What makes ecological systems reactive?

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ABSTRACT

Although perturbations from a stable equilibrium must ultimately vanish, they can grow initially, and the maximum initial growth rate is called reactivity. Reactivity thus identifies systems that may undergo transient population surges or drops in response to perturbations; however, we lack biological and mathematical intuition about what makes a system reactive. This paper presents upper and lower bounds on reactivity for an arbitrary linearized model, explores their strictness, and discusses their biological implications. I find that less stable systems (i.e. systems with long transients) have a smaller possible range of reactivities for which no perturbations grow. Systems with more species have a higher capacity to be reactive, assuming species interactions do not weaken too rapidly as the number of species increases. Finally, I find that in discrete time, reactivity is determined largely by mean interaction strength and neither discrete nor continuous time reactivity are sensitive to food web topology.

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1. Introduction

Traditionally, ecologists have focused on the long-term dynamics of ecological systems, such as the existence of equilibria and their stability. However, there is growing recognition that long-term dynamics may not be a good guide to short-term behavior. Even if an equilibrium or stage distribution is stable, a perturbation from that state may grow before subsiding, producing transient surges or drops in population levels. Furthermore, short-term behavior is important. A population surge may represent a pest outbreak, and a drop may put a population at risk of stochastic extinction. Additionally, since most experiments and monitoring programs observe only short-term dynamics, it is difficult to connect theory with experiment if theoretical predictions address only long-term behavior.

Reactivity, defined as the maximum initial rate at which a small perturbation can grow, is a common way to measure the tendency for perturbations to be amplified (Neubert and Caswell, 1997; Caswell and Neubert, 2005). Systems with positive reactivity are said to be reactive—some perturbations will grow. Reactivity gives a worst-case estimate: not all perturbations will grow so rapidly or even at all. Reactivity has been observed in models of food webs (Neubert and Caswell, 1997; Chen and Cohen, 2001; Rozdilsky et al., 2004), host-parasitoid systems (Caswell and Neubert, 2005), advective systems (Anderson et al., 2008), and invasibility (Marvier et al., 2004), while others have developed means for estimating reactivity from time series data (Ives et al., 2003; Neubert et al., 2009).

Can we develop our intuition about why some systems are reactive and about characteristics that might make a system prone to being reactive? Neubert et al. (2004) take us partway there by showing that a food web model must be reactive if there is at least one species with density-independent growth. Likewise, Neubert et al. (2002) have shown that systems with spatial patterns generated by Turing instabilities must be reactive. Are there other characteristics that signal reactivity?

After an introduction to reactivity, I present upper and lower bounds on reactivity and use these to understand what mathematical and biological characteristics promote reactivity. I then explore how strict these bounds are, using stochastic food web models. I have made the analysis as general as possible. We often lack a detailed understanding of a system's dynamics; this paper presents what can be inferred even in the absence of detailed knowledge. I consider linear systems with any number of species or life-history stages in discrete and continuous time. Linearized models have been widely used by both theorists and empiricists to describe dynamics near an equilibrium (Gurney and Nisbet, 1998; Caswell, 2001). (They are called "Jacobians" in the theoretical literature, "interaction matrices" or "community matrices" in some of the food web literature (e.g. May, 1973; Yodzis, 1988).)

Mathematically, I find that systems that are weakly stable and have strong interactions have a greater capacity to be reactive. These characteristics arise from the upper and lower bounds: reactivity is bounded from below by a perturbation's long-run growth rate, large Jacobian elements increase reactivity's upper bound, and in discrete time, large Jacobian elements also increase the lower bound. In simulations of a common food web model (the Lotka–Volterra cascade model) matrix structure has little effect on reactivity, and in discrete time, reactivity appears largely

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determined by mean Jacobian element size. Finally, using an upper bound related to the condition number of the eigenvectors, one can show that a Jacobian must be non-normal to be reactive, i.e. that its eigenvectors must be non-orthogonal. This requirement has been reported elsewhere (e.g. Trefethen et al., 1993; Caswell and Neubert, 2005; Schmid, 2007), but I include it here as it helps complete the intuitive picture of why some systems are reactive.

Biologically, this means that the range of possible reactivities which do not allow perturbations to grow is narrower for systems with longer transients. If we can assume that a system must be finely tuned for its reactivity to lie within a narrow range (and this would need to be proved on a case by case basis), then we can say that systems with longer transients are more likely to be reactive. More species-rich systems are able to reach higher reactivities, assuming that species interactions do not weaken too precipitously as the number of species increases. Furthermore, if the dynamics near equilibrium are governed by a Jacobian with only one large element and reproduction is pulsed (a discrete-time model), then we can attribute the system's reactivity to whatever biological process is represented by the large element. Finally, empirical data, while limited, does back up the findings from the simulated food webs: reactivity is largely determined by a food web's average interaction strength. Indeed, the empirical data shows this relationship for both discrete- and continuous-time reactivity.

2. An introduction to reactivity

Let us first consider discrete time, so that

$$\mathbf{n}(t + 1) = \mathbf{J}\mathbf{n}(t). \tag{1}$$

Here $\mathbf{n}$ typically represents a vector of perturbations from an equilibrium and $\mathbf{J}$ correspondingly represents a Jacobian. The largest factor by which the starting perturbation, $\mathbf{n_0}$, may initially be amplified is

$$\max_{\mathbf{n_0} \neq 0} \frac{\|\mathbf{n}(t = 1)\|}{\|\mathbf{n_0}\|} = \max_{\mathbf{n_0} \neq 0} \frac{\|\mathbf{J}\mathbf{n_0}\|}{\|\mathbf{n_0}\|}, \tag{2}$$

where the maximum is over all starting vectors $\mathbf{n_0}$ and in the absence of any further notation, $\| \cdot \|$ represents the 2-norm: $\sqrt{n_1^2 + n_2^2 + \cdots}$. Expression (2) is, by definition, $\|\mathbf{J}\|$, the 2-norm of matrix $\mathbf{J}$, which is in turn equal to the square root of the largest eigenvalue of the conjugate transpose of $\mathbf{J}$ times $\mathbf{J}$: $\sqrt{\lambda_1(\mathbf{J}^\dagger \mathbf{J})}$ (e.g. Meyer, 2000). Reactivity is ordinarily defined as the maximum growth rate of $\mathbf{n_0}$, not its maximum finite growth rate, and so

$$\text{reactivity} = \ln \left(\max_{\mathbf{n_0} \neq 0} \frac{\|\mathbf{n}(t = 1)\|}{\|\mathbf{n_0}\|} \right) = \ln \|\mathbf{J}\| \tag{3}$$

(Caswell and Neubert, 2005).

Now consider continuous time, so that

$$\frac{d\mathbf{n}}{dt} = \mathbf{J}\mathbf{n}(t), \tag{4}$$

where again, $\mathbf{J}$ typically represents the Jacobian of some model linearized about equilibrium. Reactivity is defined as the maximum initial growth rate of the perturbation:

$$\max_{\mathbf{n_0} \neq 0} \frac{1}{\|\mathbf{n_0}\|} \left. \frac{d\|\mathbf{n}(t)\|}{dt} \right|_{t=0}. \tag{5}$$

It can be shown (e.g. in Neubert and Caswell, 1997) that

$$\text{reactivity} = \lambda_1(H(\mathbf{J})), \tag{6}$$

where $H(\mathbf{J}) = (\mathbf{J} + \mathbf{J}^\dagger)/2$ is the Hermitian part of $\mathbf{J}$ and $\mathbf{J}^\dagger$ is the conjugate transpose of $\mathbf{J}$.

Note that if $\mathbf{n}$ represents actual population sizes instead of a perturbation from equilibrium, then reactivity represents the largest possible instantaneous growth rate. While this is potentially interesting, the usual motivation for studying reactivity is to predict transient surges or drops in response to a perturbation—surges or drops that cannot be predicted by traditional stability analysis. Therefore, I will focus my discussion on cases where $\mathbf{n}$ represents a perturbation.

3. Lower bounds: reactivity and stability

3.1. Mathematics

Discrete time: The 2-norm of $\mathbf{J}$ is greater than or equal to the spectral radius of $\mathbf{J}$:

$$\|\mathbf{J}\| \geq \rho(\mathbf{J}), \tag{7}$$

where spectral radius $\rho(\mathbf{J})$ is the largest magnitude of the eigenvalues of $\mathbf{J}$: $\max_i |\lambda_i| = \max_i \sqrt{\text{Re}\,\lambda_i^2 + \text{Im}\,\lambda_i^2}$ and where $\|\mathbf{J}\| = \rho(\mathbf{J})$ if and only if $\mathbf{J}$ is normal, meaning that $\mathbf{J}^\dagger \mathbf{J} = \mathbf{J}\mathbf{J}^\dagger$. (A derivation can be found in the Appendix.)

In the long run, after the transient dynamics have passed, $\|\mathbf{n}\|(t + 1) \approx \rho(\mathbf{J})\|\mathbf{n}\|(t)$ (see, for example, Caswell, 2001, Sec. 4.5.2), so the logarithm of the spectral radius represents the long-run growth rate of a perturbation away from equilibrium. Inequality (7) therefore means that the closer the perturbation's long-run growth rate is to 0 (i.e., the closer $\rho(\mathbf{J})$ is to 1), the narrower the range of possible reactivities which would not result in some perturbations growing initially. If we can assume that the Jacobian would have to be carefully adjusted for its norm to fall in a narrow window (a proposition which seems reasonable but which would need to be proven on a case by case basis), then we can say that less stable systems are more likely to have some perturbations which grow initially.

Continuous time: The same conclusion is true in continuous time. It can be shown that the smallest eigenvalue of $H(\mathbf{J})$ is less than or equal to the real parts of all of the eigenvalues of $\mathbf{J}$, which are less than or equal to the largest eigenvalue of $H(\mathbf{J})$ (Hogben, 2007, ch. 14). In particular, then,

$$\lambda_1(H(\mathbf{J})) \geq \text{Re}\,\lambda_1(\mathbf{J}), \tag{8}$$

with equality only when $\mathbf{J}$ is normal.

In the long run, after the transient dynamics have passed, $\|\mathbf{n}\|$ grows or shrinks as $\exp(\text{Re}\lambda_1(\mathbf{J})t)$, and so once again, reactivity is greater than or equal to the long-run growth rate of the perturbation.

3.2. Biological implications

Mathematically, we have found that reactivity is at least as large as the long-run growth rate of a perturbation away from equilibrium. What implications does this have?

If the equilibrium is stable, then by definition, the long-run growth rate of a perturbation is negative (i.e. $\rho(\mathbf{J})$ must be <1 in discrete time and $\text{Re}\lambda_1$ must be <0 in continuous time), and therefore, the lower bound on reactivity is also negative. This means that we can never use inequalities (7) or (8) to prove that dynamics near a given stable equilibrium will be reactive. However, the longer the system takes to return to equilibrium (i.e. the closer $\rho(\mathbf{J})$ is to 1 in discrete time or the closer $\text{Re}\lambda_1$ is to 0 in continuous time), the less room there is for the dynamics not to be reactive: the floor keeps rising.

We can say even more if $\mathbf{J}$ is normal. Recall that if $\mathbf{J}$ is normal, then the reactivity is equal to the long-run growth rate. Thus, a normal system can never be reactive around a stable equilibrium.

4. Upper and lower bounds: reactivity and the size of matrix elements

4.1. Mathematics

Discrete time: The Frobenius norm ($\|\mathbf{J}\|_F$) provides both upper and lower bounds for the 2-norm: for an $n \times n$ matrix $\mathbf{J}$,

$$\frac{1}{\sqrt{n}} \|\mathbf{J}\|_F \leq \|\mathbf{J}\| \leq \|\mathbf{J}\|_F, \tag{9}$$

where the Frobenius norm is the square root of the matrix element sum of squares:

$$\|\mathbf{J}\|_F = \sqrt{\text{Tr}(\mathbf{J}^\dagger \mathbf{J})} = \sqrt{\sum_{i,j=1}^{n} |J_{ij}|^2}. \tag{10}$$

(A derivation can be found in the Appendix.) Recall that in discrete time, a system is reactive if $\ln \|\mathbf{J}\|$ is positive, so we are interested in the conditions under which $\|\mathbf{J}\| > 1$. As the magnitude of any matrix element increases, the Frobenius norm increases, and thus so do the bounds enclosing reactivity. These bounds are not tight if the number of species or stages, n, is large, but if there are only two species or stages, $\|\mathbf{J}\|$ must lie within 70% to 100% of $\|\mathbf{J}\|_F$. This means that although reactivity need not increase with small increases in the Frobenius norm, large increases in $\|\mathbf{J}\|_F$ will force an increase in reactivity.

Even a single large matrix element can ensure large reactivity. In the same way that one proves inequality (9), one can show that

$$\|\mathbf{J}\|_{\max} \leq \|\mathbf{J}\| \leq n \|\mathbf{J}\|_{\max}, \tag{11}$$

where $\|\mathbf{J}\|_{\max}$ is simply the largest matrix element magnitude.

Note that when there is only a single large matrix element, $\|\mathbf{J}\|_F$ is not much larger than $\|\mathbf{J}\|_{\max}$, and so the combination

$$\|\mathbf{J}\|_{\max} \leq \|\mathbf{J}\| \leq \|\mathbf{J}\|_F \tag{12}$$

can provide very tight bounds on reactivity.

It is important to realize that large matrix elements can increase reactivity without changing stability. It is true that larger matrix elements allow for larger dominant eigenvalues and so can produce higher reactivity by making the system less stable: for all eigenvalues λ of $n \times n$ matrix $\mathbf{J}$, $|\lambda| \leq n \max_{i,j} |a_{ij}|$ (Hirsch and Bendixson, 1902). However, it is also true that for a given level of stability, increasing matrix element size can induce greater reactivity. For example,

$$\mathbf{J} = \begin{pmatrix} 15.048 & -14.098 \\ 14.548 & -13.598 \end{pmatrix} \quad \text{and} \quad \mathbf{B} = \begin{pmatrix} 0.728 & 0.221 \\ 0.229 & 0.721 \end{pmatrix} \tag{13}$$

both have eigenvalues 0.95 and 0.5, but $\|\mathbf{J}\| = 28.666$ (extremely reactive) and $\|\mathbf{B}\| = 0.950$ (non-reactive).

Continuous time: The Frobenius and max norms also provide an upper bound to reactivity in continuous-time systems, though not a lower bound. The solution to $\frac{d\mathbf{n}}{dt} = \mathbf{J}\mathbf{n}$ is $\mathbf{n}(t) = \exp(\mathbf{J}t)\mathbf{n_0}$, and so

$$\lambda_1(H(\mathbf{J})) = \max_{\|\mathbf{n_0}\| \neq 0} \frac{1}{\|\mathbf{n_0}\|} \frac{d\|\mathbf{n}\|}{dt}\bigg|_{t=0}$$

$$= \max_{\|\mathbf{n_0}\| \neq 0} \lim_{t \to 0} \frac{1}{\|\mathbf{n_0}\|} \frac{\|e^{\mathbf{J}t}\mathbf{n_0}\| - \|\mathbf{n_0}\|}{t}. \tag{14}$$

By definition, the maximum value of $\frac{1}{\|\mathbf{n}\|}\|\mathbf{B}\mathbf{n}\|$ is $\|\mathbf{B}\|$, so that we obtain

$$\lambda_1(H(\mathbf{J})) = \lim_{t \to 0} \frac{1}{t}\left(\|e^{\mathbf{J}t}\| - \|\mathbf{I}\|\right). \tag{15}$$

Taylor expanding the matrix exponential, we find $\lambda_1(H(\mathbf{J})) \approx \lim_{t \to 0} \frac{1}{t}(\|\mathbf{I} + \mathbf{J}t\| - \|\mathbf{I}\|)$, and because the 2-norm is subadditive,

$$\lambda_1(H(\mathbf{J})) \leq \lim_{t \to 0} \frac{1}{t}(\|\mathbf{I}\| + \|\mathbf{J}t\| - \|\mathbf{I}\|) = \lim_{t \to 0} \frac{1}{t}\|\mathbf{J}t\|$$

$$= \|\mathbf{J}\| \leq \|\mathbf{J}\|_F \text{ and } n\|\mathbf{J}\|_{\max}. \tag{16}$$

I have been unable to find a lower bound for continuous time reactivity that is tighter than $\text{Re}\lambda_1(\mathbf{J})$. Furthermore, examples show that $\lambda_1(H(\mathbf{J}))$ can be orders of magnitude lower than $\|\mathbf{J}\|_F$. I suspect that increasing the size of matrix elements need not increase reactivity in continuous time except via the effects this may have on stability. While I cannot prove this, it makes intuitive sense. Large Jacobian elements produce large changes in species or stage growth rates. In continuous time, these large instantaneous growth rates can be rapidly adjusted so that they don't result in large changes in population: the system can remain unreactive. However, in discrete time, a large growth rate must produce large changes in population and so the system must be reactive.

4.2. Biological implications

We have seen that increasing the sum of the squares of matrix elements increases both an upper and lower bound on discrete-time reactivity but only an upper bound on continuous-time reactivity. Furthermore, if there is only one large matrix element, then in discrete time, reactivity is roughly equal to the natural log of this element. What does this mean biologically?

Jacobian elements represent the strength of the effect that one population has on the per capita growth rate of another population when both are near equilibrium. The effect of population 1 on population 2 can be large because the per capita effect of population 1 on population 2 is large (e.g. strong competitive effects, high predation rate) or because population 1 is large at equilibrium, so that a small per capita effect produces a large total effect. However, these effects are typically confounded: e.g. stronger density-dependence will change the equilibrium sizes of the populations, and a larger equilibrium population size will change the strength of density dependence. It is therefore difficult to say anything general about what will produce large Jacobian elements.

However, increasing the number of species or life history stages will increase the number of matrix elements, generally increasing the sum of their squares. This increases the upper bound on reactivity: more species-rich food webs have the capacity to be more reactive. Of course, exceptions are possible. Suppose the average magnitude of the Jacobian elements decreases with the number of species, n. If the average magnitude decreases faster than $1/\sqrt{n}$, then the average sum of squares decreases as we increase the number of species, reducing the capacity of the system to be reactive.

What else can we glean from the mathematics? If we do know the values of the Jacobian elements and there is only one large element and reproduction is pulsed, then the bounds presented in the previous subsection continue to provide insight, even though we can calculate reactivity directly. As discussed in the previous subsection, if there is only one large matrix element, then the upper and lower bounds in Eq. (12) are very close together, so that reactivity is approximately equal to the log of the large element. This means that the system's reactivity is caused by whatever biological process is represented by this element.

5. The role of non-normality (and one more upper bound)

A linear system cannot be reactive unless it is non-normal (Trefethen et al., 1993; Caswell and Neubert, 2005; Schmid, 2007). Understanding why this is the case provides insight, even though

normality cannot be determined by inspection and there is no easy biological interpretation of normality.

First, let us verify mathematically that non-normality is necessary. We can rewrite $\mathbf{J}$ as $\mathbf{E}\mathbf{\Lambda}\mathbf{E}^{-1}$, where $\mathbf{\Lambda}$ is a diagonal matrix containing the eigenvalues of $\mathbf{J}$ and the columns of $\mathbf{E}$ are the respective eigenvectors. Because the 2-norm is submultiplicative,

$$\|\mathbf{J}\| \leq \|\mathbf{E}\|\|\mathbf{\Lambda}\|\|\mathbf{E}^{-1}\|. \tag{17}$$

The norm of $\mathbf{\Lambda}$ is the absolute value of its largest eigenvalue, $|\lambda_1(\mathbf{J})| = \rho(\mathbf{J})$, and $\|\mathbf{E}\|\|\mathbf{E}^{-1}\|$ is the condition number of $\mathbf{E}$, denoted by $\kappa(\mathbf{E})$, so

$$\|\mathbf{J}\| \leq \kappa(\mathbf{E})\rho(\mathbf{J}). \tag{18}$$

We recall from the previous section that $\lambda_1(H(\mathbf{J})) \leq \|\mathbf{J}\|$, so for both discrete and continuous time, reactivity is less than or equal to $\kappa(\mathbf{E})\rho(\mathbf{J})$.

Given appropriately normalized eigenvectors, the condition number $\kappa(\mathbf{E})$ is 1 when the eigenvectors are orthogonal – i.e. if $\mathbf{J}$ is normal – and becomes large as the eigenvectors of $\mathbf{J}$ become more nearly parallel – i.e. as $\mathbf{J}$ becomes less normal. To understand this, note that if $\mathbf{J}$ has parallel eigenvectors, then $\det \mathbf{E} = 0$ and $\|\mathbf{E}^{-1}\|$ is infinite. If $\mathbf{J}$ has nearly parallel eigenvectors, then $\det \mathbf{E}$ is small and $\|\mathbf{E}^{-1}\|$ is very large.

How, on an intuitive level, can non-normality cause a system to be reactive? Consider Fig. 1, inspired by the excellent treatment in Schmid (2007). For both the normal matrix and the non-normal matrix, we suppose that $\mathbf{n}(t) = \lambda_1^t \mathbf{w}_1 - \lambda_2^t \mathbf{w}_2$ and that $\lambda_2 < \lambda_1 < 1$. When $\mathbf{w}_1$ and $\mathbf{w}_2$ are orthogonal, $\mathbf{n}(t)$ shrinks as $\lambda_1^t \mathbf{w}_1$ and $\lambda_2^t \mathbf{w}_2$ shrink, but when $\mathbf{w}_2$ is partially aligned with $\mathbf{w}_1$, then the fact that $\lambda_2^t \mathbf{w}_2$ shrinks faster than $\lambda_1^t \mathbf{w}_1$ means that $\mathbf{n}(t)$ initially becomes longer, even though it must ultimately approach zero.

6. How strict are the bounds?

6.1. Mathematics

How strict are these bounds in practice? In particular, what might we expect for the sorts of random matrices used to model food webs?

The ideal situation might be to simulate community assembly, as in Law and Morton (1996); however, such an approach becomes computationally intensive quickly. Instead, I have used variants of the oft-studied Lotka–Volterra cascade model (Cohen et al., 1990), in which

$$\frac{dn_i}{dt} = n_i \left(r_i + \sum_j a_{ij} n_j \right), \quad i = 1, \ldots, n. \tag{19}$$

The sign of a_{ij} determines whether an increase in species j has a negative or a positive effect on species i while r_i represents species i's intrinsic growth rate. This model has Jacobian elements

$$J_{ij} = a_{ij} n_i^*, \tag{20}$$

where n_i^* is the equilibrium population of species i. Note that the Jacobian is independent of the r_i, which can be chosen however we wish. By choosing the equilibrium populations from a uniform distribution from 0 to 10, we can ensure that all species have positive equilibrium populations. There is no way to guarantee stability. For the figures in this section, I rejected any matrix that did not represent a stable system.

I have considered two patterns of species interaction (hierarchical and random interaction) and two patterns of connectivity (random and compartmentalized). Connectivity type determines whether species will affect each other. With random connectivity, a_{ij} is nonzero with probability c and zero otherwise. In the compartmentalized version, the n species are divided into equal sized

compartments. Species interact with all other species in their compartment, but there are no interactions between compartments. The Jacobian thus consists of nonzero submatrices along the diagonal.

Interaction type determines how species will affect each other, if they do affect each other. With hierarchical interactions, low-ranked species have a positive effect on high-ranked species and high-ranked species have a negative effect on low-ranked species: nonzero interaction elements a_{ij} are uniformly distributed between $-g$ and 0 if $i \leq j$ and between 0 and g if $i > j$. With random interactions, nonzero elements a_{ij} are uniformly distributed between $-g$ and g, regardless of species labels.

I find that the upper bound provided by the Frobenius norm (Eqs. (9) and (16)) is almost always stricter than the upper bounds provided by the degree of non-normality (Eq. (18)) or the maximum element size (Eq. (11)). For continuous-time systems, the only lower bound is given by stability (Eq. (8)), a rather weak bound. However, for discrete-time systems, the Frobenius norm or the maximum element size give stronger lower bounds. Thus, for continuous time systems, the tightest bounds are given by $\text{Re}\lambda_1(\mathbf{J}) \leq \text{reactivity} \leq \|\mathbf{J}\|_F$ (Eqs. (8) and (16)), while for discrete time systems, $\max\left(\ln\left(\frac{\|\mathbf{J}\|_F}{\sqrt{n}}\right), \ln(\max(|J_{ij}|))\right) \leq \text{reactivity} \leq \ln(\|\mathbf{J}\|_F)$ (Eqs. (9) and (11)). (Of these, $\ln(\max(|J_{ij}|))$ tends to be the tighter lower bound for large matrices with a few strong interactions — i.e. typical empirical food webs.) Let us now focus on how strict these bounds are.

Results for the random interaction models are shown in Fig. 2. The hierarchical interaction models show very similar results, which can be found in the electronic supplement. Regardless of connectivity or interaction patterns, discrete time reactivity hovers in the top half of its allowed range. Continuous time reactivity, on the other hand, is always in the bottom half of its range. There must be exceptions to these patterns, for we know that normal matrices cannot be reactive. However, there are many more ways to be non-normal than normal, especially as the number of species increases, and it's difficult to imagine any biological reason that a Jacobian should be normal.

Both upper and lower bounds for discrete time reactivity increase with Jacobian element size, so the fact that reactivity roughly tracks the movement of these bounds as element size increases suggests that reactivity may increase with mean element size in discrete time. Plotting reactivity against mean element size indeed shows a strong positive relationship (Fig. 3). We note again the absence of a relationship between reactivity and connectivity or compartmentalization, save for the fact that more connected food webs have a higher mean element size.

The lower bound on continuous time reactivity is not related to Jacobian element size, so the fact that reactivity hovers in the lower half of its possible range as element size changes does not necessarily mean that element size determines continuous-time reactivity. Fig. 3 confirms that there is no discernable relationship between mean element size and continuous time reactivity.

6.2. Biological implications

To what degree do real food webs follow these patterns? Parameterizing food webs is difficult, but the data that we have is consistent with the simulations: reactivity is near the top of its possible range for discrete time and near the bottom of its possible range for continuous time (Fig. 4). We also see a strong relationship between interaction strength (mean element size) and reactivity for both discrete and continuous-time reactivity (Fig. 5). It is not clear why the continuous time reactivity is so tightly connected to mean element size for the empirical data but not for the simulations.
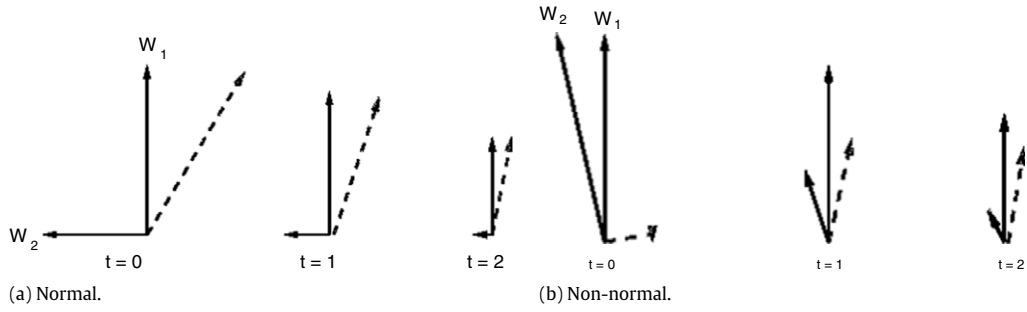
Fig. 1. Transient dynamics in normal and non-normal systems. The dashed vector is equal to the dominant eigenvector, $\mathbf{w}_1$, minus the subdominant eigenvector, $\mathbf{w}_2$. For every time step, each eigenvector is multiplied by its eigenvalue, where $\lambda_2 < \lambda_1 < 1$. In the normal system, the eigenvectors are orthogonal and the dashed vector shrinks monotonically. In the non-normal system, the eigenvectors are not orthogonal, and the dashed vector grows initially.
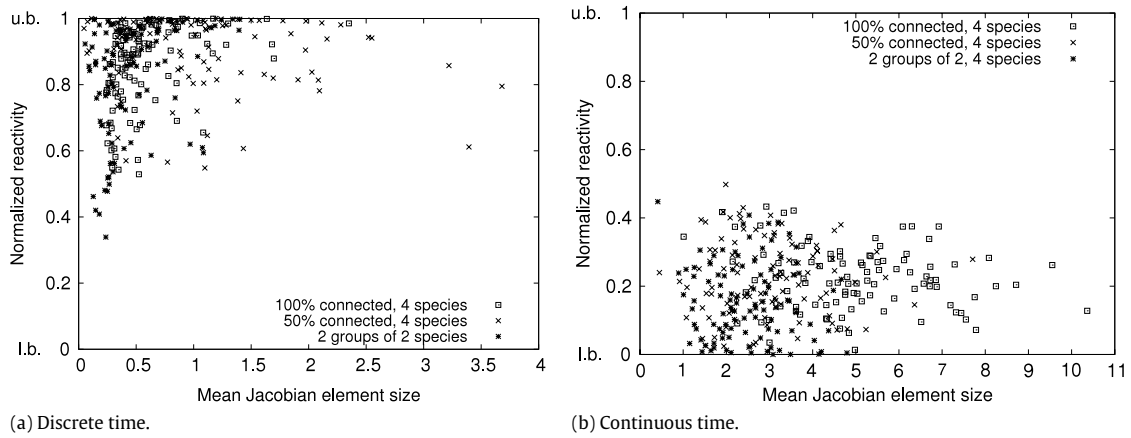

Fig. 2. Reactivity as a proportion of the distance from the lower bound (l.b.) to the upper bound (u.b.) for the random interactions food web models: (reactivity−l.b.)/(u.b.−l.b.). For discrete time systems, l.b. = $\max\left(\ln\left(\frac{\|\mathbf{J}\|_F}{\sqrt{n}}\right), \ln(\max(|J_{ij}|))\right)$ and u.b. = $\ln(\|\mathbf{J}\|_F)$ (Eqs. (9) and (11)). For continuous time systems, l.b. = $\mathrm{Re}\lambda_1(\mathbf{J})$ and u.b. = $\|\mathbf{J}\|_F$ (Eqs. (8) and (16)). Maximum interaction strength $g = 2$. I use only 4 species, as finding stable systems with more than 4 species become computationally prohibitive when the food web is 100% connected.
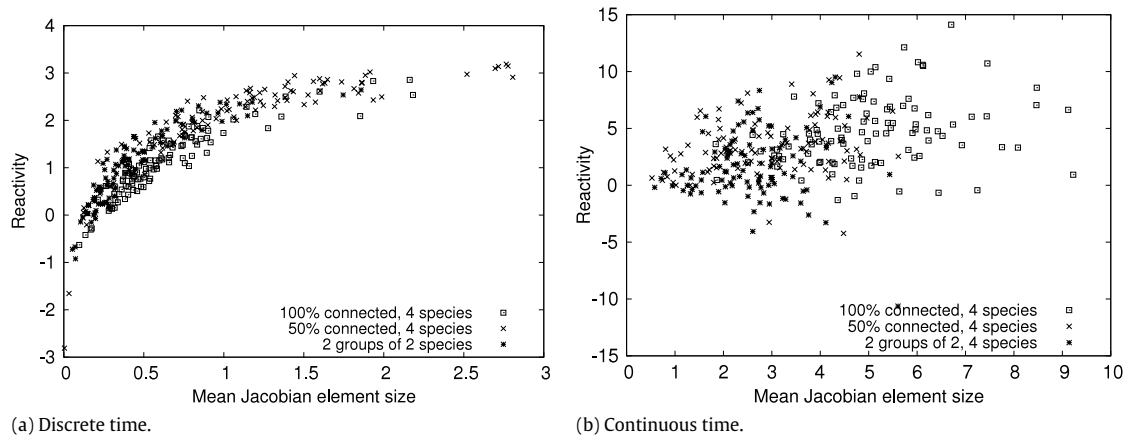

Fig. 3. Reactivity vs. mean Jacobian element size for the random interactions food web models, maximum interaction strength $g = 2$.

These results suggest that reactivity is strongly influenced by interaction strength and but not by food web topology. This is in stark contrast to other food web properties such as stability (May, 1972; Lawler, 1980), robustness to extinctions (Dunne et al., 2002; Allesina and Bodini, 2004), and the quality of ecosystem services (Montoya et al., 2003), all of which depend strongly on food web topology.

7. Discussion

Mathematical summary: In summary, we have found that less stable systems have a narrower range of negative reactivities.

(Mathematically, reactivity is bounded from below by a perturbation's long-run growth rate.) If it is true that the system must be carefully tuned for its reactivity to lie within a narrow range (a proposition which must be proven case by case), then less stable systems are more likely to be reactive. Continuous-time systems with large Jacobian elements have a greater capacity to be reactive. (Upper bounds on reactivity increase.) Discrete-time systems with large Jacobian elements are more likely to be reactive, in the sense that increasing element size causes upper and lower bounds on reactivity to increase, and having sufficiently large Jacobian elements can force a system to be reactive. For discrete time, reactivity increases with mean element size and remains in the upper half of
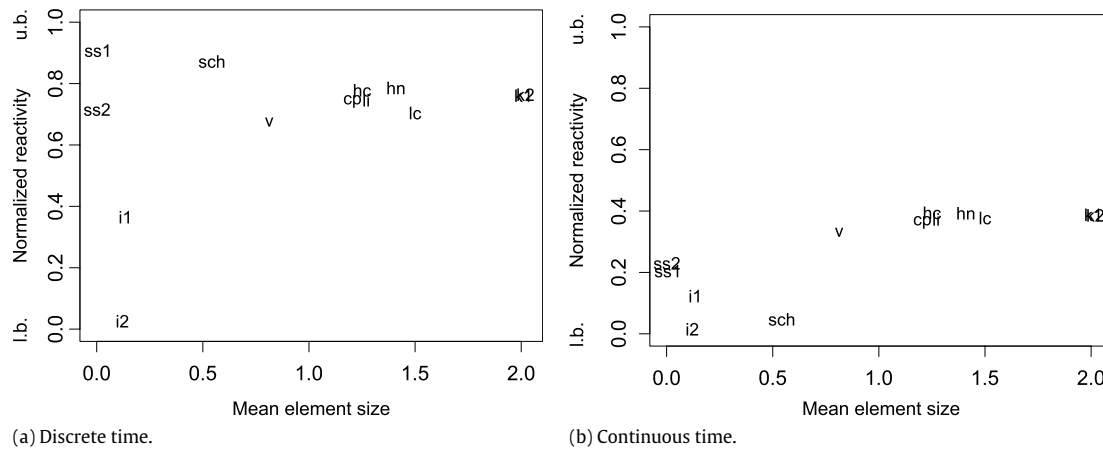
Fig. 4. Reactivity as a proportion of the distance from lower bound to upper bound for empirically parameterized food webs: (reactivity − l.b.)/(u.b. − l.b.). Bounds are as in Fig. 2. Data sources: i1 and i2: (Ives et al., 1999); sch: (Schmitz, 1997); v: (Vandermeer, 1969); ss1 and ss2: (Seifert and Seifert, 1976); cp, lc, li, hc, hn, k1, k2: (de Ruiter et al., 1998). These are continuous-time systems; the discrete-time reactivity is provided for comparison with the stochastic models.

Fig. 5. Reactivity vs mean Jacobian element size. Data sources: i1 and i2: (Ives et al., 1999); sch: (Schmitz, 1997); v: (Vandermeer, 1969); ss1 and ss2: (Seifert and Seifert, 1976); cp, lc, li, hc, hn, k1, k2: (de Ruiter et al., 1998). These are continuous-time systems; the discrete-time reactivity is provided for comparison with the stochastic models.
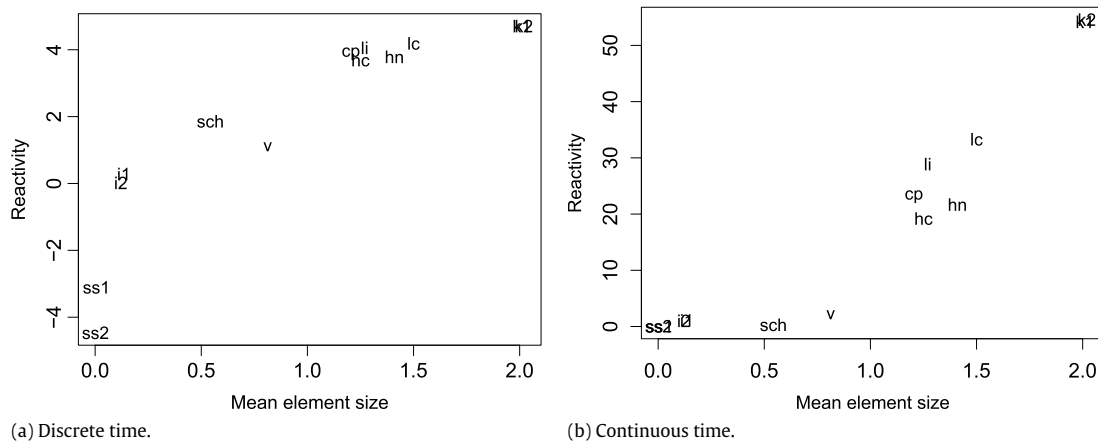
its possible range. For continuous time, reactivity has no clear relationship with mean element size but remains within the lower half of its range. In neither case does reactivity appear to be influenced by matrix structure, save that more connected networks (represented by matrices with fewer nonzero elements) typically have a larger mean element size. If there is only one large Jacobian element, the upper and lower bounds in Eq. (12) are very close, so that reactivity is approximately equal to the log of the large Jacobian element. Finally, Jacobians must be non-normal to be reactive.

These statements begin to paint an intuitive picture of reactivity. Perturbations are more likely to grow initially if the forces that bring populations back to equilibrium are weak. It is as though the system were tethered to equilibrium by a weak rubber band, and flicking the system away from equilibrium would cause it to go on a large excursion before the rubber band could pull it back in. Perturbations grow initially because small changes in one species or stage produce large changes in the growth of another species or stage. (I.e., there are large Jacobian elements.) If reproduction is continuous, these instantaneously large growth rates might be rapidly adjusted, so that the system may yet be unreactive. If reproduction comes in yearly pulses, however, a large growth rate must produce a large change in population, and so the system must be reactive. Finally, eigenvectors must be non-orthogonal for a system to be reactive — Fig. 1 explains this more succinctly than can be done in words.

Biological summary: These mathematical statements have several biological consequences. Systems with long transients have a narrower range of possible negative reactivities, so that unless reactivity is increasingly squeezed toward its lower bound, systems are more likely to be reactive as they become less stable. More species-rich systems can reach larger reactivities. If reproduction is pulsed, adding species can force an increase in reactivity.[1] If reproduction is pulsed and there is only one large Jacobian element, we can attribute the system's reactivity to whatever biological process is represented by that element. Finally, it appears that in discrete time, reactivity is determined largely by mean interaction strength and not by food web topology. Simulations suggest that in continuous time, reactivity is determined by neither mean interaction strength nor food web topology, although the limited empirical data available shows a strong positive relationship with interaction strength for discrete- and continuous-time reactivity.

This work may be particularly useful in understanding the expected behavior of stochastic food webs. From the time of May's initial papers on random food webs (May, 1972, 1973) to more sophisticated current models, stochastic food webs have been used to understand how generic structural properties of food webs influence their dynamics. For example, two recent studies

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[1] These predictions about species richness are true if species interactions do not weaken too rapidly as the number of species is increased — specifically, if the average Jacobian element magnitude does not decrease faster than $1/\sqrt{n}$, where n is the number of species.

of stochastic competitive food webs (negative interactions only) have shown that the expected reactivity (Chen and Cohen, 2001) and the expected probability of reactivity (Chen and Cohen, 2001; Rozdilsky et al., 2004) increase with the number of species in the food web. Increasing the number of species increases the food web's capacity for reactivity, so this behavior is expected.

Finally, readers are reminded that this paper presents bounds, not estimates. It is a complement to, not a substitute for, other recent papers on reactivity. If the Jacobian is known, one should simply calculate reactivity, as in Neubert and Caswell (1997) and Caswell and Neubert (2005). Likewise, to understand the effects of small parameter changes on reactivity, it is best to use the sensitivity calculations presented in Caswell (2007) and Verdy and Caswell (2008). What this paper provides is intuition and a way to think about how reactivity may behave when the Jacobian's numerical values cannot be known (as in stochastic models).

Acknowledgments

Appendix A. Derivations

Derivation of Eqs. (7), (18): Rewrite $\mathbf{J}$ as $\mathbf{E\Lambda E}^{-1}$, where $\mathbf{\Lambda}$ is a diagonal matrix containing the eigenvalues of $\mathbf{J}$ and the columns of $\mathbf{E}$ are the respective eigenvectors. Because matrix norms are sub-multiplicative, $\|\mathbf{J}\| \leq \|\mathbf{E}\|\|\mathbf{\Lambda}\|\|\mathbf{E}^{-1}\|$. The norm of a diagonal matrix is the largest magnitude of its eigenvalues, so $\|\mathbf{\Lambda}\| = \rho(\mathbf{J})$. If $\mathbf{J}$ is normal, then it can be diagonalized by a unitary matrix, so that $\|\mathbf{E}\| = \|\mathbf{E}^{-1}\| = 1$. If $\mathbf{J}$ is not normal, then $\|\mathbf{E}\|\|\mathbf{E}^{-1}\|$ is greater than 1. (To see this, note that $\|\mathbf{E}\|\|\mathbf{E}^{-1}\|$ can be written as $\sigma_{\max}(\mathbf{E})/\sigma_{\min}(\mathbf{E})$, where $\sigma_{\max}(\mathbf{E})$ and $\sigma_{\min}(\mathbf{E})$ are the maximum and minimum singular values of $\mathbf{E}$.)

Derivation of Eq. (9): This derivation follows the outline given in Meyer (2000, ch. 5). Let S_F^n be the set of all $n \times n$ matrices $\mathbf{B}$ such that $\|\mathbf{B}\|_F = 1$ and let $\mu = \min_{\mathbf{B} \in S_F^n} \|\mathbf{B}\| > 0$. We can write

$$\|\mathbf{J}\| = \|\mathbf{J}\|_F \frac{\|\mathbf{J}\|}{\|\mathbf{J}\|_F} = \|\mathbf{J}\|_F \left\|\frac{\mathbf{J}}{\|\mathbf{J}\|_F}\right\|. \tag{21}$$

However, $\mathbf{J}/\|\mathbf{J}\|_F \in S_F^n$, so $\|\mathbf{J}\| \geq \|\mathbf{J}\|_F\,\mu$. What is μ? If $\mathbf{J} \in S_F^n$, then $\|\mathbf{J}\|_F = \text{Tr}(\mathbf{J}^\dagger\mathbf{J}) = \sum_{j=1}^n \lambda_j(\mathbf{J}^\dagger\mathbf{J}) = 1$. Thus, μ is the smallest value of $\|\mathbf{J}\| = \sqrt{\lambda_1(\mathbf{J}^\dagger\mathbf{J})}$ such that $\sum_{j=1}^n \lambda_j(\mathbf{J}^\dagger\mathbf{J}) = 1$. Because $\lambda_j \leq \lambda_1$, λ_1 is smallest if all eigenvalues equal $1/n$, so that $\mu = 1/\sqrt{n}$ and $\|\mathbf{J}\| \geq \|\mathbf{J}\|_F/\sqrt{n}$.

By a similar argument,

$$\|\mathbf{J}\| = \|\mathbf{J}\|_F \left\|\frac{\mathbf{J}}{\|\mathbf{J}\|_F}\right\| \leq \|\mathbf{J}\|_F \max_{\mathbf{B} \in S_F^n} \|\mathbf{B}\|. \tag{22}$$

The eigenvalues of $\mathbf{B}^\dagger\mathbf{B}$ (i.e. the singular values of $\mathbf{B}$) must be non-negative, so that if the trace of $\mathbf{B}^\dagger\mathbf{B}$ is held at 1, then $\lambda_1(\mathbf{B}^\dagger\mathbf{B})$ is largest when $\lambda_1 = 1$ and $\lambda_{j \neq 1} = 0$. Thus $\max_{\mathbf{B} \in S_F^n} \|\mathbf{B}\| = 1$ and $\|\mathbf{J}\| \leq \|\mathbf{J}\|_F$.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tpb.2010.03.004.

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