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Exact probabilities for the indeterminacy of complex networks as perceived through press perturbations

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Abstract We consider the goal of predicting how complex networks respond to chronic (press) perturbations when characterizations of their network topology and interaction strengths are associated with uncertainty. Our primary result is the derivation of exact formulas for the expected number and probability of qualitatively incorrect predictions about a system's responses under uncertainties drawn form arbitrary distributions of error. Additional indices provide new tools for identifying which links in a network are most qualitatively and quantitatively sensitive to error, and for determining the volume of errors within which predictions will remain qualitatively determinate (i.e. sign insensitive). Together with recent advances in the empirical characterization of uncertainty in networks, these tools bridge a way towards probabilistic predictions of network dynamics.

Keywords Press perturbations · Net effects · Loop analysis · Sign sensitivity · Qualitative indeterminacy · Ecosystem-based management · Community matrix · Intraguild predation · Trophic chain · Sherman–Morrison · Matrix perturbation · Inverse · Sign pattern

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1 Introduction

The need to understand and predict how complex networks respond to perturbations of their constituent entities pervades many disciplines, including applications in communications, human health, and fisheries management (Strogatz 2001; Ives and Carpenter 2007). Many of these perturbations involve sustained, chronic changes imposed on particular nodes of the network (a.k.a. 'press perturbations' Bender et al. 1984), which can propagate rapidly via both direct and indirect pathways. Ecosystem-based fisheries management, for example, entails the need to consider not only how alternative harvesting scenarios will alter the abundance of a particular focal species or stock, but also how such perturbations ripple through the ecosystem to affect non-targeted species (Travis et al. 2014).

Predicting how networks respond to press perturbations is hindered by a number of compounding sources of uncertainty (Petchey et al. 2015). It has long been appreciated, for example, that predictions can depend crucially on knowing both the network topology and the strengths of the interactions that connect each pair of species (Lawlor 1979; Yodzis 1988). Even low-complexity networks entail an inordinate number of indirect pathways (Borrett and Patten 2003). When combined with uncertainty in a network's topology and interaction strengths, these indirect pathways can quickly render a targeted perturbation's net effects as indeterminate, leaving little predictive certainty in the magnitude or even the sign (increase or decrease) of each species' ultimate response (Dambacher et al. 2002; Novak et al. 2011).

Here, our goal is to understand the effect of uncertainty on the steady state variation of a complex network presumed to be well-described by a system of ordinary differential equations. The variation of interest is either the quantitative or qualitative response of each system variable to a sustained perturbation of another system variable. More specifically, given a system of interacting variables defined by $\frac{dN_i}{dt} = f_i(\vec{N}) + u_i$ for i = 1, ..., n variables, we are interested in determining the sign or magnitude of $\frac{\partial N_i}{\partial u_j}$. In the context of ecological networks, N_i is the abundance of species i, $f_i(\vec{N})$ is a function describing the interactions between species i and a vector of other species, and u_i is a scalar representing a constant rate of external input to (or removal of) species i. The relationship between (the sign of) $\frac{\partial N_i}{\partial u_j}$ and the vector valued function \vec{f} encapsulates the (sign) sensitivity of a system's predicted dynamics to uncertainty in the species interactions. Qualitative indeterminacy refers to the situation when the direction of a species' response cannot be predicted without quantitative knowledge of \vec{f} .

Previous efforts to understand the sign sensitivity of ecological networks such as food webs have fallen into two primary categories. Both are based on the characterization of species interactions by means of the so-called Community matrix (Levins 1968), with $A_{i,j} = \frac{\partial f_i(\vec{N})}{\partial N_j}$ reflecting a Jacobian of the system's i = 1, ..., n population growth rate equations (Novak et al. 2016). Assuming asymptotically stable steady state conditions, the community matrix (when evaluated at or near the equilibrium) affords insight into a press perturbation u_j 's net propagation along all direct and indirect pathways by means of $-A^{-1} = \frac{\partial N_i}{\partial u_j}$ (Yodzis 1988). Each (i, j) entry of $-A^{-1}$

encapsulates a first-order approximation to the net change in species *i*'s steady state abundance due to a sustained increase in species *j*'s population growth rate, assuming no bifurcations are incurred (Novak et al. 2016). The elements of $-A^{-1}$ are related to how species are expected to respond to perturbations of their abundances (Lawlor 1979), per capita growth rates (Barabás et al. 2014), and carrying capacities (Levins 1968) by a scaling relationship between diagonal and off-diagonal matrix elements (Novak et al. 2016).

Tractable algebraic insight into $\frac{\partial N_i}{\partial u_i}$ (e.g., Dambacher et al. 2002; Cortez and Abrams 2016) is limited to small networks. Hence, beginning with Levins (1974), the first approach, typically referred to as 'loop analysis' or 'qualitative modeling', has been to focus on the influence of network topology alone by specifying the elements of A by their sign (i.e. $A_{i,i} = 1, 0, \text{ or } - 1$). On this basis, it was reasoned in Dambacher et al. (2002, 2003) that the relative frequency of positive and negative feedback loops between species provides insight into the likelihood of observing a net increase or decrease for a given species in response to a press perturbation elsewhere in its network. That is, net effects emanating from a near equal summation of positive and negative feedback loops are inferred to be more qualitatively indeterminate than are net effects that are dominated by one or the other. The approach is widely used (Carey et al. 2014; Marzloff et al. 2016), with benefits including the ability to more easily analyze alternative network topologies, and that empirical estimates of interaction strength are unnecessary. Drawbacks include the need to compute the matrix permanent of A for the total summation of feedback loops, which quickly becomes computationally challenging for large networks (Jerrum et al. 2004; Novak et al. 2011). Furthermore, simulations have shown that the 'weighted feedback matrix', which encapsulate the metric of positive versus negative feedback loops, quickly loses utility as its entries rapidly diminish to values of zero, implying complete indeterminacy, as network complexity increases (Novak et al. 2011). Extensions of the approach help to reduce this indeterminacy in applications where prior information or knowledge of a subset of net effects is available (Hosack et al. 2008; Raymond et al. 2011).

Beginning with Yodzis (1988), the second approach has been to assume that network topology and some aspect of the quantitative elements of A are known, and to use simulations to assess the sign sensitivity of $-A^{-1}$ to uncertainty in A. For example, Dambacher et al. (2003), Melbourne-Thomas et al. (2012), Raymond et al. (2011) used simulations in which the values of A were drawn from predefined (typically uniform) distributions, interpreting the most frequently observed sign of each entry in the resultant $-A^{-1}$ matrices as the most probable perturbation response. Others have used simulations to compare the sign structure of $-A^{-1}$ given an assumed 'true' A to those produced after introducing varying degrees of error to the elements of A, randomly drawing these errors from log-uniform distributions (Novak et al. 2011; Iles and Novak 2016). The benefits of such 'quantitative models' include consideration of the extreme variation of the $A_{i, i}$ magnitudes that is known to occur in nature (Wootton and Emmerson 2005), and that this approach typically exhibits less qualitative indeterminacy on average, given the assumed ranges of uncertainty, than do corresponding 'qualitative models' (Dambacher et al. 2002; Novak et al. 2011). However, the approach provides less clarity into the contribution of topology and requires extensive simulations or permutation tests to achieve insight. Recently, Giordano et al. (2016) have developed an algorithm for determining which entries of A are sign insensitive (qualitatively determinate) to quantitative uncertainty on the assumption that a BDC decomposition of A is possible.

Here we provide exact formulas for the expected number and probability of making qualitatively incorrect predictions about a system's responses given by $-A^{-1}$ when the entries of A are associated with error drawn from arbitrary distributions. Assessments of alternative network topologies, as considered by loop analysis, may be considered as special cases of these error distributions. Our approach does not rest on simulations or algorithms for determining indeterminacy. Focusing on two particularly illustrative network motifs—a four-species trophic chain (TC) and a four-species intraguild predation (IGP) motif (Fig. 1)—which are pervasive in food webs (Stouffer et al. 2007), we provide computationally accessible methods for determining which entries of A are most sensitive to error, and for determining the magnitude and volume of entrywise errors that will incur no sign switches for any distribution of errors. That is, we focus on identifying the entries of A that need to be estimated most accurately in order to avoid a sign switch somewhere in $-A^{-1}$, rather than identifying the location of entries that switch sign, which is also possible with our approach but not pursued here. The methods we develop enable us to demonstrate and explain the seemingly counterintuitive result that, for the parameterizations owing to Takimoto et al. (2007), Novak et al. (2016), the TC motif is in fact more quantitatively sensitive than is the IGP motif, despite the TC motif being entirely sign insensitive to any error in its $A_{i,i}$ entries. We relate this result to the variance of the entries of $-A^{-1}$ as well as to the singular values and the variance of the entries of A, which reflect a system's asymptotic stability (Allesina and Tang 2012). Note that, for consistency with the mathematical literature, we henceforth use the term *perturbation* to refer to an error of magnitude ϵ in the entries of A (i.e. $A_{i,i} + \epsilon_{i,i}$).

The results we obtain are organized as follows: Sect. 3 is dedicated to investigating the case when a single entry of A is perturbed. We begin in Sect. 3.1 by applying the well-known Sherman–Morrison formula for the inverse of a rank 1 perturbation of a matrix. This allows us obtain an inequality that determines when the sign of the (i, j) entry of the inverse of the perturbed matrix differs from the sign of the (i, j) entry of the inverse of the unperturbed matrix. Using this, we calculate explicitly the probability of a sign switch in the (i, j) entry of the inverse when the perturbation is taken according to some arbitrary distribution. In Sect. 3.2, we then study the limiting behavior of the total number of sign switches in the inverse of the perturbed matrix as the perturbation grows to infinity and explicitly quantify how large the perturbation must be to reach this limiting number of sign switches. We also numerically determine the expected fraction of sign switches using independent Gaussian matrices and compare this with the two motivating motif examples. In Sect. 3.3, we investigate how perturbing a single entry of a given matrix affects the norm of the inverse, relative to the norm of the inverse of the unperturbed matrix. We use the entry-wise (vectorized) 1norm and the (spectral) 2-norm to investigate these characterizations of quantitative sensitivity.



Fig. 1 a The four-species trophic chain (TC) network motif and **b** the intraguild predation (IGP) network motif depicted as signed digraphs. *Arrowheads* and *circles* respectively indicate the positive and negative direct effects between species as encapsulated by *A*. Following Novak et al. (2016), we let $A_{1,1} = -0.237$, $A_{2,2} = A_{3,3} = A_{4,4} = -0.015$, $A_{1,2} = A_{2,3} = A_{3,4} = -1$ and $A_{2,1} = A_{3,2} = A_{4,3} = 0.1$ for both motifs, and $A_{2,4} = -1$ and $A_{4,2} = 0.045$ for the IGP motif. All other entries are set to zero

In Sect. 3.4, we investigate the case of perturbing multiple entries of *A*. Utilizing an iterative application of the Sherman–Morrison formula, we show how to obtain a system of inequalities that describes when sign switches will occur in the inverse of the perturbed matrix. Looking at the region of "perturbation space" where no sign switch occurs gives an indication of the "sign sensitivity" of the matrix, and we define two indices reflecting this quantity.

In Sect. 4, we derive conditions on a tridiagonal matrix that ensure that the sign pattern of the inverse of the matrix depends only on the sign pattern of the original matrix. This defines a class of matrices in which arbitrary perturbations (as long as they don't change the sign pattern of the original matrix) will *not* cause the inverse of the perturbed matrix to have a different sign pattern than that of the inverse of the unperturbed matrix. The trophic chain (TC) motif provides an illustrative special case.

Finally, in Sect. 5, we provide an indication of why the IGP motif exhibits a high proclivity for switching signs under any set of perturbations, as is demonstrated in Sect. 3.4. We accomplish this by illustrating a way to decompose this matrix into a sum of terms that can be individually analyzed using the techniques developed in Sects. 3 and 4.

Throughout this paper, unless otherwise stated, we assume that A is invertible and that for $A_{i,j}^{-1}$, the (i, j) entry of A^{-1} , we have $-A_{i,j}^{-1} \neq 0$ for each *i* and *j*. When we consider a perturbation by another matrix B, we assume that A + B is invertible. We typically think of A as a square, $n \times n$ real matrix. For notational simplicity, we consider A^{-1} and not $-A^{-1}$ as this choice does not effect the determination of a sign switch.

2 Motivating examples

Consider a four-species system (Fig. 1b) described by the following set of differential equations:

$$f_{1} = \frac{dN_{1}}{dt} = I + (r_{1} + a_{1,2}N_{2})N_{1}$$

$$f_{2} = \frac{dN_{2}}{dt} = (r_{2} + a_{2,1}N_{1} + a_{2,2}N_{2} + a_{2,3}N_{3} + a_{2,4}N_{4})N_{2}$$

$$f_{3} = \frac{dN_{3}}{dt} = (r_{3} + a_{3,2}N_{2} + a_{3,3}N_{3} + a_{3,4}N_{4})N_{3}$$

$$f_{4} = \frac{dN_{4}}{dt} = (r_{4} + a_{4,2}N_{2} + a_{4,3}N_{3} + a_{4,4}N_{4})N_{4}$$
(2.1)

with $a_{i,j}, r_i, I \in \mathbb{R}$ and where at time $t \in \mathbb{R}$ the abundance of species *i* is given by $N_i(t) \in \mathbb{R}$ (Takimoto et al. 2007; Novak et al. 2016). The $a_{i,j}, r_i$, and *I* parameters respectively represent the per capita strengths of the species' interactions, the species' intrinsic per capita growth (death) rates, and a density-independent influx to the basal species.

The direct effects between each pair of species can be given in terms of this system's Jacobian with $A_{ij} = \frac{\partial f_i}{\partial N_i}$:

$$A = \begin{pmatrix} A_{1,1} & A_{1,2} & 0 & 0\\ A_{2,1} & A_{2,2} & A_{2,3} & A_{2,4}\\ 0 & A_{3,2} & A_{3,3} & A_{3,4}\\ 0 & A_{4,2} & A_{4,3} & A_{4,4} \end{pmatrix}.$$
 (2.2)

The structural form of the equations given in (2.1) and summarized in the matrix A in (2.2) (with variable $A_{i,j}$'s) is referred to as the intraguild predation motif (or IGP motif). A realization of this motif is given by fixing values for the $A_{i,j}$. Given fixed values for all $A_{i,j}$, the sign pattern of $-A^{-1}$ is equivalent to the sign pattern of adj(-A).

Given fixed values for the $A_{i,j}$'s, we wish to study the change in $-A^{-1}$ as a function of perturbing (adding error to) the $A_{i,j}$'s: replacing $A_{i,j}$ with $A_{i,j} + \epsilon$ representing the uncertainty in the value of $A_{i,j}$. Note that the sign pattern of $-A^{-1}$ can be derived from that of A^{-1} . For example, using a realization of the IGP motif given by

$${}^{\text{IGP}}\!A = \begin{pmatrix} -0.237 & -1 & 0 & 0\\ 0.1 & -0.015 & -1 & -1\\ 0 & 0.1 & -0.015 & -1\\ 0 & 0.045 & 0.1 & -0.015 \end{pmatrix}$$
(2.3)

implies that

$${}^{\text{IGP}}\!A^{-1} = \begin{pmatrix} 12.05 & 38.56 & -44.24 & 378.95 \\ -3.86 & -9.14 & 10.49 & -89.81 \\ 1.67 & 3.97 & -4.70 & 48.96 \\ -0.41 & -0.97 & 0.12 & -9.72 \end{pmatrix},$$
(2.4)

reflecting the response of the species in row *i* to a press perturbation of the species in column *j*. For comparison, perturbing the (4, 2) entry of ^{IGP}A by an error of -0.04 leads to

$$A_{\epsilon}^{-1} = \begin{pmatrix} -0.68 & 8.40 & -9.63 & 82.52 \\ -0.84 & -1.99 & 2.28 & -19.56 \\ 0.029 & 0.069 & -0.23 & 10.66 \\ -0.084 & -0.20 & -0.77 & -2.12 \end{pmatrix},$$

demonstrating that such a perturbation leads to a sign change in two entries of the perturbed system (entries (1, 1) and (4, 3), while remaining asymptotically stable.

For illustrative comparisons to the IGP motif, we use the following realization of the trophic chain motif (Fig. 1a):

$${}^{\mathrm{Tri}}A = \begin{pmatrix} -0.237 & -1 & 0 & 0\\ 0.1 & -0.015 & -1 & 0\\ 0 & 0.1 & -0.015 & -1\\ 0 & 0 & 0.1 & -0.015 \end{pmatrix}.$$
 (2.5)

Note that ^{Tri}A is obtained from ^{IGP}A by setting $A_{2,4} = A_{4,2} = 0$.

3 Sign switches of the inverse of an arbitrary matrix under perturbation

We begin by introducing our technique for determining the number of sign switches that perturbations in the entries of A will incur. To compute the inverse of the sum of two matrices $(A + B)^{-1}$ when the inverse of one, say A^{-1} , is known, we use a result of Miller (1981). Here, we think of B as a perturbation of A.

Theorem 3.1 [Lemma 1 of Miller (1981)] Let A and A + B be nonsingular matrices where B is rank one. Let $g = \text{tr}(BA^{-1}) = \sum_{i,j} B_{j,i}A_{i,j}^{-1}$. Then $g \neq -1$ and

$$(A+B)^{-1} = A^{-1} - \frac{1}{1+g}A^{-1}BA^{-1}.$$
(3.1)

This formula is also known as the Sherman–Morrison formula. Note that a variety of perturbations can be expressed as the addition of a rank one matrix *B*. Indeed, the Sherman–Morrison formula holds for any perturbation of the form $B = w^t \cdot v$ where w and v are row vectors and the superscript "t" denotes the transpose (Eq. (5.2) gives such an example). We, however, will mainly be concerned with perturbing a single entry as perturbing multiple entries can be combined by using Theorem 3.9 below.

3.1 Perturb single entry

We apply Theorem 3.1 in the case of perturbing a single entry of the matrix A. That is, for $\delta_{k,l}$ being the matrix (of same size as A) of zeros save a single 1 in the (k, l) entry and zero otherwise, $B = \epsilon \delta_{k,l}$ where ϵ is the magnitude of the perturbation. Applying Theorem 3.1, we have the (i, j) entry of $(A + \epsilon \delta_{k,l})^{-1}$ given by:

$$(A + \epsilon \delta_{k,l})_{i,j}^{-1} = A_{i,j}^{-1} - \frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{1 + \epsilon A_{l,k}^{-1}}.$$
(3.2)

Upon dividing by $A_{i,i}^{-1}$, this leads to the following Lemma:

Lemma 3.2 Given a fixed invertible matrix A and an invertible perturbation $A + \epsilon \delta_{k,l}$ such that for each *i*, *j*, $A_{i,j}^{-1} \neq 0$ and that $A_{l,k}^{-1} \neq \frac{-1}{\epsilon}$, the (*i*, *j*)th entry of A^{-1} will have a different sign from the (*i*, *j*)th entry of $(A + \epsilon \delta_{k,l})^{-1}$ if and only if

$$1 - \frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} \left(1 + \epsilon A_{l,k}^{-1}\right)} < 0.$$
(3.3)

In words, this means that an error to the direct effect of species l on species k will cause a qualitatively incorrect prediction to be made for the net effect of any jth species on any ith species if and only if the ratio of: 1. the product of the error and the net effects of k on i and of j on l, and 2. the net effect of j on i times one plus the product of the error and the net effect of k on l, is greater than 1.

If ϵ is not a fixed quantity but rather drawn according to some distribution, then Lemma 3.2 can be utilized to calculate the probability of a sign switch in the (i, j)th entry of $(A + \epsilon \delta_{k,l})^{-1}$. For notational simplicity, let $C = A^{-1}$, then assuming that ϵ is drawn from a uniform distribution on [0, 1], and, for example, assuming that $C_{l,k} < -1$ and $C_{i,j} < 0$, we have the probability that $A_{i,j}^{-1}$ differs in sign from $(A + \epsilon \delta_{k,l})_{i,j}^{-1}$ given by 1 - p where p has the value:

$$p = \begin{cases} 1 + \frac{1}{C_{l,k}}, & \text{if } (C_{i,k} < 0 \lor C_{l,j} > 0) \land \\ (C_{i,k} > 0 \lor C_{l,j} \le 0) \land \frac{C_{i,k}C_{l,j}}{C_{i,j}} \le C_{l,k} + 1 \\ -\frac{C_{i,j}}{C_{i,k}C_{l,j} + C_{i,j}C_{l,k}} - \frac{1}{C_{l,k}}, & \text{if } (C_{i,k} > 0 \land C_{l,j} \le 0) \lor \\ (C_{i,k} < 0 \land C_{l,j} > 0) \\ -\frac{C_{i,j}}{C_{i,j}C_{l,k} + C_{i,k}C_{l,j}} + \frac{1}{C_{l,k}}, & \text{Otherwise.} \end{cases}$$

Observe that this formula is explicitly given in terms of the entries of $C = A^{-1}$.

Furthermore, if ϵ is a random variable, one can use the expression in Eq. (3.3) to define another random variable indicating if a sign switch has occurred:

$$\mathbb{1}_{\text{switch}(A,\epsilon,i,j,k,l)} = \begin{cases} 1, & \text{if } 1 - \frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} (1 + \epsilon A_{l,k}^{-1})} < 0\\ 0, & \text{if } 1 - \frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} (1 + \epsilon A_{l,k}^{-1})} > 0. \end{cases}$$
(3.4)

Summing over *i* and *j* will return the number of sign switches that have occurred in A^{-1} when perturbing the (k, l) entry of *A* by magnitude ϵ :

$$NS(A, \epsilon, k, l) = \sum_{i,j} \mathbb{1}_{switch(A, \epsilon, i, j, k, l)}.$$
(3.5)

Note that the number of switches $NS(A, \epsilon, k, l)$ is a deterministic (non-random) function of A and ϵ . For fixed k, l, and A, the value of $NS(A, \epsilon, k, l)$ is an integer. Hence, for random ϵ , calculating the expected number of sign switches can be accomplished as follows: Let f_{ϵ} be the probability density function of the random variable ϵ , then the expected total number of sign switches in A^{-1} when perturbing the (k, l) entry by a magnitude given by (the random variable) ϵ is given by:

$$\mathbb{E}(\mathrm{NS}(A,\epsilon,k,l)) = \int \mathrm{NS}(A,x,k,l) f_{\epsilon}(x) \, dx.$$
(3.6)

Remark 1 In order to give biologically meaningful results, the probability density f_{ϵ} should only be supported on those values where the resulting Jacobian has eigenvalues with negative real part in order to guarantee the asymptotic stability of the system. Furthermore, the probability density used in NS(A, ϵ, k, l) should be zero whenever the signs of $A_{k,l}$ and $A_{k,l} + \epsilon$ differ. Such a probability density is utilized in the examples below. Note, however, that the function NS(A, ϵ, k, l) is still defined for ϵ values where the system is unstable.

The contrapositive of Theorem 3.1 can be used to facilitate finding the interval of single-entry perturbation values that contains zero and maintains the asymptotic stability of the matrix A. In particular, consider perturbing a single entry $A_{k,l}$ with $sign(A_{k,l}) = sign(A_{k,l} + \epsilon)$. Then the largest interval I of perturbation values ϵ that cause $(A + \epsilon \delta_{k,l})$ to remain asymptotically stable satisfies:

$$I \subseteq \begin{cases} \begin{bmatrix} -A_{k,l}, \frac{-1}{A_{l,k}^{-1}} \end{bmatrix} & \text{if } A_{k,l} > 0 \text{ and } A_{k,l}^{-1} < 0 \\ \begin{bmatrix} \frac{-1}{A_{l,k}^{-1}}, -A_{k,l} \end{bmatrix} & \text{if } A_{k,l} < 0 \text{ and } A_{k,l}^{-1} > 0 \end{cases}$$

with other such interval estimates possible for other combinations of signs of $A_{k,l}$ and $A_{l,k}^{-1}$.

Remark 2 Picturing the number of switches $NS(A, \epsilon, k, l)$ as a function of ϵ for various k and l reveals which entries (k, l) cause the most sign switches in A^{-1} when they are perturbed. For example, the number of expected sign switches as a function of



Fig. 2 The number of sign switches as a function of the error in the (k, l) entry of ^{IGP}A for (k, l) = (4, 3) and (k, l) = (2, 3). Overlain on these are truncated normal probability distributions which are non-zero only when the corresponding system is stable. These error distributions describe an illustrative and empirically-likely case of errors being clustered around $A_{k,l}$ but not changing its sign. Such a distribution of errors for the two entries respectively results in getting approximately 8 and 5% of predictions in $-A^{-1}$ being qualitatively incorrect

 ϵ for the matrix ^{IGP}A from Eq. (2.3) is illustrated in Fig. 2. Also shown in Fig. 2 is an illustrative distribution for $\epsilon_{k,l}$: For the (k, l) entry, we numerically calculate the interval $I_{k,l}$ of $\epsilon_{k,l}$ values (containing zero) for which A is asymptotically stable and $A_{k,l}$ and $A_{k,l} + \epsilon_{k,l}$ do not differ in sign. We then let f_{ϵ} be the probability density corresponding to the truncated normal distribution with variance $|I_{k,l}|/2$.

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It follows that the expected fraction of sign switches, over all n^2 entries in the matrix, is given by:

$$\frac{1}{n^2} \mathbb{E} \left(\text{NS} \left(A, \epsilon, k, l \right) \right)$$
(3.7)

For the example matrix ^{IGP}A, this leads to:

$$\frac{1}{4^2} \mathbb{E}\left(\mathrm{NS}\left({}^{\mathrm{IGP}}A, \epsilon, 4, 3\right)\right) = 0.081$$
$$\frac{1}{4^2} \mathbb{E}\left(\mathrm{NS}\left({}^{\mathrm{IGP}}A, \epsilon, 2, 3\right)\right) = 0.048.$$

This means, for example, that perturbing the (4, 3) entry in ^{IGP}A according to the aforementioned distribution will cause an average of 8.1% of the predictions to be qualitatively incorrect.

In Fig. 3 we include heat maps of the percent of expected sign switches $100\% \times \frac{1}{4^2}\mathbb{E}(NS(A, \epsilon, k, l))$ over all k and l for each example matrix. The distribution over which the expectation is taken is given in Remark 2. Figure 3a illustrates that the qualitative dynamics of the TC motif realization are entirely sign insensitive to any quantitative uncertainty in ^{Tri}A. Figure 3b illustrates, for example, how the qualitative dynamics of the IGP motif realization are less sign sensitive to uncertainty in top-down direct effect of the top-predator (species 4) on the intermediate consumer (species 3) (i.e. $A_{3,4}$) as compared to uncertainty in the reciprocal bottom-up effect of the intermediate dynamics of the IGP motif realization (i.e. $A_{4,3}$). Figure 3b similarly illustrates how the qualitative dynamics of the IGP motif realization (i.e. $A_{4,3}$). Figure 3b similarly illustrates how the qualitative dynamics of the IGP motif realization are generally less sign sensitive to uncertainty in the interspecific interactions (off-diagonal elements) than in the species' self-effects (diagonal elements). These insights are to be compared to the quantitative response sensitivities illustrated in Fig. 5.

3.2 Limiting value of NS

In this section, we focus on describing the behavior of the number of sign switches $NS(A, \epsilon, k, l)$ as $\epsilon \to \pm \infty$ and quantify how large ϵ must be to reach this limiting value. Before describing the limiting behavior, we prove a Lemma that gives an expression for $NS(A, \epsilon, k, l)$. In the following, we often use the *k*-minors of a matrix, defined as follows.

Definition 3.1 (*k*-*Minors*) For an $n \times n$ matrix A, an integer k < n, unique integers $1 < i_1, i_2, \ldots, i_k \le n$, and unique integers $1 \le j_1, j_2, \ldots, j_k \le n$, let $A_{[i_1 \cdots i_k, j_1 \cdots j_k]}$ be the sub-matrix of A obtained by deleting rows i_1 through i_k and columns j_1 through j_k . By a *k*-minor, we mean a determinant of the form det $(A_{[i_1 \cdots i_k, j_1 \cdots j_k]})$. By a minor, we mean a 1-minor (i.e. determinant after deleting one row and one column).

We first note that for certain values of *i* and *j*, the inequality in Eq. (3.3) reduces to an expression not involving *i* or *j*. As a consequence, depending only on the perturbation magnitude ϵ and the size of the entry $A_{l,k}^{-1}$, perturbing the entry in the *k*th row and *l*th

 ^{Tri}A



(a)

Lemma 3.3 For an invertible $n \times n$ matrix A such that no entry of A^{-1} is zero, for $1 \le i, j, k, l \le n$ such that i = l, or j = k, or $det(A_{[ki,lj]}) = 0$, then the expression

Fig. 3 Heat maps for the

average percent of sign switches (defined in Eq. (3.7)) induced by perturbation of each (k, l) entry.

$$1 - \frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} \left(1 + \epsilon A_{l,k}^{-1}\right)} < 0$$
(3.8)

is true if and only if the logical expression

$$\left(\epsilon < 0 \text{ and } A_{l,k}^{-1} > \frac{-1}{\epsilon}\right) \text{ or } \left(\epsilon > 0 \text{ and } A_{l,k}^{-1} < \frac{-1}{\epsilon}\right)$$
 (3.9)

is true.

This result implies that once an error associated with the direct effect of species l on species k causes a qualitatively incorrect prediction to be made for *any one* of the network's net effects that either emanate from species k or affect species l, then *all* predictions for the net effects emanating from k and affecting l will be qualitatively incorrect (and hence can be corrected by making the opposite qualitative prediction).

Proof The proof of this Lemma is via computation utilizing Lemma 3.2. Namely, when i = l,

$$1 - \frac{\epsilon A_{l,k}^{-1} A_{l,j}^{-1}}{A_{l,j}^{-1} \left(1 + \epsilon A_{l,k}^{-1}\right)} = 1 - \frac{\epsilon A_{l,k}^{-1}}{1 + \epsilon A_{l,k}^{-1}}.$$
(3.10)

Note that $1 - \frac{\epsilon A_{l,k}^{-1}}{1 + \epsilon A_{l,k}^{-1}} < 0$ if and only if either $\epsilon < 0$ and $A_{l,k}^{-1} > \frac{-1}{\epsilon}$ or $\epsilon > 0$ and $A_{l,k}^{-1} < \frac{-1}{\epsilon}$. A similar calculation takes care of the case when j = k. In the case that det $(A_{[ki,lj]}) = 0$, by Theorem 2.5.2 in Prasolov (1994), det $(A_{[ki,lj]}) = 0$ if and only if $A_{i,k}^{-1}A_{l,j}^{-1} = A_{i,j}^{-1}A_{l,k}^{-1}$, hence

$$1 - \frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} \left(1 + \epsilon A_{l,k}^{-1}\right)} = 1 - \frac{\epsilon A_{i,j}^{-1} A_{l,k}^{-1}}{A_{i,j}^{-1} \left(1 + \epsilon A_{l,k}^{-1}\right)} = 1 - \frac{\epsilon A_{l,k}^{-1}}{1 + \epsilon A_{l,k}^{-1}}$$
(3.11)

which, as before, is less than zero if and only if either $\epsilon < 0$ and $A_{l,k}^{-1} > \frac{-1}{\epsilon}$ or $\epsilon > 0$ and $A_{l,k}^{-1} < \frac{-1}{\epsilon}$.

This Lemma allows us to obtain an expression for NS(A, ϵ, k, l) by separating the terms where det($A_{[ki,lj]}$) = 0. In the following, let $N(k, l) = |\{1 \le i, j \le n : i \ne l, j \ne k, \det(A_{[ki,lj]}) = 0\}|$ be the number of 2-minors equal to zero involving the *k*th row and *l*th column (with $i \ne l$ and $j \ne k$).

Theorem 3.4 For an invertible $n \times n$ matrix A such that no entry of A^{-1} is zero, and for $1 \le k, l \le n$, and $\epsilon \in \mathbb{R}$,

$$NS(A, \epsilon, k, l) = \sum_{\substack{i \neq l \\ j \neq k \\ \det(A_{[ki,lj]}) \neq 0}} \mathbb{1}_{\left\{\frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} (1 + \epsilon A_{l,k}^{-1})} > 1\right\}}$$
(3.12)
+ $(2n - 1 + N(k, l)) \mathbb{1}_{\left\{\left(\epsilon < 0 \land A_{l,k}^{-1} > \frac{-1}{\epsilon}\right) \lor \left(\epsilon > 0 \land A_{l,k}^{-1} < \frac{-1}{\epsilon}\right)\right\}}$

This Theorem allows us to determine the limiting behavior of the number of switches $NS(A, \epsilon, k, l)$. In particular, after a certain point, increasing the magnitude of the perturbation ϵ no longer causes a sign switch in the inverse of the perturbed matrix when compared to the original matrix.

Corollary 3.5 For an invertible $n \times n$ matrix A such that no entry of A^{-1} is zero, and for $1 \le k, l \le n$, if $\epsilon_1, \epsilon_2 \in \mathbb{R}$ such that

$$|\epsilon_{1}|, |\epsilon_{2}| > \max_{\substack{i \neq l \\ j \neq k \\ \det(A_{[ki,lj]}) \neq 0}} \left| \frac{A_{i,j}^{-1}}{A_{i,k}^{-1}A_{l,j}^{-1} - A_{i,j}^{-1}A_{l,k}^{-1}} \right|$$

then

$$NS(A, \epsilon_1, k, l) = NS(A, \epsilon_2, k, l).$$

In particular, when $sign(\epsilon_1) = sign(A_{k,l})$ (i.e. the error changes the magnitude of $A_{k,l}$ but not its sign), we have

$$NS(A, \epsilon_{1}, k, l) = \sum_{i \neq l, j \neq k: det(A_{[ki,lj]}) \neq 0} \mathbb{1} \left\{ \frac{A_{i,k}^{-1}A_{l,j}^{-1}}{A_{i,j}^{-1}A_{l,k}^{-1}} \right\}$$

$$+ (2n - 1 + N(k, l)) \mathbb{1} \left\{ sign(A_{l,k}^{-1}) \neq sign(A_{k,l}) \right\}.$$
(3.13)

Proof First, note that as a function of ϵ , the quantity $\frac{\epsilon A_{l,k}^{-1} A_{l,j}^{-1}}{A_{l,j}^{-1}(1+\epsilon A_{l,k}^{-1})}$ is monotonic (depending on the sign of $\frac{A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1}}$) with a discontinuity at $\epsilon = -\frac{1}{A_{l,k}^{-1}}$. Furthermore, $\frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1}(1+\epsilon A_{l,k}^{-1})} = 1$ if and only if $\epsilon = \frac{1}{\frac{A_{i,k}^{-1} A_{l,j}^{-1}}{A_{l,j}^{-1}} - A_{l,k}^{-1}} = \frac{A_{i,j}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} - A_{l,k}^{-1}}$. Now we know

that

$$\lim_{\epsilon \to \pm \infty} \frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} \left(1 + \epsilon A_{l,k}^{-1}\right)} = \frac{A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} A_{l,k}^{-1}},$$
(3.14)

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hence, for $i \neq l, j \neq k$ and such that $det(A_{[ki,lj]}) \neq 0$, we have that as long as

$$|\epsilon_{1}| > \max_{\substack{i \neq l \\ j \neq k \\ \det(A_{[ki,lj]}) \neq 0}} \left| \frac{A_{i,j}^{-1}}{A_{i,k}^{-1}A_{l,j}^{-1} - A_{i,j}^{-1}A_{l,k}^{-1}} \right|$$

we have that

$$\frac{A_{i,k}^{-1}A_{l,j}^{-1}}{A_{i,j}^{-1}A_{l,k}^{-1}} > 1 \quad \text{if and only if} \quad \frac{\epsilon_1 A_{i,k}^{-1}A_{l,j}^{-1}}{A_{i,j}^{-1}\left(1+\epsilon_1 A_{l,k}^{-1}\right)} > 1. \tag{3.15}$$

Combining this with the definition given in line (3.5) proves the first part of the Corollary. The second part of the Corollary is proved by applying this observation to Theorem 3.4 and noting that as $|\epsilon| \to \infty$, the expression $(\epsilon < 0 \land A_{l,k}^{-1} > \frac{-1}{\epsilon}) \lor (\epsilon > 0 \land A_{l,k}^{-1} < \frac{-1}{\epsilon})$ is true if and only if sign $(A_{l,k}^{-1}) \neq \text{sign}(\epsilon) = \text{sign}(A_{k,l})$.

A useful application of Corollary 3.5 is when the matrix *A* has all its entries drawn independently from a continuous distribution, such as the standard normal distribution (i.e. each entry of *A* is drawn from an independent standard normal random variable). In the limit, the expected fraction of entries that experience a sign switch has an especially compact representation. Here, we do not concern ourselves with asymptotic stability of the matrices utilized as we wish only to understand the behavior of NS over a background distribution of matrices.

Corollary 3.6 For an $n \times n$ matrix A with entries drawn independently from a continuous distribution (such as independent standard normal random variables), the asymptotic expected fraction of sign switches is given by

$$\lim_{n \to \infty} \lim_{|\epsilon| \to \infty} \mathbb{E}_A \left(\text{NS}(A, \epsilon, k, l) \right) / n^2 = \lim_{n \to \infty} \frac{1}{n^2} \sum_{i, j=1}^n \mathbb{P} \left(\frac{A_{i,k}^{-1} A_{l,j}^{-1}}{A_{i,j}^{-1} A_{l,k}^{-1}} > 1 \right).$$
(3.16)

Thus, for a matrix with size approaching infinity with all entries drawn independently from a standard normal distribution, the proportion of qualitatively incorrect predictions can be expressed in a form that eases theoretical and computational calculations.

Proof For fixed *k* and *l*, the set of matrices *A* such that there exist *i*, *j* such that det($A_{[ki,lj]}$) = 0 has positive codimension in the set of all real, invertible $n \times n$ matrices and hence has probability zero for the continuous distribution under consideration. Hence the quantity (2n - 1 + N(k, l)) in line (3.13) is equal to 2n - 1 corresponding to the cases i = l or j = k. However, since $\frac{2n-1}{n^2} \to 0$ as $n \to \infty$, applying the expectation to Corollary 3.5 leads to the result.

Remark 3 Unfortunately, it appears not to be straightforward to exactly compute the quantity $\mathbb{P}\left(\frac{A_{i,k}^{-1}A_{l,j}^{-1}}{A_{i,j}^{-1}A_{l,k}^{-1}} > 1\right)$ for each *i*, *j*. Nevertheless, the expression in Eq. (3.16) does



Fig. 4 Histogram of $\frac{1}{n^2}$ NS(A, ϵ, k, l) obtained by sampling A with independent standard normal entries and evaluating the right hand side of Eq. (3.16) 7000 times using n = 200, k = 25, and l = 70. The probability density function for a beta (3.4088, 6.7448) distribution is overlaid this histogram as a *blue line* (color figure online)

give a convenient way to sample the limiting expected fraction of switches (as the right hand side is free from the perturbation value ϵ). To demonstrate, we fixed n = 200 and k = 25, l = 70 and computed the right hand side of Eq. (3.16) for 7000 draws of matrices with independent standard normal entries. The resulting distribution is show in Fig. 4 and does not appear to depend significantly on the chosen k and l. Interestingly, the average percent of sign switches in this computation was approximately 33%, and the resulting distribution appears to be similar to a beta distribution (shown in Fig. 4 with a blue line) indicating that further simplifications of (3.16) may be possible.

In comparison, even for small n such as when n = 4, using Corollary 3.5, the mean (averaged over k and l and 5000 draws of a entry-wise independent standard normal distribution) expectation of signs switches is give by,

$$\lim_{|\epsilon|\to\infty} \frac{1}{4^2} \sum_{k,l} \mathbb{E}_A \left(\text{NS}(A,\epsilon,k,l) \right) \approx 0.33$$

We compare this value to our two example network motifs. For these it only makes sense to perturb the non-zero entries (k, l) such that $A_{k,l} \neq 0$, and only such that $sign(\epsilon) = sign(A_{k,l})$. For the trophic chain motif, ^{Tri}A, for each k and l,

$$\lim_{\epsilon \to \infty} \operatorname{NS}\left(\operatorname{Tri} A, \operatorname{sign}\left(\operatorname{Tri} A_{k,l}\right) \epsilon, k, l\right) = 0.$$

Hence, no sign switches will occur for any choice of non-zero (k, l) entries; the trophic chain is entirely sign insensitive to error in its $A_{k,l}$ magnitudes (see also Fig. 3a). The reason for this is given in Theorem 4.2.

In contrast, for the intraguild predation motif ^{IGP}A the average (over all non-zero k and l) fraction of sign switches is given by using Corollary 3.5 which results in:

$$\lim_{\epsilon \to \infty} \frac{1}{12} \sum_{k,l \text{ s.t. } IGP_{A_{k,l} \neq 0}} \frac{1}{4^2} NS\left({}^{IGP}A, \operatorname{sign}\left({}^{IGP}A_{k,l}\right)\epsilon, k, l\right) = 0.427,$$

showing that for this matrix, perturbing a single entry leads to a higher average fraction of sign switches than is expected on average when using independent standard normal distributions for the entries. An explanation for this is given in Sect. 5.

3.3 How perturbation affects the norm of the inverse

We now aim to investigate how perturbing a single entry in *A* affects the norm of the inverse. We do this for a few different norms, each useful in describing how *quantitatively* different the inverse of the perturbed matrix is from the inverse of the unperturbed matrix (i.e. how sensitive predictions of species' quantitative responses are to error in *A*). Recall our standing assumptions that *A* is invertible, for each *i* and j, $A_{i,j}^{-1} \neq 0$, and when we consider a perturbation by another matrix *B*, we assume that A + B is invertible.

3.3.1 Entry-wise 1-norm

We first investigate the effect perturbation has on the entry-wise (vectorized) 1-norm. We use the atypical notation $||A||_T$ to emphasize that this means the *total* absolute value of the entries of the matrix A, and to differentiate it from the operator 1-norm $||A||_1$.

Definition 3.2 For an $n \times m$ matrix A, let

$$||A||_{\mathrm{T}} = \sum_{i=1}^{n} \sum_{j=1}^{m} |A_{i,j}|.$$

A few other matrix norms will be helpful:

Definition 3.3 Let A be an $n \times m$ matrix, and $1 \le p \le \infty$. Then the operator p-norm of A is given by

$$||A||_p = \max_{x \neq 0} \frac{||Ax||_p}{||x||_p}$$

where $|| \cdot ||_p$ is the standard vector *p*-norm.

Recall that $||A||_1 = \max_{1 \le j \le n} \sum_{i=1}^n |A_{i,j}|$ is the maximum absolute column sum of A and $||A||_{\infty} = \max_{1 \le i \le n} \sum_{j=1}^n |A_{i,j}|$ is the maximum absolute row sum of A.

Remark 4 In this section, we do not incorporate the asymptotic stability of the perturbed matrix as we aim to study arbitrarily large perturbations. This will result in a global indication of how perturbation affects change in the value of a given norm. It is also straightforward to demonstrate that the norm expressions considered (such as in Eq. (3.19) below) can, as functions of ϵ , be decomposed to be piecewise monotone with at most three pieces, so estimation of the norm as $\epsilon \to \infty$ provides bounds for any other perturbation value (such as when the perturbations are restricted to those that retain asymptotic stability).

As $|\epsilon|$ approaches infinity, the entry-wise 1-norm (total magnitude) of the difference between A^{-1} and the perturbed matrix (i.e. the difference in the total summed responses of all species) reaches a (finite) fixed value. Indeed, using Eq. (3.2) we find that

$$||A^{-1} - (A + \epsilon \delta_{k,l})^{-1}||_{\mathrm{T}} = \sum_{i,j=1}^{n} \left| A_{i,j}^{-1} - (A + \epsilon \delta_{k,l})_{i,j}^{-1} \right|$$
(3.17)

$$=\sum_{i,j=1}^{n} \left| \frac{\epsilon A_{i,k}^{-1} A_{l,j}^{-1}}{1 + \epsilon A_{l,k}^{-1}} \right|$$
(3.18)

$$= \left| \frac{\epsilon}{1 + \epsilon A_{l,k}^{-1}} \right| \sum_{i=1}^{n} |A_{i,k}^{-1}| \sum_{j=1}^{n} |A_{l,j}^{-1}|$$
(3.19)

$$\xrightarrow[\epsilon \to \pm \infty]{} \frac{1}{|A_{l,k}^{-1}|} \sum_{i=1}^{n} |A_{i,k}^{-1}| \sum_{j=1}^{n} |A_{l,j}^{-1}|.$$
(3.20)

This means that quantitative sensitivity is reduced by having the absolute value of the net effect of k on l be large relative to the sum of k's absolute net effects on all species and the sum of the absolute net effects of all species on l.

Further estimations are possible, including the observation that Eq. (3.20) implies that

$$\lim_{\epsilon \to \infty} ||A^{-1} - (A + \epsilon \delta_{k,l})^{-1}||_{\mathsf{T}} \le \frac{1}{|A_{l,k}^{-1}|} ||A^{-1}||_1 ||A^{-1}||_{\infty}.$$

Similarly, if all entries of *A* are nonzero, summing the relative total magnitude differences gives:

$$\lim_{\epsilon \to \infty} \sum_{k,l} \frac{\|A^{-1} - (A + \epsilon \delta_{k,l})^{-1}\|_{\mathrm{T}}}{\|A^{-1}\|_{\mathrm{T}}} = \|A^{-1}\|_{\mathrm{T}} \|1/A^{-1}\|_{\mathrm{T}}$$

where by $1/A^{-1}$ we mean the matrix whose (i, j) entry is equal to $\frac{1}{A_{i,j}^{-1}}$. This leads to the following measure of quantitative sensitivity of a matrix:

Definition 3.4 For an invertible $n \times n$ matrix A, let M be the number of non-zero entries in A: $M = |\{(i, j) \text{ s.t. } A_{i,j} \neq 0\}|$. By the magnitude response sensitivity, we mean

$$MRS(A) = \frac{1}{M \cdot ||A^{-1}||_{T}} \sum_{k,l \text{ s.t. } A_{k,l} \neq 0} \frac{1}{|A_{l,k}^{-1}|} \sum_{i=1}^{n} |A_{i,k}^{-1}| \sum_{j=1}^{n} |A_{l,j}^{-1}|.$$
(3.21)

The quantity MRS(*A*) gives the mean (averaged over all individually perturbed entries) relative total magnitude difference between the inverse of the unperturbed matrix and the inverse of the matrix resulting from letting one entry be perturbed in an arbitrarily large fashion. Note that for matrices with no zero entries, the quantity MRS(*A*) is minimized for matrices *A* with all entries equal in absolute value: any minimizer of the quantity $||A^{-1}||_T||1/A^{-1}||_T$ has the property that $A^{-1} = aD$ for $a \in \mathbb{R}$ and *D* an invertible matrix with entries in the set $\{-1, 1\}$. Conversely, matrices *A* with large variation (in absolute value) in their entries will exhibit large values of MRS(*A*), and hence larger quantitative sensitivity.

Using this definition, we can calculate the average (over all perturbed k and l) total relative error between A^{-1} and $(A + \epsilon \delta_{k,l})^{-1}$. For ^{Tri}A, we have that

$$\mathrm{MRS}\left(^{\mathrm{Tri}}A\right) = 3.53.$$

This indicates that, on average, perturbing (to infinity) a single nonzero entry of $^{\text{Tri}A}$ will result in the values of the inverse being off by factor of approximately 3.53 when compared to the unperturbed matrix. For $^{\text{IGP}}A$, we find that

$$\mathrm{MRS}\left(^{\mathrm{IGP}}A\right) = 1.63.$$

This indicates that, on average, perturbing (to infinity) a single nonzero entry of ^{IGP}A will result in the values of the inverse being off by a factor of only approximately 1.63 when compared to the unperturbed matrix.

Hence, while ^{IGP}A is more sign sensitive to large ϵ perturbations (see the remark at the end of Sect. 3.2), the matrix ^{Tri}A exhibits significantly less total change in magnitude when perturbed; the trophic chain is more quantitatively sensitive to error than is the intraguild predation motif. Figure 5, where the individual relative errors $\lim_{\epsilon \to \infty} \frac{||A^{-1} - (A + \epsilon \delta_{k,l})^{-1}||_{T}}{||A^{-1}||_{T}}$ are depicted in a heat map for each k and l, visualizes which entries are the cause of this quantitative sensitivity. For example, the quantitative dynamics of the trophic chain are clearly most sensitive to uncertainty in the top-down effect of species 3 (the intermediate consumer) on the primary consumer (species 2) (i.e. $A_{2,3}$), and relatively insensitive to uncertainty in the reciprocal interaction of these two species (i.e. $A_{3,2}$). Compare this to the qualitative sensitivities shown in Fig. 3. **Fig. 5** Heat maps for the (quantitative) magnitude response sensitvity between the perturbed and unperturbed matrices:

 $\lim_{\epsilon \to \infty} \frac{||A^{-1} - (A + \epsilon \delta_{k,l})^{-1}||_{\mathrm{T}}}{||A^{-1}||_{\mathrm{T}}}.$ **a** The trophic chain motif. **b** The

a The topinc chain holf. B The intraguild predation motif. The average quantitative relative error of the intraguild predation motif is roughly half as large as the average quantitative relative error of the trophic chain



3.3.2 Spectral norm

We now study how perturbing the matrix A affects the spectral norm ($|| \cdot ||_2$ from Definition 3.3) of the inverse matrix. While the spectral norm has no clear ecological interpretation, our goal is to relate the spectral norm of $A^{-1} - (A + \epsilon \delta_{k,l})^{-1}$ with the singular values of A whose importance and properties are well known. We first define our notation.

Definition 3.5 (*Singular values*) For a real matrix $A \in \mathbb{R}^{\times m}$ the singular values $\sigma_i(A)$ are the square roots of the eigenvalues of $A^T A$ listed (with their multiplicities) in non-increasing order

$$\sigma_1(A) \ge \sigma_2(A) \ge \cdots \ge \sigma_n(A).$$

We will at times write $\sigma_{\max}(A)$ and $\sigma_{\min}(A)$ for $\sigma_1(A)$ and $\sigma_n(A)$ respectively. Recall that the spectral norm $||A||_2$ is equal to the dominant singular value: $||A||_2 = \sigma_1(A)$. We will also have need of the Frobenius norm.

Definition 3.6 (*Frobenius norm*) For a real matrix $A \in \mathbb{R}^{m \times n}$, let

$$||A||_F = \left(\sum_{i=1}^m \sum_{j=1}^n |A_{i,j}|^2\right)^{1/2}$$

Recall that for any matrix $A \in \mathbb{R}^{m \times n}$, $||A||_F = \left(\sum_{i=1}^{\min\{m,n\}} \sigma_i(A)^2\right)^{1/2}$ and so $||A||_2 \le ||A||_F$ with equality if and only if A is rank 1.

We aim to sum the norm $||A^{-1} - (A + \epsilon \delta_{k,l})^{-1}||_2$ over all *k* and *l* entries to thereby estimate the Euclidean distances between the unperturbed and perturbed inverse matrices. We consider the ecologically realistic case where we only perturb the non-zero entries of *A* and ensure that the perturbation to the (k, l) entry does not change the sign of $A_{k,l}$. Hence, when perturbing the (k, l) entry, let t > 0 be a variable real number and define $\epsilon_{k,l}(t) = \text{sign}(A_{k,l})t$, recalling that for a scalar *x*, sign(*x*) is equal to 1 if x > 0, -1 if x < 0, and 0 if x = 0.

Theorem 3.7 Let $A \in \mathbb{R}^{n \times n}$ be an invertible real matrix such that for each $k, l = 1, ..., n, A_{k,l}^{-1} \neq 0$. Let $t \in \mathbb{R}_{>0}$ and for each k, l = 1, ..., n, let $\epsilon_{k,l}(t) = \text{sign}(A_{k,l})t$. Then

$$\lim_{t \to \infty} \sum_{k,l=1}^{n} \left| \left| A^{-1} - \left(A + \epsilon_{k,l}(t) \delta_{k,l} \right)^{-1} \right| \right|_{2}^{2} \le \max_{k,l} \frac{1}{|A_{k,l}^{-1}|^{2}} \left(\sum_{i=1}^{n} \frac{1}{\sigma_{i}(A)^{2}} \right)^{2}$$

This means that the maximum difference between the inverse of the perturbed and the inverse of the unperturbed matrix (as quantified by the spectral norm) is inversely related to the absolute values of the inverse of the unperturbed matrix and to the singular values of the unperturbed matrix.

Proof Observe that the matrix with (i, j) entry equal to $\frac{\epsilon A_{l,k}^{-1} A_{l,k}^{-1}}{1+\epsilon A_{l,k}^{-1}}$, has rank equal to 1 as it is equal to a scalar times an outer product involving a column and a row of A^{-1} . Combining this fact with Theorem 3.1 allows us to relate the spectral norm of $A^{-1} - (A + \epsilon \delta_{k,l})^{-1}$ with the Frobenius norm of the outer product of the *k*th column and *l*th row of A^{-1} . Calculating:

$$\sum_{k,l=1}^{n} \left\| A^{-1} - \left(A + \epsilon_{k,l}(t) \delta_{k,l} \right)^{-1} \right\|_{2}^{2}$$
(3.22)

$$=\sum_{k,l=1}^{n}\sum_{i,j=1}^{n}\left\|\left|A_{i,j}^{-1}-\left(A_{i,j}^{-1}-\frac{\epsilon_{k,l}(t)A_{i,k}^{-1}A_{l,j}^{-1}}{1+\epsilon_{k,l}(t)A_{l,k}^{-1}}\right)\right\|_{2}^{2}$$
(3.23)

$$=\sum_{k,l=1}^{n}\sum_{i,j=1}^{n}\left|\frac{\epsilon_{k,l}(t)A_{i,k}^{-1}A_{l,j}^{-1}}{1+\epsilon_{k,l}(t)A_{l,k}^{-1}}\right|^{2}$$
(3.24)

$$=\sum_{k,l=1}^{n} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^{2} \sum_{i,j=1}^{n} \left| A_{i,k}^{-1}A_{l,j}^{-1} \right|^{2}$$
(3.25)

$$\leq \max_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 \sum_{k,l=1}^n \sum_{i,j=1}^n \left| A_{i,k}^{-1} A_{l,j}^{-1} \right|^2$$
(3.26)

$$= \max_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 \sum_{i,k=1}^n \left| A_{i,k}^{-1} \right|^2 \sum_{l,j=1}^n \left| A_{l,j}^{-1} \right|^2$$
(3.27)

$$= \max_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 \left| \left| A^{-1} \right| \right|_F^4$$
(3.28)

$$= \max_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 \left(\sum_{i=1}^n \sigma_i (A^{-1})^2 \right)^2.$$
(3.29)

Recalling that we defined $\epsilon_{k,l}(t) = \operatorname{sign}(A_{k,l})t$, we have

$$\lim_{t \to \infty} \max_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t) A_{l,k}^{-1}} \right|^2 = \lim_{t \to \infty} \max_{k,l} \left| \frac{t}{1 \pm t A_{l,k}^{-1}} \right|^2 = \max_{k,l} \frac{1}{|A_{k,l}^{-1}|^2}.$$

Finally, using the fact that $\sigma_i(A^{-1}) = 1/\sigma_i(A)$ for all *i*, and taking the limit as $t \to \infty$, the result follows.

In the case where no entry of A is zero, we have a lower bound as well.

Theorem 3.8 Let $A \in \mathbb{R}^{n \times n}$ be an invertible real matrix such that for each k, l = 1, ..., n, both $A_{k,l} \neq 0$ and $A_{k,l}^{-1} \neq 0$. Let $t \in \mathbb{R}_{>0}$ and for each k, l = 1, ..., n, let $\epsilon_{k,l}(t) = \operatorname{sign}(A_{k,l})t$. Then

$$\lim_{t \to \infty} \sum_{k,l=1}^{n} \left\| \left| A^{-1} - \left(A + \epsilon_{k,l}(t) \delta_{k,l} \right)^{-1} \right\|_{2}^{2} \ge \min_{k,l} \frac{1}{|A_{k,l}^{-1}|^{2}} \frac{1}{\sigma_{\min}(A)^{4}}.$$

Therefore, the minimum difference between the inverse of the perturbed and the inverse of the unperturbed matrix (as quantified by the spectral norm) is also inversely related

to the absolute values of the inverse of the unperturbed matrix (as in Theorem 3.7) and to the smallest singular value of the unperturbed matrix.

Proof The proof follows from a calculation similar to that in the proof of Theorem 3.7:

$$\sum_{k,l=1}^{n} \left\| \left| A^{-1} - \left(A + \epsilon_{k,l}(t) \delta_{k,l} \right)^2 \right\|_2^2$$
(3.30)

$$=\sum_{k,l=1}^{n}\sum_{i,j=1}^{n}\left|\frac{\epsilon_{k,l}(t)A_{i,k}^{-1}A_{l,j}^{-1}}{1+\epsilon_{k,l}(t)A_{l,k}^{-1}}\right|^{2}$$
(3.31)

$$=\sum_{k,l=1}^{n} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^{2} \sum_{i,j=1}^{n} |A_{i,k}^{-1}|^{2} |A_{l,j}^{-1}|^{2}$$
(3.32)

$$\geq \min_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 ||A^{-1}||_F^4$$
(3.33)

$$\geq \min_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 ||A^{-1}||_2^4$$
(3.34)

$$= \min_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 \sigma_{\max}(A^{-1})^4$$
(3.35)

$$= \min_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1 + \epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 \frac{1}{\sigma_{\min}(A)^4}.$$
 (3.36)

Since each entry of *A* is nonzero, this implies that for all *k*, *l*, $\epsilon_{k,l}(t) = \operatorname{sign}(A_{k,l})t$, and hence $\lim_{t\to\infty} \min_{k,l} \left| \frac{\epsilon_{k,l}(t)}{1+\epsilon_{k,l}(t)A_{l,k}^{-1}} \right|^2 > 0$. Taking limits as $t \to \infty$ leads to the result.

3.4 Perturbing multiple esntries

Up to this point we have assumed that only a single entry of A is perturbed at a time. However, in most applications, multiple if not all entries will have some level of uncertainty associated. Fortunately, Theorem 3.1 can be applied iteratively to compute $(A + B)^{-1}$ when B is of rank r by writing B as a sum of rank 1 matrices. This leads to the following result:

Theorem 3.9 [Theorem 1 of Miller (1981)] Let A and A + B be nonsingular matrices where $B = B_{(1)} + \cdots + B_{(r)}$ has rank r and each $B_{(i)}$ has rank 1 for $i = 1, \ldots, r$. Let $C_{(k+1)} = A + B_{(1)} + \cdots + B_{(k)}$ for $k = 1, \ldots, r$ and $C_{(1)} = A$. Then with $g_{(k)} = \frac{1}{1 + \operatorname{tr}(C_{(k)}^{-1}B_{(k)})}$,

$$C_{(k+1)}^{-1} = C_{(k)}^{-1} - g_{(k)}C_{(k)}^{-1}B_{(k)}C_{(k)}^{-1}.$$

In particular,

$$(A+B)^{-1} = C_{(r)}^{-1} - g_{(r)}C_{(r)}^{-1}B_{(r)}C_{(r)}^{-1}.$$

Utilizing Theorem 3.9 allows one to programmatically compute the inverse of $(A + B)^{-1}$, an arbitrary set of perturbations of the matrix A with any entry $B_{i,j} = \epsilon_{i,j}$ being either a fixed real number or a suitably chosen random variable. This allows results similar to Lemma 3.2 to be obtained through the assistance of a computer algebra system. Similarly, formulas for the generalization of the number of switches NS and the expected number of switches $\mathbb{E}(NS)$, while notationally unwieldy, are computationally straightforward to utilize, as they still only depend on the entries of A^{-1} and the values of $B_{i,j} = \epsilon_{i,j}$.

3.4.1 Index of sign sensitivity

We next perturb more than one entry to obtain an index of sign sensitivity which characterizes the overall proclivity of an arbitrary perturbation to cause sign switches in the inverse of the perturbed matrix. We motivate this using our example motifs, recalling for convenience that the definition of ^{IGP}A given in Eq. (2.3) is:

$${}^{\text{IGP}}\!A = \begin{pmatrix} -0.237 & -1 & 0 & 0\\ 0.1 & -0.015 & -1 & -1\\ 0 & 0.1 & -0.015 & -1\\ 0 & 0.045 & 0.1 & -0.015 \end{pmatrix}.$$
 (3.37)

We first consider a perturbation to ^{IGP}A of B, defined by

$$B = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \epsilon_{2,4} \\ 0 & 0 & 0 & 0 \\ 0 & \epsilon_{4,2} & 0 & 0 \end{pmatrix},$$
 (3.38)

where $\epsilon_{2,4}$ and $\epsilon_{4,2}$ range over the given intervals. This case is ecologically relevant and is illustrative to consider as it represents the case where all entries of ^{IGP}A are known exactly, except the (2, 4) and (4, 2) entries, and where the signs of these entries are known, but where their magnitudes are allowed to vary over an arbitrarily chosen interval. Applying Theorem 3.9 allows one to obtain a (large) formula for the inverse of ^{IGP}A + B.

To illustrate, we focus on the (1, 1) entry of $(^{IGP}A + B)^{-1}$ and compare this to the (1, 1) entry of $(^{IGP}A)^{-1}$ to see what values of $\epsilon_{2,4}$ and $\epsilon_{4,2}$ cause the sign of this entry to switch. Utilizing a computer algebra system and Theorem 3.9, we find that the (1, 1) entry will not switch sign when either of the following two inequalities are satisfied:



Fig. 6 Depiction of the region where the perturbation values $\epsilon_{2,4}$ and $\epsilon_{4,2}$ cause a sign switch in the (1, 1) entry of $\left({}^{\text{IGP}}A + B\right)^{-1}$ in comparison to the sign of the (1, 1) entry of $\left({}^{\text{IGP}}A\right)^{-1}$. Values of $\epsilon_{2,4} > 1$ and $\epsilon_{4,2} < -0.045$ are not biologically relevant because they alter the sign structure of *A*, but are depicted here for clarity. Note that the motif ${}^{\text{Tr}i}A$ corresponds to the highlighted special case where the two errors are of equal magnitude but opposite in sign to their respective entries in ${}^{\text{IGP}}A$. Hence this depiction also represents an assessment of alternative network topologies

$$\frac{142.392}{3\epsilon_{2,4}+197} - 0.712 < \epsilon_{4,2} < -\frac{0.000025(85400\epsilon_{2,4}+250573)}{3\epsilon_{2,4}+197}$$

or
$$-\frac{0.000025(85400\epsilon_{2,4}+250573)}{3\epsilon_{2,4}+197} < \epsilon_{4,2} < \frac{142.39}{3\epsilon_{2,4}+197} - 0.712.$$

Plotting the region where this expression is false leads to a depiction of the *region of* sign sensitivity (i.e. sign indeterminacy): the region where values of $\epsilon_{2,4}$ and $\epsilon_{4,2}$ cause a sign switch in the (1, 1) entry of the perturbation $(^{IGP}A + B)^{-1}$ when compared to the (1, 1) entry of $(^{IGP}A)^{-1}$ (Fig. 6).

For general *A*, we can generalize the approach to where $B_{ij} = \epsilon_{ij}$ is a matrix of same size as *A* with each $\epsilon_{i,j}$ taking on values in a given interval (while still preserving the sign of A + B in comparison to *A*) and consider the resulting inequalities for all entries of $(A + B)_{ij}^{-1}$. Comparing the volume of the region where this systems of inequalities is not all true to the total volume of the perturbation space leads to an index of *sign sensitivity*:

Definition 3.7 Given a fixed invertible $m \times n$ matrix A and an $m \times n$ matrix with entries $B_{i,j} = \epsilon_{i,j}$ whose values range over the region $\mathcal{R} \subset \mathbb{R}^{m+n}$, let S be the subregion in \mathcal{R} satisfying:

$$(\epsilon_{1,1},\ldots,\epsilon_{m,n}) \in \mathbb{S} \iff \exists i, j, (A+B)_{i,i}^{-1}$$
 has the opposite sign as $A_{i,i}^{-1}$. (3.39)

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Then define the sign sensitivity of A as

$$SS(A) = \frac{\operatorname{vol}(S)}{\operatorname{vol}(\mathcal{R})}.$$
(3.40)

This index is interpreted as the percentage of perturbation space in which some entry of the perturbed matrix inverse $(A + B)^{-1}$ changes sign in comparison to A^{-1} . This definition can be extended by incorporating a probability distribution over \mathcal{R} (and subsequently S as well):

Definition 3.8 Given a fixed invertible $m \times n$ matrix A and an $m \times n$ matrix with entries $B_{i,j} = \epsilon_{i,j}$ whose values range over the region $\mathcal{R} \subset \mathbb{R}^{m+n}$ according to the multivariate distribution \mathcal{D} supported on \mathcal{R} . Let \mathcal{S} be the subregion in \mathcal{R} satisfying:

$$(\epsilon_{1,1},\ldots,\epsilon_{m,n}) \in \mathbb{S} \iff \exists i, j, (A+B)_{i,j}^{-1}$$
 has the opposite sign as $A_{i,j}^{-1}$. (3.41)

Then define the distributional sign sensitivity of A as

$$SS_{\mathcal{D}}(A) = \mathbb{P}_{\mathcal{D}}(S) \tag{3.42}$$

Due to Theorem 3.9 and the subsequent discussion, both SS(A) and $SS_{\mathcal{D}}(A)$ can be computed explicitly and hence efficiently via Monte-Carlo sampling.

For example, for \mathcal{D} being the product of independent uniform distributions over intervals of length 0.01 that do not change the signs of the original matrix A and set to zero when the perturbation causes the system to become asymptotically unstable, we calculate the distributional sign sensitivity of ^{IGP}A to be

$$\mathrm{SS}_{\mathcal{D}}\left(^{\mathrm{IGP}}A\right)\approx 0.37,$$

indicating that approximately 37% of all perturbation values incur sign changes in $(^{IGP}A)^{-1}$ due to this error distribution. Equivalently, this means if each $\epsilon_{i,j}$ is a uniform random variable in the interval $[-^{IGP}A_{i,j}, 1 - ^{IGP}A_{i,j}]$ for $^{IGP}A_{i,j} > 0$ and $[-1 - ^{IGP}A_{i,j}, - ^{IGP}A_{i,j}]$ for $^{IGP}A_{i,j} < 0$, and a point mass on 0 if $^{IGP}A_{i,j} = 0$, then the probability of at least one sign switch occurring in $(^{IGP}A + B)^{-1}$ in comparison to $(^{IGP}A)^{-1}$ is equal to 0.37.

In comparison, for the trophic chain motif $^{\text{Tri}}A$ and a similarly defined distribution \mathcal{D} ,

$$SS_{\mathcal{D}}\left(^{Tri}A\right) = 0.$$

This corresponds to Theorem 4.2 wherein we show that for this topology, the signs of the inverse do not depend on the magnitudes of the $A_{i,j}$ entries. Note that, just as in Corollary 3.6, the index of distributional sign sensitivity may be applied using any other distributions of errors as well.

4 The sign sensitivity of tridiagonal matrices

The trophic chain motif corresponds to a tridiagonal matrix. We will subsequently utilize this fact for decomposing networks to understand their sensitivity. In this Section we therefore investigate the qualitative sensitivity of tridiagonal matrices.

A number of authors have derived explicit formulas for the inverse of a tridiagonal matrix (Usmani 1994a, b; Fonseca 2007; Lewis 1982). We use the notation of Fonseca (2007) for the following Theorem:

Theorem 4.1 [Lemma 3 of Usmani (1994b)] *Given an* $n \times n$ *nonsingular tridiagonal matrix*

$$T = \begin{pmatrix} a_1 & b_1 & & & \\ c_1 & a_2 & b_2 & & \\ & c_2 & \ddots & \ddots & \\ & & \ddots & \ddots & b_{n-1} \\ & & & c_{n-1} & a_n \end{pmatrix},$$
(4.1)

let θ_i *satisfy the recurrence relation*

$$\theta_i = a_i \theta_{i-1} - b_{i-1} c_{i-1} \theta_{i-2}, \quad i = 2, \dots, n$$
(4.2)

with initial conditions $\theta_0 = 1$, $\theta_1 = a_1$. Let ψ_i satisfy the recurrence relation

$$\psi_i = a_i \psi_{i+1} - b_i c_i \psi_{i+2}, \quad i = n - 1, \dots, 1$$
(4.3)

with initial conditions $\psi_{n+1} = 1$, $\psi_n = a_n$. Then

$$\left(T^{-1}\right)_{i,j} = \begin{cases} (-1)^{i+j} b_i \cdots b_{j-1} \theta_{i-1} \psi_{j+1} / \theta_n & \text{if } i \le j \\ (-1)^{i+j} c_j \cdots c_{i-1} \theta_{j-1} \psi_{i+1} / \theta_n & \text{if } i > j. \end{cases}$$

$$(4.4)$$

Using this result, we can demonstrate when no entry of T^{-1} will change sign as the elements of T are perturbed. For a given matrix A, by sign(A) we mean a matrix with (i, j)th entry equal to sign $(A_{i,j})$. We now show that for certain tridiagonal matrices T, the sign pattern of T^{-1} depends only on the sign pattern of T and not on the magnitudes of the entries of T.

Theorem 4.2 Let T be a nonsingular tridiagonal matrix as in Theorem 4.1 such that for all i and j, if $a_i \neq 0$ and $a_j \neq 0$, then $\operatorname{sign}(a_i) = \operatorname{sign}(a_j)$, and if $c_i \neq 0$ and $b_i \neq 0$, then $\operatorname{sign}(c_i) = -\operatorname{sign}(b_i)$. Then $\operatorname{sign}(T_{i,j}^{-1})$ can be calculated directly from $\operatorname{sign}(T)$.

In other words, the qualitative net effects between species in a trophic chain motif are determined completely by the topology of the motif and not by the magnitudes of the interaction strengths.

Proof We sketch the proof for the case where for all $i, a_i \le 0, b_i \le 0$, and $c_i \ge 0$ as the other cases proceed similarly. Using the same notation as in equation (4.1),

$$\theta_1 = a_1 \le 0 \tag{4.5}$$

$$\theta_2 = a_2\theta_1 - c_1b_1\theta_0 = \widetilde{a_2a_1} - \widetilde{c_1b_1} \ge 0$$
(4.6)

negative

$$\theta_3 = \overbrace{a_3\theta_2}^{\text{positive}} - \overbrace{c_2b_2\theta_1}^{\text{positive}} \le 0.$$
(4.7)

Continuing in this fashion, one can see that

$$\operatorname{sign}(\theta_i) = \begin{cases} 1 & \text{if } i \text{ is even} \\ -1 & \text{if } i \text{ is odd} \end{cases}$$
(4.8)

Proceeding in a similar fashion for ψ_i , one can observe that

$$\operatorname{sign}(\psi_i) = \begin{cases} 1 & \text{if } i \neq n \mod 2\\ -1 & \text{if } i \equiv n \mod 2 \end{cases}.$$
(4.9)

Thus, since $T_{i,j}^{-1}$ is equal to a product of terms whose signs do not depend on the magnitude of a_k , b_k , or c_k , the Theorem immediately follows.

For the matrix ^{Tri}A, this implies that if we perturb the entries of ^{Tri}A without changing their signs, the resulting inverse will have the same sign pattern as that of the inverse of the unperturbed matrix: $\operatorname{sign}\left(\binom{\operatorname{Tri}A}{l}^{-1}\right)$. This indicates why we previously found that the sign sensitivity $\operatorname{SS}_{\mathcal{D}}\left(\operatorname{Tri}A\right) = 0$, and that for any k, l, the value $\lim_{\epsilon \to \infty} \operatorname{NS}\left(\operatorname{Tri}A, \operatorname{sign}\left(\operatorname{Tri}A_{k,l}\right)\epsilon, k, l\right) = 0$. This insight extends to any linear chain of species interactions, including the motifs of apparent competition and exploitative competition (Holt 1977).

In terms of asymptotic stability, many ecologically relevant tridiagonal matrices *T* (as given in expression (4.1)) are asymptotically stable no matter the perturbation magnitude (while still preserving the sign pattern of *T*). Indeed, if *T* has a negative main diagonal and symmetric off-diagonal entries of opposite sign, we can define the diagonal matrix *M* by: $M_{1,1} = 1$, $M_{2,2} = \sqrt{\frac{c_1}{b_1}}$, $M_{n,n} = \sqrt{\frac{c_{n-1}c_{n-2}}{b_{n-1}b_{n-2}}}$ for n > 2, and $M_{i,j} = 0$ otherwise. Then *T* can be decomposed as $T = M^{-1}(S + D)M$ where *S* is a skew-symmetric matrix and *D* is a diagonal matrix with negative main diagonal. The eigenvalues of such matrices all have strictly negative real part (Horn and Johnson 2012).

5 The sign sensitivity of the IGP motif

In Sect. 3.4 it was seen that even slight perturbations of the entries of the ^{IGP}A matrix caused sign switches in it inverse (i.e. the sign sensitivity $SS_{\mathcal{D}}(^{IGP}A) \approx 0.37$). We

here provide the means to understand why this is so by combining the use of Theorems 3.1 and 4.1.

For convenience, recall that

$${}^{\text{IGP}}\!A = \begin{pmatrix} -0.237 & -1 & 0 & 0\\ 0.1 & -0.015 & -1 & -1\\ 0 & 0.1 & -0.015 & -1\\ 0 & 0.045 & 0.1 & -0.015 \end{pmatrix}.$$
 (5.1)

This matrix can be written as the sum of tridiagonal matrix plus a rank one matrix:

$${}^{\text{IGP}}A = \begin{pmatrix} -0.237 & -1 & 0 & 0\\ 0.1 & 0.435 & -1 & 0\\ 0 & 0.1 & -0.015 & -1\\ 0 & 0 & 0.1 & -1.015 \end{pmatrix} + \begin{pmatrix} 0\\ -1\\ 0\\ 1 \end{pmatrix} \cdot \begin{pmatrix} 0 & 0.045 & 0 & 1 \end{pmatrix}.$$
(5.2)

Let *T* be the tridiagonal matrix in this decomposition:

$$T = \begin{pmatrix} -0.237 & -1 & 0 & 0\\ 0.1 & 0.435 & -1 & 0\\ 0 & 0.1 & -0.015 & -1\\ 0 & 0 & 0.1 & -1.015 \end{pmatrix}$$
(5.3)

and let B be the rank one matrix which is the outer product of u and v,

$$u = \begin{pmatrix} 0\\-1\\0\\1 \end{pmatrix}$$
(5.4)

$$v' = \begin{pmatrix} 0 & 0.045 & 0 & 1 \end{pmatrix}$$
(5.5)

$$B = uv' = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & -0.045 & 0 & -1 \\ 0 & 0 & 0 & 0 \\ 0 & 0.045 & 0 & 1 \end{pmatrix}.$$
 (5.6)

The matrix *B* can therefore be thought of as a perturbation to a certain subset of entries in *A*, a situation that can be analyzed by the techniques developed in Sect. 3.4. We therefore also have $^{IGP}A = T + B$, such that the matrix ^{IGP}A can be viewed as a perturbation of the tridiagonal matrix *T*. Observe that Theorem 4.1 indicates that the signs of the entries of T^{-1} depend on the magnitude of the entries of *T*. This is due critically to the entry $T_{2,2} = 0.435$ which causes the entries on the main diagonal of *T* to *not* all have the same sign. It is because $T_{2,2}$ is positive that *T* is sign sensitive, as seen in the proof of Theorem 4.2. The addition of the rank 1 perturbation *B* makes ^{IGP}*A* even more sign sensitive (Sect. 3). Indeed, the decomposition of ^{IGP}*A* into *T* and *B* reveals that the sign sensitivity of ^{IGP}*A* would be most reduced by having the magnitude of $T_{4,2}$ be less than the magnitude of $T_{2,2}$ as then only the sign sensitivity of *B* would be of consequence. In contrast, perturbations to the $T_{2,4}$ entry will not affect the sign sensitivity of ^{IGP}*A* because $T_{2,4}$ has the same sign as $T_{4,4}$. In ecological terms, the sign sensitivity of the intraguild predation motif is driven by the sensitivity of the bottom-up effect of the basal resource on the top consumer rather than by the reciprocal top-down effect, which is consistent with our observations in Fig. 3.

More generally, utilizing Theorem 3.1, we have a formula for the inverse of ^{IGP}A:

$$\left({}^{\text{IGP}}A\right)^{-1} = (T+B)^{-1} = T^{-1} - \frac{1}{1+v'T^{-1}u}T^{-1}vv'T^{-1}.$$
 (5.7)

Since the signs of T^{-1} depend on the magnitudes of the entries of T, the above formula indicates that the signs of $(^{IGP}A)^{-1}$ must also depend on the magnitudes of the entries of ^{IGP}A . This is why the signs of the inverse of ^{IGP}A are sensitive to uncertainty in the entries of the original matrix.

6 Conclusions

The primary contributions of this work are four indices that characterize the qualitative and quantitative sensitivity of press perturbation responses to uncertainty (or intrinsic variation) in a system's interaction strengths and topology:

- 1. NS(A, ϵ, k, l), which denotes the number of sign switches incurred by an estimation error of magnitude ϵ to the (k, l) entry of A,
- the magnitude response sensitivity MRS(A), which quantifies the relative total magnitude difference between a system's true press perturbation responses and those predicted with estimation error, and
- the sign sensitivity indices SS(A) and SS_D(A), which quantify the percentage of possible error magnitude space in which at least one sign switch will occur, with error respectively considered as either a volume or a distribution of magnitudes.

The NS(A, ϵ , k, l) index, which underlies much of our approach, enables one to identify the most sensitive interactions within the network which must be estimated most accurately to produce qualitatively robust predictions. Importantly, these indices are exact and may be computed with relative ease, thereby obviating the need for simulations in assessing the indeterminacy of complex networks. A key advance is the separation of the estimation error magnitudes from their frequency distribution. Together with recent statistical advances in the empirical characterization of uncertainty in ecological networks (Wolf et al. 2015; Poisot et al. 2016), our study thereby bridges the way to probabilistic predictions of ecosystem dynamics (Novak et al. 2016).

Applications of the indices to two well-studied food web motifs provide a proof-ofconcept demonstration for how the indeterminacy of larger, truly complex networks

may be decomposed and understood. They also illustrate the useful insights the indices can provide. For example, the observation that the trophic chain realization is more quantitatively sensitive to uncertainty than is the intraguild predation realization, despite the trophic chain being entirely sign insensitive to any error, may be ascribed to the top-down link between the intermediate consumer and the secondary consumer (i.e. $TriA_{2,3}$, Fig. 5a). It is this interaction that will need to be estimated most accurately for accurate quantitative predictions to be made. Similarly, our approach also elucidates why the qualitative dynamics of the IGP realization are less sign insensitive to uncertainty in the top-down direct effect of the top-predator on the intermediate consumer $(^{IGP}A_{3,4})$ than to uncertainty in the reciprocal bottom-up effect of the intermediate consumer on the top-predator $(^{IGP}A_{4,2})$ as shown in Fig. 3b), and explained in Sect. 5). This particular insight indicates that qualitative predictions for this motif are more sensitive to error in the characterization of the top-predator's numerical response (i.e. the efficiency with which the predator converts consumed prey to offspring) than to error in the characterization of its functional response (i.e. the rate at which the predator consumes prey). Future work will need to address the degree to which this conclusion is dependent on the specific choice of parameters used in our example, or is general to the structure of the motif itself.

It is important to note that not all of our treatments of indeterminacy considered the stability and feasibility of the perturbed matrix. In interpreting the quantitative (norm) sensitivities of the ^{Tri}A and ^{IGP}A motifs we ignored the requirement that no bifurcations are affected by the addition of errors via *B*. The network properties that control these important attributes of complex networks remain an active area of research (Allesina and Tang 2012; Rohr et al. 2014). That these attributes are directly related to a network's quantitative sensitivity is evidenced by the influence of the singular values in determining the upper and lower bounds of the spectral norm difference between the inverse of the perturbed and unperturbed matrices (Theorems 3.8 and 3.7). Indeed, this observation suggests that a network's quantitative sensitivity may be of empirical use as an early warning indicator of bifurcation events across which qualitative predictions will surely be inaccurate (Novak et al. 2016; Scheffer et al. 2012).

More generally, our theorems highlight how the analysis of qualitative models (i.e. loop analysis) represents a special case of the analysis of quantitative models using our approach. As evidenced in Fig. 6, the assessment of alternative network topologies reflects the case in which the assumed magnitudes of the $\epsilon_{i,j}$ errors correspond exactly to the negative magnitudes of their respective $A_{i,j}$ elements. Likewise, the addition of new links corresponds to the perturbation of the zero entries of *A*. More specifically, alternative network topologies reflect alternative perturbations of each other, as illustrated in Sect. 5 by the decomposition of the intraguild predation motif into the trophic chain motif. The ability to characterize the region of parameter space within which no sign switches occur by analytical means (see Sect. 3.4) will thus be particularly useful in applications where quantitative estimates of interaction strengths are unavailable, enabling a more robust determination of the consequences of characterizing interactions by only their sign and a unit-magnitude strength.

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