_i}) = 0$$

$$\implies p_{\boldsymbol{M}}(\lambda_{M_i}) = p_{\boldsymbol{C}}(-\lambda_{M_i}),$$

where the coefficients for all the odd powers between $p_{\boldsymbol{M}}$ and $p_{\boldsymbol{C}}$ differ solely by sign.

The discriminant of a polynomial allows us to determine whether there is a complex root. Therefore, considering the general characteristic polynomial for a 3×3 matrix,

$$a_0 x^3 + a_1 x^2 + a_2 x + a_3 = 0,$$

then the discriminant of the characteristic polynomial for a scaled matrix (where $a_0 = 1$ and $a_1 = 0$) is given as

(3.1) $$\Delta = -4a_2^3 - 27a_3^2.$$

Whether there exists a complex-valued eigenvalue pair is determined by whether $\Delta < 0$. The sign of the discriminant is determined by the values of the respective coefficients a_2 and a_3, which reflect the form of the underlying matrix.

The general, scaled, 3×3 matrices of mutualistic, competitive, and predator-prey (brought in for completion for the remaining discussion) systems are

$$
\begin{array}{ccc}
\text{Mutualistic} & \text{Competitive} & \text{Predator-Prey} \\
\begin{bmatrix} 0 & b & c \\ d & 0 & e \\ f & g & 0 \end{bmatrix} &
\begin{bmatrix} 0 & -b & -c \\ -d & 0 & -e \\ -f & -g & 0 \end{bmatrix} &
\begin{bmatrix} 0 & b & c \\ -d & 0 & e \\ -f & -g & 0 \end{bmatrix}
\end{array}
$$

As described more fully in Appendix C, an eigenvalue ordering such as (r, c, c) consists of a real-valued eigenvalue (r), and then a complex conjugate pair (c, c), with the ordering based on the smallest eigenvalue located on the left (in numeric terms) and the largest eigenvalue on the right. As shown below (along with the possible eigenvalue orderings and coefficient signs), the mutualistic and competitive matrices result in the same form of the discriminant, even while differing in their sign of coefficient a_3 (see Figure 2).

Mutualistic:
$$
\begin{array}{ll}
(c, c, r) & a_2 < 0, a_3 < 0, \Delta > 0, \text{or } \Delta < 0 \\
(r, r, r)' & \Delta = 4(eg + cf + bd)^3 - 27(bef + cdg)^2,
\end{array}
$$

Competitive:
$$
\begin{array}{ll}
(r, c, c) & a_2 < 0, a_3 > 0, \Delta > 0, \text{or } \Delta < 0 \\
(r, r, r)' & \Delta = 4(eg + cf + bd)^3 - 27(bef + cdg)^2,
\end{array}
$$

Predator-Prey:
$$
\begin{array}{ll}
(r, c, c) & a_2 > 0, \Delta < 0 \\
(c, c, r)' & \Delta = -4(eg + cf + bd)^3 - 27(cdg - bef)^2.
\end{array}
$$

As can be seen above and in Figure 2, the predator-prey 3×3 systems can have a complex conjugate pair in two possible positions, and therefore no assurance that a complex-valued eigenvalue is leading. Mutualistic systems can of course only have a real-valued leading eigenvalue. But with the 3×3 (and no higher n) scaled competitive matrix we can be assured that when there is a complex-valued eigenvalue, it is leading. In this specific case, the ratio of the values of the a_2 and a_3 coefficients in the discriminant determines when there is a leading complex-valued eigenvalue:

$$
(3.2) \qquad \frac{4(eg + cf + bd)^3}{27(bef + cdg)^2} \begin{cases} > 1 : \text{all eigenvalues are real-valued,} \\ < 1 : \text{leading eigenvalue is complex-valued.} \end{cases}
$$

The feedback in a system is found by multiplying the matrix entries that make up a circuit, and these in turn, through their summation of each feedback level, or circuit size, are represented by the coefficients of the characteristic polynomial [1], [16], [27]. The coefficients
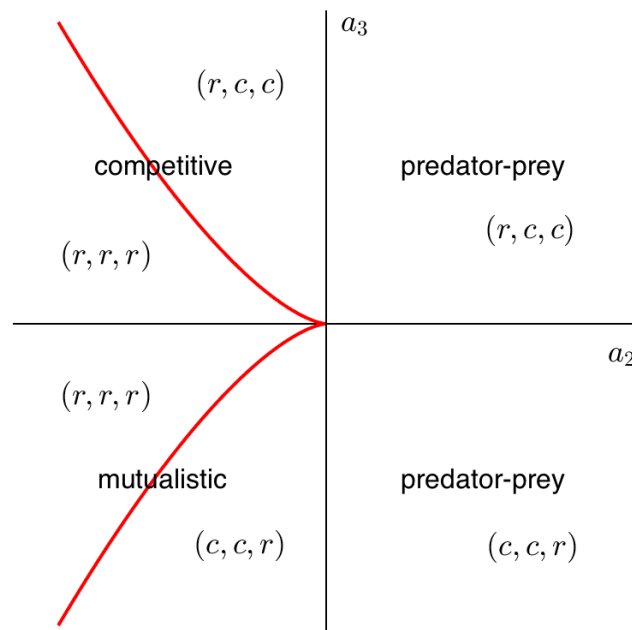
Figure 2. *The regions for the eigenvalue signatures (the eigenvalue orderings as described in Appendix C) depending on the sign of the respective coefficients (a_2 and a_3) of the different forms (mutualistic/competitive/predator-prey) for general, scaled 3×3 community matrices. The red curve indicates where the discriminant given by (3.1) is zero. In the region to the left of the red curve, the discriminant is positive and there are three real eigenvalues.*

of a_2 and a_3 in (3.2) not only reflect different sized circuits, but since they come from a competitive system, the underlying feedback inherent in each coefficient differs fully as well. Thus, greater positive feedback (a_2, the numerator in (3.2)) results in real-valued leading eigenvalues, while increasing the negative feedback (a_3, the denominator in (3.2)) will eventually lead to complex-leading eigenvalues.

4. Conclusion. Empirical food web models must contain self-damping terms, which may represent widely different time scales, to be ecologically relevant. Once these are included, in order to compare differing community matrices, a normalization of the diagonal terms is needed. A matrix scaling technique outlined in Neutel and Thorne [27] translates the self-damping terms on the diagonal into the interspecific off-diagonal terms, followed by a linear shift. In most cases, the resulting leading eigenvalue of the scaled matrix, when applied as the diagonal multiplying factor in the original unscaled matrix, brings the system to a stability tipping point. We have now explored this relation between the leading eigenvalue of the scaled matrix and the diagonal multiplying factor of the original matrix.

The applicability of the scaling method has been contested. Smith et al. [34] argued that

the wide range of time scales of the differing species prevented the technique from being valid. This can now be disregarded due to the relation between (2.7) and (2.8). Haydon [8] argued that dividing each row by its diagonal term (see, e.g., [33]) will not preserve the dynamics in any way [13]. But there is no expectation that the scaled matrices have the same dynamics as the unscaled matrices, only that they carry valuable information on the original matrices.

For mathematical closure, it is necessary to allow the diagonal variable σ to be complex-valued. Yet to be ecologically sensible, it is ideal for σ, and therefore the leading eigenvalue of the scaled matrix, to be real-valued. That is, $\sigma = s$, the real-valued s as in the original numerical formulation of the problem. In mutualistic matrices, this will always be the case. We have shown that in small 3×3 scaled competitive systems, the field of the leading eigenvalue (i.e., $\lambda_{\max(\bar{A}_0)} \in \mathbb{R}$ or $\lambda_{\max(\bar{A}_0)} \in \mathbb{C}$) is determined by whether the system is driven by positive or negative feedback. Resolving to what extent, if any, the field of the leading eigenvalue is determined by the feedback for systems in general remains an interesting problem.

Since the scaling method can be applied to all square matrices with negative diagonal terms, such a technique should find relevance beyond the scope of ecological theory.

Appendix A. Construction of a community matrix.
While the use of the term community matrix stems from Levins [15], it has been used since to mean a wide range of differing constructions [29]. We describe here one widely used approach.

We begin with the governing equations. Everything that follows can easily be generalized to any number of species, but as an example, consider a Lotka–Volterra system of equations for three species,

$$\dot{x}_1 = b_1 x_1 + c_{11} x_1^2 + c_{12} x_1 x_2 + c_{13} x_1 x_3 = F_1(x_1, x_2, x_3) = x_1 G_1(x_1, x_2, x_3),$$
$$\dot{x}_2 = b_2 x_2 + c_{21} x_2 x_1 + c_{22} x_2^2 + c_{23} x_2 x_3 = F_2(x_1, x_2, x_3) = x_2 G_2(x_1, x_2, x_3),$$
$$\dot{x}_3 = b_3 x_3 + c_{31} x_3 x_1 + c_{32} x_3 x_2 + c_{33} x_3^2 = F_3(x_1, x_2, x_3) = x_3 G_3(x_1, x_2, x_3),$$

where the x_i represent the population density of each species, b_i the birth/death rates, $c_{ii} \leq 0$ the self-regulation rates, and c_{ij} $(i \neq j)$ the predation rates. The c_{ij} $(i \neq j)$ can be positive or negative (or zero) depending on whether the system is mutualistic, predator-prey, or competitive.

The equilibrium or steady states of this Lotka–Volterra system are found by setting the right-hand side of all the governing equations equal to zero $(F_i = 0)$. This three-species system possesses eight possible steady states: a coexistence equilibrium, $(x_1 \neq 0, x_2 \neq 0, x_3 \neq 0)$, where all three species coexist; three different equilibria, where one species is extinct, e.g., $(x_1 \neq 0, x_2 \neq 0, x_3 = 0)$; three equilibria where two of the species are extinct, e.g., $(x_1 \neq 0, x_2 = 0, x_3 = 0)$; and finally, an equilibrium where all the species are extinct, $(x_1 = 0, x_2 = 0, x_3 = 0)$. Generally, the equilibrium of interest, and which we show below, is where all the species coexist, designated (x_1^*, x_2^*, x_3^*).

We then approximate the governing equations using the Jacobian, $\mathcal{J}$, to linearize the

system, where

$$\boldsymbol{\mathcal{J}} = \begin{bmatrix} \dfrac{\partial F_1}{\partial x_1} & \dfrac{\partial F_1}{\partial x_2} & \dfrac{\partial F_1}{\partial x_3} \\[2mm] \dfrac{\partial F_2}{\partial x_1} & \dfrac{\partial F_2}{\partial x_2} & \dfrac{\partial F_2}{\partial x_3} \\[2mm] \dfrac{\partial F_3}{\partial x_1} & \dfrac{\partial F_3}{\partial x_2} & \dfrac{\partial F_3}{\partial x_3} \end{bmatrix}.$$

The community matrix, $\boldsymbol{\mathcal{J}}^*$, is the Jacobian evaluated at a steady state, i.e., $\boldsymbol{\mathcal{J}}^* = \boldsymbol{\mathcal{J}}|_{(x_1^*, x_2^*, x_3^*)}$. For the three-species example where the coexistence equilibrium means that $F_i = 0$ and $x_i \neq 0$, and therefore $G_i = 0$ for all i, the community matrix is

$$\boldsymbol{\mathcal{J}}^* = \begin{bmatrix} c_{11}x_1^* & c_{12}x_1^* & c_{13}x_1^* \\[2mm] c_{21}x_2^* & c_{22}x_2^* & c_{23}x_2^* \\[2mm] c_{31}x_3^* & c_{32}x_3^* & c_{33}x_3^* \end{bmatrix}.$$

In section 2, equation (2.1) is $\boldsymbol{\mathcal{J}}^*$ for a predator-prey system.

Appendix B. In mutualistic systems the leading eigenvalue is always real-valued.
Mutualistic systems are represented by square matrices with positive off-diagonal elements and negative or zero diagonal elements. If all the diagonal elements are zero, such as after the scaling process, then one may apply the Perron–Frobenius theorem, which ensures that for nonnegative matrices, the leading eigenvalue is real-valued, and is in fact the spectral radius of the matrix [9]. If the diagonal elements are negative, we need to prove an extension to the Perron–Frobenius theorem.

Theorem. Matrices of mutualistic systems with negative diagonal elements have leading eigenvalues that are real-valued.

Proof. The Perron–Frobenius theorem states that for any positive or nonnegative matrix $\boldsymbol{A}$ there exists a unique, real-valued eigenvalue λ_{max}, its size equalling the spectral radius of $\boldsymbol{A}$, such that all the other eigenvalues ϕ_j (possibly complex) are smaller in modulus than λ_{max} ($|\phi_j| < \lambda_{max}$).

From a mutualistic matrix with negative diagonal elements $\boldsymbol{A}$, we form a new matrix as follows: choose an α (real) so that the new matrix $\boldsymbol{A} + \alpha \boldsymbol{I}$ is nonnegative. By the Perron–Frobenius theorem, this new matrix $\boldsymbol{A} + \alpha \boldsymbol{I}$ has a unique, real-valued leading eigenvalue, λ_δ.

We know from the standard eigenvalue-eigenvector equation that

$$(\boldsymbol{A} + \alpha \boldsymbol{I})\boldsymbol{x} = \lambda_\delta \boldsymbol{x},$$

which can be rewritten as

$$\boldsymbol{A}\boldsymbol{x} = (\lambda_\delta - \alpha)\boldsymbol{x} = \lambda_\gamma \boldsymbol{x},$$

where $\lambda_\gamma = \lambda_\delta - \alpha$ is real-valued and is an eigenvalue of $\boldsymbol{A}$.

To prove that λ_γ is leading, we need to show that all the other eigenvalues $\{\phi_1, \ldots, \phi_{n-1}\}$ of $\boldsymbol{A}$ have real part less than λ_γ ($\mathrm{Re}(\phi_i) < \lambda_\gamma$). Since ϕ_i is an eigenvalue of $\boldsymbol{A}$, $\phi_i + \alpha$ is an eigenvalue of $\boldsymbol{A} + \alpha \boldsymbol{I}$. By the Perron–Frobenius theorem, we know that

$$|\phi_i + \alpha| < \lambda_\delta = \lambda_\gamma + \alpha.$$

By the triangle inequality, and the fact that α is real and positive,

$$|\phi_i + \alpha| \leq |\phi_i| + |\alpha| = |\phi_i| + \alpha < \lambda_\gamma + \alpha \implies |\phi_i| < \lambda_\gamma.$$

Since $\mathrm{Re}(\phi_i) \leq |\phi_i|$, then $\mathrm{Re}(\phi_i) < \lambda_\gamma$. ∎

Appendix C. Combinatorial argument for the field of the leading eigenvalue in scaled competitive systems.

Below we provide a combinatorial argument for the number of possible arrangements that result in either leading real- or complex-valued eigenvalues in scaled competitive systems. By Perron–Frobenius, the leading eigenvalue of a scaled mutualistic system is always real-valued. Therefore, the minimal eigenvalue in a scaled competitive system is real-valued, as described in section 3. Consider an ordered set of eigenvalues associated with an $n \times n$ scaled competitive matrix. Since we know that the minimal eigenvalue must be real-valued, there remain $n - 1$ eigenvalues which can either be a single real value, or a complex value that must lie adjacent to its complement.

For example, given a 6×6 competitive matrix, we have eight possibilities for the ordering of the eigenvalues. With c denoting a single complex-valued eigenvalue, and r denoting a real-valued eigenvalue, then the possible combinations are $(rrcccc)$, $(rccrcc)$, $(rccccr)$, $(rrrrcc)$, $(rrrccr)$, $(rrccrr)$, $(rccrrr)$, and $(rrrrrr)$. Here, the ordering is based on the smallest eigenvalue (which we know is real-valued) located on the left and the largest (real part) eigenvalue on the right. This means that three of the possibilities have a complex-valued leading eigenvalue, while the remaining five possibilities have a real-valued leading eigenvalue.

Considering the possibilities from the smallest 2×2 matrices, we know that there must be at least one real-valued eigenvalue, and therefore there can be no complex-valued eigenvalue. We can denote this as $(0{:}1)$, where the first value denotes the total number of possibilities where there is a complex-valued leading eigenvalue and the second value denotes the total number of possibilities where there is a real-valued leading eigenvalue. There are two possibilities for 3×3 matrices: $\{(rcc), (rrr)\}$, so that the total number of complex- and real-valued possibilities is given as $(1{:}1)$. 4×4 matrices have one complex to two real possibilities, $(1{:}2)$, and 5×5 matrices have $(2{:}3)$. We saw above that 6×6 matrices are $(3{:}5)$, and continuing to 7×7 matrices, which are $(5{:}8)$, we get the beginning of a recurrent sequence: $\{(0:1), (1:1), (1:2), (2:3), (3:5), (5:8), \ldots\}$, each part of which should be familiar as the beginning of the Fibonacci numbers.

To generalize the above, we need to construct a combinatoric argument for the two forms (real- and complex-valued leading eigenvalue orderings). We start by placing the real-valued, minimal eigenvalue in the left-most position for all of the $n \times n$ orderings, leaving $n - 1$ positions free. When we consider each of the eigenvalue orderings containing a complex conjugate pair, we may reduce the number of spaces needed to be considered by 1. For example, in the $n = 6$ case, once one positions the real-valued left-most position, there are

five possible openings to place an eigenvalue. But if one positions a complex-valued eigenvalue, then there are only four possible openings where a conjugate pair (c, c) can be placed: $\{(r, r, r, r, c, c), (r, r, r, c, c, r), (r, r, c, c, r, r), (r, c, c, r, r, r)\}$. So for an $n \times n$ matrix, there are $n - 1 - 1$ places where one complex pair may be placed. Likewise, there are $n - 1 - 2$ positions where two complex pairs may be placed, $n - 1 - 3$ positions where three complex pairs may be placed, and so on. Finally, there is one possible eigenvalue ordering for the situation where all the eigenvalues are real, which may be added at the end. Therefore, the total number of possible eigenvalue orderings for all $n \times n$ matrices is given by

$$(\text{C.1}) \qquad p = \sum_{j=1}^{n-1-j \geq j} \binom{n-1-j}{j} + 1.$$

The number of cases where the leading eigenvalue is complex-valued is similarly argued. The simplest case would see all the positions containing real-valued eigenvalues, except for a leading complex conjugate pair, $(r, r, \ldots, r, c, c)$, found in all eigenvalue sets where $n \geq 3$ and added accordingly after the combinatorial sum. The remaining number of positions to be considered in an ordering after eliminating the left-most real-valued eigenvalue and the right-most complex conjugate pair is therefore $n - 1 - 2$. Following the argument as before we can now construct a function in which we successively add complex pairs and count their possible positions. For an additional complex pair (in addition to the leading pair), there will be $n - 1 - 2 - 1$ openings, and with two other sets of complex conjugate pairs there will be $n - 1 - 2 - 2$ openings, and so on. The number of orderings in which the leading eigenvalue is complex is

$$(\text{C.2}) \qquad q = \begin{cases} n = 2: & 0, \\ n \geq 3: & \sum_{j=1}^{n-3-j \geq j} \binom{n-3-j}{j} + 1. \end{cases}$$

Therefore, the recurrent sequence of complex-valued to real-valued leading eigenvalues is $(q : p - q)$ for a given n and where the successive set for $n + 1$ is $(p - q : p)$. Of course, this states nothing about the weighted likelihood for a given ordering.

Supplementary materials. The supplementary file containing the various community matrices depicted in Figure 1 are found in the accompanying file M135548_01.zip ([local/web 7.00KB]).

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