Characterizing Species Interactions to Understand Press Perturbations: What Is the Community Matrix?

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Abstract

The community matrix is among ecology's most important mathematical
abstractions, formally encapsulating the interconnected network of effects
that species have on one another's populations. Despite its importance, the
term "community matrix" has been applied to multiple types of matrices that
have differing interpretations. This has hindered the application of theory
for understanding community structure and perturbation responses. Here,
we clarify the correspondence and distinctions among the Interaction matrix,
the Alpha matrix, and the Jacobian matrix, terms that are frequently used
interchangeably as well as synonymously with the term "community matrix."

We illustrate how these matrices correspond to different ways of characterizing interaction strengths, how they permit insights regarding different types of press perturbations, and how these are related by a simple scaling relationship. Connections to additional interaction strength characterizations encapsulated by the Beta matrix, the Gamma matrix, and the Removal matrix are also discussed. Our synthesis highlights the empirical challenges that remain in using these tools to understand actual communities.

1. INTRODUCTION

The community matrix is among ecology's most important mathematical abstractions. From its encapsulation of all the pairwise interactions between species, one can deduce the first-order consequences of all the direct and indirect effects that propagate through a community in response to a perturbation. For much of its history, the community matrix has therefore occupied a central position in our conceptual understanding of the mechanisms that govern the response of communities to pulse perturbations (Allesina & Tang 2015, May 1972). In contrast, its capacity to provide insight into the effects of press perturbations, such as eutrophication, harvest, and climate change, has received much less attention (Ives & Carpenter 2007). This discrepancy is beginning to change as ecologists have renewed efforts to understand and predict how species and whole communities respond to such sustained disturbances, particularly in the context of multiple stressors in conservation and ecosystem-based management (e.g., Berg et al. 2011, Dambacher et al. 2015, Melbourne-Thomas et al. 2012, Metcalf 2010, Montoya et al. 2009, Petchey et al. 2015, Reum et al. 2015, Schmitz 1997, Vázquez et al. 2015).

Despite its long-standing importance, the term "community matrix" has been used loosely to describe different mathematical objects. These objects (i.e., matrices) characterize the strengths of species interactions in different ways, each having distinct theoretical derivations and empirical interpretations. In particular, the term "community matrix" as coined by Levins (1968) has been used interchangeably with the terms "interaction matrix," "alpha matrix," and "Jacobian matrix." This loose usage has resulted in decades of confusion, which persists today (see discussions in Clark & Hallam 1982, Laska & Wootton 1998, Vázquez et al. 2015). All three matrices—as well as others, which we also discuss—describe the effects that species have on one another. Nevertheless, their interaction strength characterizations entail sometimes subtle differences that are important in both the quantitative and qualitative uses of interaction networks to understand the dynamics of real communities.

Here we provide a synthesis of the literature to clarify the distinctions between alternative characterizations of species interaction strengths. (See **Table 1** for a summary and **Supplemental Tables 1** and **2** for glossaries of symbols and key terms; follow the **Supplemental Material link** in the online version of this article or at **http://www.annualreviews.org**). Our motivation is to unify terminology and show how each of these characterizations may be used to gain insight into how species respond to chronic disturbances of their community (i.e., press perturbations, sensu Bender et al. 1984). Because the real-world relevance of this body of theory is not manifestly obvious (Doak et al. 2008, Maurer 1999), we specifically consider when and how its tools and derived insights may be most optimistically applied.

Our review is organized as follows: We first provide an overview of the use of matrix methods to understand press perturbations and the pathways through which species affect one another's populations. These methods build on the study of pulse perturbations, for which numerous descriptions exist (e.g., Allesina & Tang 2015). We then provide formal definitions for the Interaction matrix,

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Pulse perturbations:
acute, short-term disturbances to one or more species of a community

Press perturbations:
chronic, long-term disturbances to one or more species of a community

Table 1 A summary of the definitions and empirical interpretations of the three alternative interaction strength characterizations that matrix A has represented in the literature; other symbols have also been used (e.g., J, M, C, Φ, Γ)

	Community matrix[a]	Interaction matrix[a]	Alpha matrix[b]
Definition (A_{ij})	$\dfrac{\partial\left(\frac{dN_i}{dt}\right)}{\partial N_j}\Big\|_{\vec{N}}$	$\dfrac{\partial\left(\frac{1}{N_i}\frac{dN_i}{dt}\right)}{\partial N_j}\Big\|_{\vec{N}}$	$\dfrac{\partial\left(\frac{K_i}{r_i N_i}\frac{dN_i}{dt}\right)}{\partial N_j}\Big\|_{\vec{N}}$
Interpretation	Direct effect of the average species j individual on species i's…		
	population growth rate	per capita growth rate	growth rate relative to i's effect on own growth rate
	…with all other species held constant.		
Net Effects matrix ($-\mathbf{A}^{-1}$)	Net effect of a sustained unit increase in species j's…		
	population growth rate (e.g., fixed-quota harvest)	per capita growth rate (e.g., fixed-effort harvest)	carrying capacity (e.g., size of marine protected area)
	…on species i's population size with all species responding.		
Normalized Net Effects matrix ($\check{\mathbf{A}}^{-1}$)	Net effect of sustained unit increase in species j's… population size (e.g., most manipulative experiments) …on species i's population size with all species responding.		

All three characterizations correspond to Jacobian matrices (in the mathematical definition) and provide insight into a community's response to acute pulse perturbations (in the form of local stability analysis, for example) and chronic press perturbations (in the form of their Net Effects matrices). Normalizing their Net Effects matrices reduces these to the same Normalized Net Effects matrix. See text for matrix synonyms and additional characterizations encapsulated by the Beta, Gamma, and Removal matrices.
[a]Defined for any model of differentiable functions.
[b]Defined for the Lotka-Volterra competition model, or more generally as the ratio of the interspecific (a_{ij}) to intraspecific (a_{ii}) elements of the Interaction matrix.

the Community matrix, and the Alpha matrix and summarize their interpretations. In particular, we clarify why the Interaction matrix, the Community matrix, the Alpha matrix, and the Jacobian matrix (as this term is frequently used in the ecological literature) are in fact all Jacobian matrices (as the term is mathematically defined). We then show how, despite differences in the way they characterize interaction strengths, the insights the three matrices provide into press perturbation responses are related by a scaling relationship among alternative perturbation forms on species growth rates and abundances. This scaling relationship highlights the differing empirical uses of the matrices as well as the differing insights they offer. We conclude by discussing the key empirical challenges that remain for putting theory into practice in using matrix methods to understand community dynamics and obtain sought-after predictions of postperturbation community structure.

2. SPECIES RESPONSES TO PRESS PERTURBATIONS

We begin by illustrating in general terms how matrix methods can provide insights into species' responses to press perturbations of their community. This section serves to motivate our subsequent consideration of alternative interaction strength definitions. It also highlights why considering these definitions is important for both quantitative and qualitative representations of interaction networks. Note that in all of these applications the community's network structure is presumed to be known, either with or without knowledge of the interaction strengths themselves.

Consider a four-species system (**Figure 1**) in which an omnivorous top predator (species 4) feeds upon an intermediate predator (species 3) and competes with it for a shared prey (species 2).
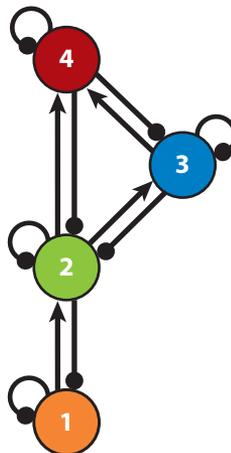
Figure 1

The direct and indirect effects that occur in the interaction network of a simple four-species trophic omnivory system are useful for illustrating the application and implicit assumptions of press perturbation theory. Species numbers correspond to their respective rows/columns in the matrices in the text. Arrowheads indicate positive direct effects; circles indicate negative direct effects.

The shared prey consumes its own resource (species 1). We assume that each species experiences negative density-dependent population growth. Other forms of intra- and interspecific interactions, such as interference competition, mutualisms, and interaction modifications (Wootton 1994), could also be incorporated (Dambacher & Ramos-Jiliberto 2007, Travis & Post 1979).

All the direct pairwise interactions between the four species can be organized into a matrix denoted by **A**,

$$\mathbf{A} = \begin{bmatrix} \alpha_{11} & \alpha_{12} & 0 & 0 \\ \alpha_{21} & \alpha_{22} & \alpha_{23} & \alpha_{24} \\ 0 & \alpha_{32} & \alpha_{33} & \alpha_{34} \\ 0 & \alpha_{42} & \alpha_{43} & \alpha_{44} \end{bmatrix}. \tag{1}$$

This matrix is interpreted as the direct effect of the species in column j on the species in row i. For example, the omnivore has a top-down negative effect on the shared prey ($\alpha_{24} < 0$) and receives a positive bottom-up effect from it ($\alpha_{42} > 0$). For now, the potentially nonlinear dynamical equations assumed to underlie these effects may remain unspecified.

Although Levins (1968) coined the term "community matrix" to refer to such a representation of an interaction network, the interpretation of what the α_{ij} elements represent has varied among authors of subsequent works, including Levins himself (e.g., Levins 1975). For now we continue to refer to this matrix simply as **A**, foretelling that the methodology of press perturbations applies to each of its interpretations.

2.1. Predictions from Quantitative Interaction Strengths

Interaction modification: an effect by which species alter one another's interactions rather than densities

When the signs and magnitudes of the elements in **A** are known, quantitative predictions can be made that describe how species abundances should be altered by a perturbation to a target species by calculating the negative of its inverse, $-\mathbf{A}^{-1}$. In the literature, this matrix has been referred to as the Net Effects matrix (our usage henceforth), the Inverse Community matrix, the Inverse Jacobian matrix, the Predictions matrix, the Sensitivity matrix, the Effective Interaction

matrix, and the matrix of Community Effects (e.g., Dambacher et al. 2002, Lawlor 1979, Nakajima 1992, Roberts & Stone 2004, Yodzis 1988a). Each element of $-\mathbf{A}^{-1}$ specifies the direction and magnitude by which the abundance of the species in row i is expected to respond to a perturbation of the species in column j. Such a perturbation is neither a one-time acute pulse disturbance, as has been the primary focus of ecological theory (e.g., May 1972), nor the typical manipulation of field experiments involving complete species removals or setting a species' abundance at a fixed value (but see Flake 1980); rather, it reflects a chronic manipulation that affects a change in species j's growth rate. If no nonperturbed species goes extinct, then $-\mathbf{A}^{-1}$ summarizes the net changes in the steady-state abundance of each ith species resulting from all the direct and indirect interactions that affect both positive and negative feedbacks between it and species j. The columns of $-\mathbf{A}^{-1}$ can be combined (added or subtracted) to understand the joint effects of simultaneous unit-strength perturbations of multiple species (Nakajima 1992).

Steady state: when long-term average abundances are unchanging in time, including fixed-point (constant) and oscillatory (e.g., limit cycle) dynamic equilibria

For example, if the direct effects of our four-species system (**Figure 1**) were

$$\mathbf{A} = \begin{bmatrix} -1 & -4.2 & 0 & 0 \\ 6.7 & -1 & -66.7 & -66.7 \\ 0 & 6.7 & -1 & -66.7 \\ 0 & 3.0 & 6.7 & -1 \end{bmatrix} \tag{2}$$

then the predicted net effects of independent perturbations to each species (across the columns) would be

$$-\mathbf{A}^{-1} = \begin{bmatrix} -2.873 & -0.581 & 0.667 & -5.709 \\ 0.919 & 0.138 & -0.158 & 1.355 \\ -0.399 & -0.060 & 0.071 & -0.738 \\ 0.098 & 0.015 & -0.002 & 0.147 \end{bmatrix} \tag{3}$$

(exact values correspond to dynamical equations and parameter values provided in **Supplemental Figure 1**). A qualitative interpretation of this Net Effects matrix is that a perturbation (increase) to the basal resource (1st column) is expected to cause a net increase in the abundance of the shared prey (2nd row) and the omnivore (4th row), and a net decrease in the abundance of the intermediate predator (3rd row) and the basal resource itself (1st row).

▶ Supplemental Material

There are a number of assumptions implicit in the interpretation of $-\mathbf{A}^{-1}$, to which we return below. For example, in making predictions of new population sizes, we typically assume that pre- and postperturbed systems are at nearby fixed-point steady states and that perturbations are sufficiently small (Hernandez 2009, Yodzis 1995). Our predictions are linear approximations to what could be strongly nonlinear responses.

A few methods for gaining insight into the temporal and species-to-species propagation of perturbations through the community (Burns et al. 2014; Higashi & Nakajima 1995; Takimoto et al. 2009; Yodzis 1988a, 1989, 1995) and for considering systems exhibiting transient and bounded oscillatory dynamics (Levins & Schultz 1996, Puccia & Levins 1991, Richard et al. 2015) have also been developed but are not discussed further here. Previous work has also emphasized how sensitive predictions are to interaction strength uncertainty (Novak et al. 2011, Roberts & Stone 2004, Yodzis 1988b).

2.2. Predictions from Qualitative Interaction Strengths

Often, community-wide knowledge of species interaction strengths is unavailable, and only the existence and signs of the interactions have been inferred. When this is the case, the matrix

corresponding to **Figure 1** is specified qualitatively as

$$°\mathbf{A} = \begin{bmatrix} -1 & -1 & 0 & 0 \\ 1 & -1 & -1 & -1 \\ 0 & 1 & -1 & -1 \\ 0 & 1 & 1 & -1 \end{bmatrix},$$

(4)

Adjugate: a matrix whose elements reflect the net number of positive and negative feedback loops that link each species pair (aka the classical adjoint)

Determinant: a single number contributing equally to all elements of the inverse that scales the magnitude of species' net responses

Qualitative indeterminacy: when a species' true response—increase, decrease, or lack of change—is indefinite (sign-indeterminate)

using $°\mathbf{A}$ to denote this specification (Dambacher et al. 2002). In what was originally termed loop analysis, Levins (1974; see also Mason 1953) developed an algorithm for computing predictions of species responses from $°\mathbf{A}$. This algorithm was in practice limited to small matrices (Pilette et al. 1987). Dambacher et al. (2002; see also Levine 1976) pointed out the correspondence of qualitative and quantitative approaches, showing the adjugate of a matrix to be scaled to its inverse by its determinant [i.e., $\mathbf{A}^{-1} = \mathrm{adj}(\mathbf{A})/\det(\mathbf{A})$]. This connection permits insights into larger qualitatively specified systems because the adjugate retains the same sign structure as the inverse. The matrix determinant, in turn, provides a measure of the community's overall sensitivity to perturbations (Barabás et al. 2014).

Specifying only the sign structure of a community's interactions can produce qualitatively different expectations than when interaction strengths are specified quantitatively. For example, if the interaction network of our four-species system were to be specified qualitatively, the Net Effects matrix would be

$$-°\mathbf{A}^{-1} = \begin{bmatrix} \frac{2}{3} & -\frac{1}{3} & \frac{1}{3} & 0 \\ \frac{1}{3} & \frac{1}{3} & -\frac{1}{3} & 0 \\ 0 & 0 & \frac{1}{2} & -\frac{1}{2} \\ \frac{1}{3} & \frac{1}{3} & \frac{1}{6} & \frac{1}{2} \end{bmatrix}.$$

(5)

A sustained input to the basal species (1st column) is therefore expected to cause a net increase in the abundance of the shared prey (2nd row) and the omnivore (4th row) and, in contrast to the situation described above (Equation 3), no net change in the intermediate predator (3rd row) and an increase in the basal resource itself (1st row). The intermediate predator's response is now qualitatively indeterminate because of two counteracting feedback loops—one having a positive effect via the shared prey and the other having a negative indirect effect via the omnivore—that sum to zero when all $\alpha_{ij} = 1, -1,$ or 0. In such situations, when the numbers of incoming positive and negative feedback loops are equal, the direction of a species' response depends on the quantitative values of the interaction strengths (Dambacher et al. 2002, Yodzis 1988b). The basal resource's expected response is similarly incorrect because the magnitudes of the contributing feedbacks are assumed equal. Novak et al. (2011) demonstrated how increasing amounts of uncertainty (or intrinsic variation) in species interaction strengths cause the ability to predict qualitative responses using quantitatively described networks to converge on the more limited success rate of qualitatively described networks.

3. CHARACTERIZING INTERACTION STRENGTHS

We now turn to interpreting the elements of matrix $\mathbf{A}$ as measures of the direct pairwise strength of species interactions. As stated above, there are four terms that have seen the most frequent use in reference to this matrix: the Interaction matrix, the Community matrix, the Alpha matrix, and the Jacobian matrix. In this section, we explain why the first three of these are all, in fact, Jacobian matrices in the mathematical sense, and then contrast their mathematical derivations and ecological interpretations. A key point is worth highlighting: It is useful to think of interaction strengths in general, and the elements of these matrices in particular, not as constants (as has

typically been done in empirical and theoretical studies) but rather as reflections of functions describing how variables and parameters (e.g., species abundances; ecosystem context; aspects of behavior, such as attack rates and handling times) contribute to determining the direct effects that species have on each other (see also Abrams 2001). This point applies equally to qualitative interaction networks.

3.1. The (Mathematical) Jacobian Matrix

Consider a community of S interacting species in which each ith species exhibits a per capita growth rate described by its own as-yet-unspecified function,

$$\frac{1}{N_i}\frac{dN_i}{dt} = f_i(\vec{N}) = f_i(N_1, N_2, \ldots, N_S). \tag{6}$$

Each f_i function relates how the rate of change of species i's abundance (on a per individual basis) is directly dependent on its own abundance (N_i) and on the abundances of the other species in the community (not necessarily all S). A powerful mathematical tool is the ability to describe each such function by means of a Taylor series—a potentially infinite sum of terms containing a function's partial derivatives with respect to a given variable evaluated at a given point along it. How the value of the function (i.e., species i's per capita growth rate) changes in response to a change in one of its variables (i.e., a change to species j's abundance by amount ΔN_j, with the abundances of all other species held unchanged) may be approximated to a desired degree of accuracy by including successively higher-order derivatives of the function evaluated at the variable's original value (i.e., N_j):

$$f_i(N_1, \ldots, N_j + \Delta N_j, \ldots, N_S) = f_i(\vec{N}) + \underbrace{\frac{\partial f_i}{\partial N_j}\bigg|_{\vec{N}}}_{\substack{ij\text{th} \\ \text{element of} \\ \text{Jacobian}}} \Delta N_j + \underbrace{\sum_{n=2}^{\infty} \frac{\partial^n f_i(\vec{N})}{\partial N_j^n}\bigg|_{\vec{N}} \frac{\Delta N_j^n}{n!}}_{\text{higher-order terms}}. \tag{7}$$

The more species j's population size is changed from its original size, the greater the number of derivatives that are needed to reasonably approximate how species i's per capita growth rate will respond (**Figure 2a–c**). If f_i is linear with respect to N_j, then the first two terms suffice fully (**Figure 2a**). Because the contribution of successively higher-order derivatives in the series ($n \geq 2$) diminishes rapidly when the size of the perturbation ΔN_j is small, and because at steady state the first (zero-order) term of the series $f_i(\vec{N}) = 0$ by definition, the first-order derivative $\frac{\partial f_i}{\partial N_j}$ will determine the sign (i.e., whether f_i increases or decreases with N_j) and dominate the magnitude of the approximation near steady state.

By its mathematical definition, a Jacobian is a matrix whose ij elements correspond to the first-order partial derivatives of each ith function with respect to each jth variable. Each matrix element reflects the ith function's tangent slope at the point where it is evaluated (**Figure 2**). For the empirical perspective, it is worth highlighting that, as encapsulated by the linear approximation of the Jacobian, species j's effect on i is short term only in that all other species abundances are assumed to have remained constant (cf. Vázquez et al. 2015). It is near steady state that a Jacobian's mathematical properties are most useful.

Although we have so far specified these f_i functions to reflect species per capita growth rates, this is by choice rather than by definition. Indeed, as we show next, the mathematical derivations of the Interaction matrix (and hence the definition of per capita interaction strengths) and the Community matrix differ only in that the Interaction matrix is based on functions describing
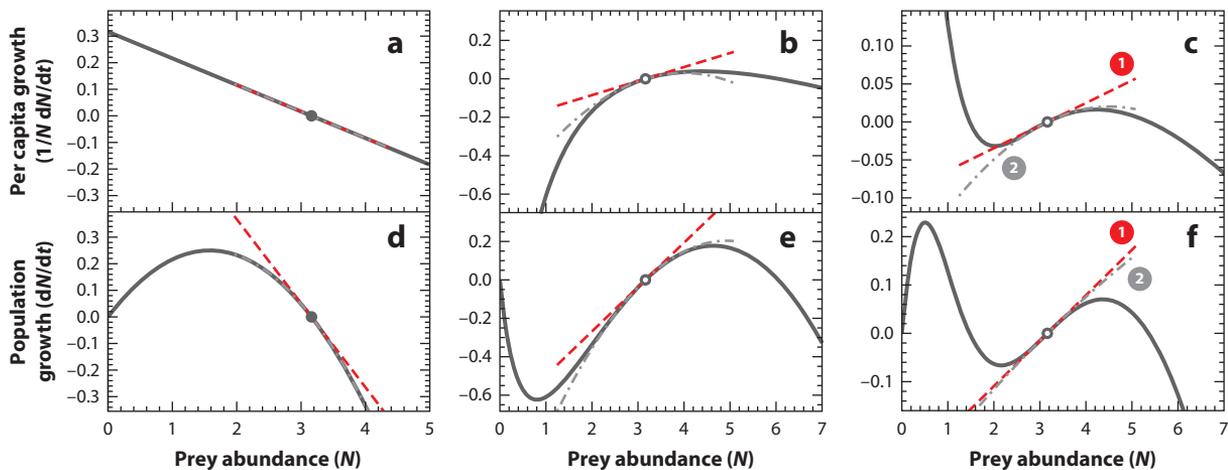
Figure 2

The matrix elements of a Jacobian reflect tangent-slope approximations to functions describing how species' growth rates respond to a change in their abundance. Each element represents the second (first-order) term of a Taylor series expansion around a focal point along such a function (①－－－), a function that may reflect a species per capita growth rate ($\frac{1}{N}\frac{dN}{dt} = f_i$) or its population growth rate ($\frac{dN}{dt} = F_i$). The first term of the Taylor series equals zero ($f_i = F_i = 0$) at both stable (*filled circle*) and unstable (*open circle*) steady states. The consideration of higher-order terms (e.g., the second-order term, ②－·－) provides a more faithful approximation. Illustrated are functions for a hypothetical predator-prey pair describing how the prey's (*a–c*) per capita and (*d–f*) population growth rate responds to its own abundance, N, and how these functions are respectively approximated within the Interaction and Community matrices. Three scenarios are illustrated in which the prey always exhibits logistic self-limitation but its predator exhibits a functional response of either a (*a,d*) Holling type I, (*b,e*) type II, or (*c,f*) type III form, with the value of the attack rate parameter specified to make the per capita strength of the interspecific effects equal in all cases (see **Supplemental Figure 2**).

Supplemental Material

species per capita growth rates ($\frac{1}{N_i}\frac{dN_i}{dt}$; **Figure 2*a–c***), whereas the Community matrix is based on functions describing population growth rates ($\frac{dN_i}{dt}$; **Figure 2*d–f***). By these definitions, the Alpha matrix of competition coefficients (Levins 1968) is neither an Interaction matrix nor a Community matrix, although each of these latter two matrices may be obtained for the model from which the Alpha matrix is derived.

3.2. Defining the Interaction Matrix

To this point we have characterized species interactions generically using matrices and unspecified functions. Indeed, the power of the above-described methods is that they do not prescribe a specific functional form to a community's interactions. Nevertheless, standard practice in both theory and empirical contexts has been to assume that the community is closed to migration, that pairwise direct interactions are constant in time and linear with respect to species densities, and that no interaction modifications between species are present. Typically these assumptions are enacted by replacing $f_i(\vec{N})$ with a generalized version of a Lotka-Volterra model written with self-limitation in all species as

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i + \sum_{j=1}^{S} a_{ij} N_j \qquad (8)$$

(e.g., Pimm & Lawton 1978). This model is implicit in most empirical approaches to estimating interaction strengths (Wootton & Emmerson 2005). Species i's observed per capita growth rate is thus a function of its intrinsic per capita growth rate (r_i), its own self-effects ($a_{ii} < 0$), its

interactions with other species ($a_{ij} < 0$ and $a_{ji} > 0$ for prey-i consumer-j pairs; a_{ij} and $a_{ji} < 0$ for competitors; a_{ij} and $a_{ji} > 0$ for mutualists), and the abundances of those species. Note that we have switched from using α to using a to represent the strength of species interactions, a subtlety arising from the distinction between the Alpha matrix and the Interaction matrix, which we clarify below.

The per capita growth rate r is the net effect of a population's per capita birth and death rates in the absence of all other explicitly considered species. Thus for species whose resources are considered implicitly (e.g., primary producers) we assume $r > 0$, whereas for species whose resources are considered explicitly (e.g., consumers) we let $r < 0$ because we have already accounted for their prey-dependent birth rates in the $\sum a_{ij} N_j$ terms. A consumer's r therefore reflects its intrinsic per capita death rate. For predator-prey interactions we typically consider the bottom-up per capita effect of prey on predators to be scaled to the predator's top-down per capita effect by a constant conversion efficiency e (i.e., $|a_{ij}| = e a_{ji}$), thereby assuming a linear numerical response.

Numerous authors have regarded the a_{ii} and a_{ij} parameters of the Lotka-Volterra model as respectively defining the diagonal and off-diagonal elements of the Interaction matrix or the Community matrix (e.g., Attayde & Hansson 2001, Berg et al. 2011, Laska & Wootton 1998, Montoya et al. 2005, Roberts & Stone 2004, Vázquez et al. 2015). However, this interpretation is only a particular case of the more general formal definition of an Interaction matrix as the first-order partial derivatives of each species' per capita growth rate with respect to each other species' abundance (Travis & Post 1979):

$$\left. \frac{\partial \left(\frac{1}{N_i} \frac{dN_i}{dt} \right)}{\partial N_j} \right|_{\vec{N}} = \frac{\partial \left(r_i + \sum a_{ij} N_j \right)}{\partial N_j} = a_{ij}. \tag{9}$$

In other words, the Interaction matrix corresponds to a (mathematical) Jacobian matrix containing the second terms from a Taylor series expansion of each species' per capita growth rate (**Figure 2a–c**). It is only for a linear Lotka-Volterra model that the Interaction matrix contains only the a_{ij} parameters of that model.

There are several ways to connect the elements of the Interaction matrix to empirical metrics of species interaction strengths. Each element reflects the direct effect that an average individual of species j has on species i's per capita rate of growth or decline; the elements define direct per capita interaction strengths (cf. Novak & Wootton 2010, Paine 1992). These permit direct comparisons between the effects of species that have different population sizes, thereby enabling the identification of keystone species whose effects are disproportionate to their abundance (Power et al. 1996). Species i's population-level rate of growth or decline is changed by the amount $a_{ij} N_i N_j$ in the absence of species j relative to when j is present and the species are in isolation. Similarly, a small change in the abundance of j will have an effect proportional to $a_{ij} N_i$ on species i's population growth rate. In the absence of all other species in a community of competitors (all resources considered implicitly), species i would eventually attain its carrying capacity $K_i = \frac{r_i}{a_{ii}}$ (Vandermeer 1975). It is worth reiterating, however, that the elements of the Interaction matrix encapsulate species j's effect on species i as being short term only in that all other species are assumed to have remained constant. As we highlight below (Section 4.2), these pairwise per capita effects are not transient but rather are equally important for understanding the long-term responses of the entire community to press perturbations.

With the formal definition of the Interaction matrix as a Jacobian of the species per capita growth rates, it becomes apparent that per capita interaction strengths need not be restricted to single parameters or constants that are independent of species' population sizes (**Figure 2a–c**). Rather, per capita interaction strengths may be linear or nonlinear functions dependent on species'

abundances and parameters other than just the per capita attack rate (Novak & Wootton 2010). Keystone status is thus more appropriately ascribed to the interactions between species, as Paine (1969) originally proposed, than to individual species themselves, as current practice maintains (Power et al. 1996). For example, the original keystone species, *Pisaster ochraceus*, has an effect on intertidal community structure only because its primary prey, *Mytilus californianus*, does not exhibit a growth rate capable of replenishing its population at the rate that *P. ochraceus* consumes it.

Nonlinear interactions complicate the simplistic extrapolation of per capita effects from the linear case implicit in most empirical methods of estimating interaction strengths. This may be illustrated by two examples considering a focal predator's functional response, described below.

In the first example, for a two-species predator-prey interaction in which the predator's feeding rate responds to changes in prey density with a Holling type II functional response (i.e., Equation 8 with $a_{ij} \to \frac{-c}{1 + cbN_i}$), the Interaction matrix of per capita interaction strengths is

$$\begin{bmatrix} a_{ii} + \frac{c^2\, bN_j}{(1 + cbN_i)^2} & \frac{-c}{1 + cbN_i} \\ \frac{ec}{(1 + cbN_i)^2} & a_{jj} \end{bmatrix}. \tag{10}$$

Here parameter c denotes the per capita attack rate that describes the rate at which the predator j's feeding rate becomes saturated, limited not by prey availability but rather by its handling time b. Thus, in contrast to the case of a linear functional response where the prey's per capita effect on itself is simply a_{ii} (representing the prey's self-limitation) and always negative (**Figure 2a**), it will now be positive if the magnitude of a_{ii} is less than $\frac{c^2 bN_j}{(1 + cbN_i)^2}$ (**Figure 2b**), which depends on species abundances and how quickly the predator's feeding rate can become saturated (as controlled by c and b). When such nonlinear interactions are present, the sign of matrix elements could easily be misspecified in the intuition-based reconstruction of a real community's qualitative interaction matrix.

In the second example, for a three-species apparent competition module in which a predator consumes two noncompeting prey species, the per capita interaction strength between the two prey species is zero when a linear Lotka-Volterra model is assumed. In contrast, when the predator j exhibits a multispecies type II functional response ($a_{ij} \to \frac{-c_{ij}}{1 + c_{ij}b_{ij}N_i + c_{kj}b_{kj}N_k}$), the corresponding element of the Interaction matrix that specifies prey k's direct per capita effect on prey i is

$$\frac{\partial f_i(\vec{N})}{\partial N_k} = \frac{-c_{ij}c_{kj}b_{kj}N_j}{\left(1 + c_{ij}b_{ik}N_i + c_{kj}b_{kj}N_k\right)^2}, \tag{11}$$

and vice versa for i's effect on k. Thus, although the two prey do not compete with each other, they directly affect each other's per capita growth rates via an interaction modification that alters the predator's feeding rate. Their per capita interaction strengths therefore consist of an apparent mutualism that could be missed in the naive reconstruction of a community's interaction matrix (Yodzis 2000).

3.3. Defining the Community Matrix

Numerous authors have also used the term "Jacobian matrix" as a synonym for "community matrix." Indeed, this has become the more typical use of the term among theoreticians (e.g., Berlow et al. 2004, Dambacher et al. 2002, de Ruiter et al. 1995, Jorgensen et al. 2000, Laska & Wootton 1998, Montoya et al. 2009, Schmitz 1997, Stone & Roberts 1991, Vázquez et al. 2015, Yodzis 1995). Although May (1972) used the term "interaction matrix" in reference to an

approximation to a (mathematical) Jacobian matrix, his paper appears to have been the origin of this usage.

The matrix in question consists of the partial derivatives of each species' population growth rate with respect to each other species abundance (**Figure 2d–f**). We henceforth refer to this matrix as the Community matrix, using $F_i(\vec{N})$ to distinguish the population growth rate functions from the per capita growth rate functions referred to above (i.e., $F_i(\vec{N}) = N_i f_i(\vec{N}) = \frac{dN_i}{dt}$). When this definition is applied to the generalized Lotka-Volterra model, the Community matrix consists of

$$\left. \frac{\partial \left(\frac{dN_i}{dt} \right)}{\partial N_j} \right|_{\vec{N}} = \begin{cases} a_{ii} N_i + f_i(\vec{N}) & i = j \\ a_{ij} N_i & i \neq j \end{cases} \tag{12}$$

(e.g., Pimm & Lawton 1977). At steady state, where $f_i(\vec{N}) = 0$, the diagonal matrix elements further simplify to $a_{ii} N_i$, corresponding to the effects of intraspecific self-limitation. Thus, some authors refer to this matrix as the Community matrix only when its elements are evaluated specifically at steady-state abundances, N^*, where its mathematical properties are most useful (e.g., Allesina & Tang 2015).

The elements of the Community matrix reflect the direct effect that an average individual of species j has on species i's population-level rate of growth or decline. They are not per capita interaction strengths (Wootton & Emmerson 2005). The potential for confusion has arisen because elements of the Community matrix have been referred to as per capita interaction strengths (e.g., de Ruiter et al. 1995) and per capita effects (Yodzis 1981, 1988b) because they reflect the effect of a single individual of species j. As for the Interaction matrix, the elements of the Community matrix reflect species i's short-term response to species j only in that the abundances of all other species are assumed to have remained constant.

As in the case of the Interaction matrix, nonlinear species interactions complicate the simplistic extrapolation of the Community matrix elements from the linear case of the generalized Lotka-Volterra model. For example, it is only in the linear case that the diagonal elements reflect just the intraspecific self-limitation effects at steady state (De Angelis 1975, Haydon 1994). Thus, for the two-species predator-prey interaction with a type II functional response (Equation 10), the corresponding Community matrix is

$$\begin{bmatrix} r_i + 2a_{ii}N_i - \frac{cN_j}{1+cbN_i} + \frac{c^2bN_iN_j}{(1+cbN_i)^2} & \frac{-cN_i}{1+cbN_i} \\ \frac{ecN_j}{(1+cbN_i)^2} & r_j + \frac{ecN_i}{1+cbN_i} + 2a_{jj}N_j \end{bmatrix}. \tag{13}$$

The prey's qualitative effect on itself may therefore be negative or positive depending on species abundances, how saturated the predator's feeding rate is, the strength of the prey's self-limitation, and its intrinsic growth rate (**Figure 2**). In the case of the three-species apparent competition module in which the predator exhibits a multispecies type II functional response, the apparent mutualistic effects between prey are as in the Interaction matrix (Equation 11) except that the affected species' abundance is also present in the numerator (Neutel & Thorne 2015, Yodzis 2000).

3.4. Defining the Alpha Matrix (the Original Community Matrix)

Neither the Interaction matrix nor the Community matrix, as just defined, corresponds to the original usage of the term "community matrix"—a term coined by Levins (1968) in reference to a system of competing species (resources considered implicitly) whose empirically inspired estimates of pairwise direct interaction strengths were derived from measures of niche overlap

(May & MacArthur 1972). Levins (1968) based his derivation on the Lotka-Volterra competition model used by Gause (1934):

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i\left(1 - \frac{\sum \alpha_{ij} N_j}{K_i}\right).$$ (14)

This model can be rewritten in the form of the generalized Lotka-Volterra model by substituting $\alpha_{ii} = a_{ii}/a_{ii} = 1$ and $\alpha_{ij} = a_{ij}/a_{ii}$ using $K_i = r_i/a_{ii}$ (Vandermeer 1975). Bender et al. (1984) used c_i to represent r_i/K_i. The original community matrix is composed of these α competition coefficients, which Levins (1968, p. 51) interpreted as "the reduction in the rate of increase of [species i] caused by an individual of [species j] compared to the effect of an individual of [species i]." The interspecific effect of j on i is expressed as a fraction of species i's intraspecific per capita effect.

Levins (1968, p. 53) defined the original community matrix by converting the Lotka-Volterra competition model (Equation 14) to matrix form at steady state, $\mathbf{A}\vec{N}^* = \vec{K}$. Levins illustrated $\mathbf{A}$ with diagonal elements $\alpha_{ii} = 1$ because in terms of the competitive niche each species is presumed to overlap completely with itself. [This intuitively appealing assumption may not be appropriate for many species (Bolnick et al. 2011)]. The off-diagonal α_{ij} elements of $\mathbf{A}$ represent interspecific niche overlap. The values of the matrix elements are made negative to reflect the negative direct effects that competing species have on one another. This original community matrix was later considered synonymous with the Alpha matrix (e.g., Lawlor 1979) and the Competition matrix (e.g., Levine 1976, May & MacArthur 1972; but see Vandermeer 1970). The former term seems preferable because competition between species may be described in numerous ways, as in the Lotka-Volterra model. The distinction between the interaction strength measures of the Alpha matrix and those of the Interaction and Community matrices are thus that the interaction coefficients of the model used by Levins to define the Alpha matrix are measures that are scaled to the a_{ii} self-effects and the r_i intrinsic growth rates of the affected species itself. This may also be shown by alternative derivations of the Alpha matrix using either a Jacobian,

$$\left.\frac{\partial\left(\frac{K_1}{r_i N_i}\frac{dN_i}{dt}\right)}{\partial N_j}\right|_{\vec{N}} = \frac{\partial\left(1 - \sum \alpha_{ij} N_j\right)}{\partial N_j} = -\alpha_{ij},$$ (15)

or by dividing the off-diagonal elements of the interaction matrix by their corresponding diagonal elements (**Table 1**). Elements of the Alpha matrix are thereby not equivalent to per capita interaction strengths as defined by Equation 9.

Introducing a similar matrix, Vandermeer (1975) presented what could be referred to as the Beta matrix, using elements $\beta_{ii} = a_{ii}/a_{jj}$ and $\beta_{ij} = a_{ij}/a_{jj}$ to represent the strength of intra- and interspecific interactions relative to the strength of the intraspecific interaction of the species affecting the competition. A different definition of Beta matrix stemming from the statistical terminology for regression coefficients refers to a matrix most analogous to an Interaction matrix reflecting responses to changes in species log-abundances ($\frac{1}{N}\frac{dN}{dt} = \frac{d\log(N)}{dt}$; Ives et al. 2003).

4. PRESS PERTURBATIONS REVISITED: GROWTH RATES VERSUS ABUNDANCES

4.1. Growth Rate Perturbations

As emphasized by many authors, inferences regarding species responses to press or pulse perturbations using matrix methods do not rest on an assumption of an underlying Lotka-Volterra model (May 1972, Yodzis 1988b); the approach is pertinent to any differentiable model (e.g., Nakajima

1992, Yodzis 2000). Furthermore, although the elements of the Interaction, Community, and Alpha matrices represent different measures of the direct, pairwise strengths of species interactions, each offers insight into a community's dynamics. It has been proven, for example, that if the Interaction matrix of a Lotka-Volterra system is asymptotically stable, then its Community matrix will be stable as well (Logofet 2005).

Because each matrix constitutes a different interaction strength characterization, however, each produces different predictions and inferences regarding a community's net responses to press perturbations in the form of $-\mathbf{A}^{-1}$ (see **Supplemental Figure 1**). These differences can have critical implications for using empirical data on species dynamics to estimate parameters of species interaction models, for example, but have not been recognized in the literature; different authors have used different matrices in their analyses.

In fact, the elements of $-\mathbf{A}^{-1}$ represent changes in species i's abundance due to a unit increase in species j's (1) per capita growth rate, when $\mathbf{A}$ is an Interaction matrix (e.g., Roberts & Stone 2004); (2) population growth rate, when $\mathbf{A}$ is a Community matrix (e.g., Higashi & Nakajima 1995); and (3) carrying capacity, when $\mathbf{A}$ is an Alpha matrix (e.g., Bender et al. 1984, Levine 1976). More specifically, they represent tangent slopes to the functions describing how abundances change in response to these perturbations (**Figure 3**). Thus, in the context of fisheries management, for example, the Net Effects matrix of the Interaction matrix may be used to gain insight into the effects of fixed-effort harvest, the Net Effects matrix of the Community matrix reflects the effects of fixed-quota harvest, and the Net Effects matrix of the Alpha matrix reflects the effects of spatial management in the form of varying marine protected area size (**Table 1**).

What the inverses of the three matrices have in common is that they each reflect perturbations to different factors affecting species' growth rates. Species i's expected net response to a press perturbation of any factor p affecting the growth rate of any number of species in the community may be determined even more generally using

$$\frac{\partial N_i^*}{\partial p} = -\sum_{k=1}^{S}\left((\mathbf{A}^{-1})_{ik} \cdot \frac{\partial F_k}{\partial p}\right) \qquad (16)$$

(Higashi & Nakajima 1995, Nakajima 1992, Yodzis 1989). In words, how species i's abundance is expected to respond to a press perturbation of its community reflects a summation over all S species of the magnitude by which each kth species' population growth rate responds directly to the perturbation ($\frac{\partial F_k}{\partial p}$, which for species-specific perturbations will equal zero for all nontargeted species) times the magnitude of species k's net effect on species i as encapsulated by $-\mathbf{A}^{-1}$ when $\mathbf{A}$ is a Community matrix. Equation 16 may be written equivalently using $\frac{\partial f_k}{\partial p}$ when $\mathbf{A}$ is an Interaction matrix (Barabás et al. 2014). It provides a powerful tool for gaining insight into the consequences of many real-world press perturbations—including harvest, eutrophication, and climate change—and their additive effects (**Figure 3**). Equation 16 also provides the basis for a first-order estimate of the perturbation magnitude that would cause a species to go extinct (Barabás et al. 2014).

4.2. Abundance Perturbations: Defining the Normalized Net Effects Matrix

Press perturbations of species growth rates are not the same as press perturbations of species abundances. The three inverse matrices are not directly interpretable for understanding how species abundances will change in response to a specific change in some particular species' abundance, which is the typical manipulation imposed in field experiments. Nonetheless, and despite their differences, the three matrices equivalently hold the necessary information for deriving expectations for these responses. We next encapsulate these expectations by introducing a new matrix, the Normalized Net Effects matrix.

Asymptotic stability: the condition whereby the size of a pulse perturbation eventually declines toward zero at a rate given by the leading eigenvalue λ_1
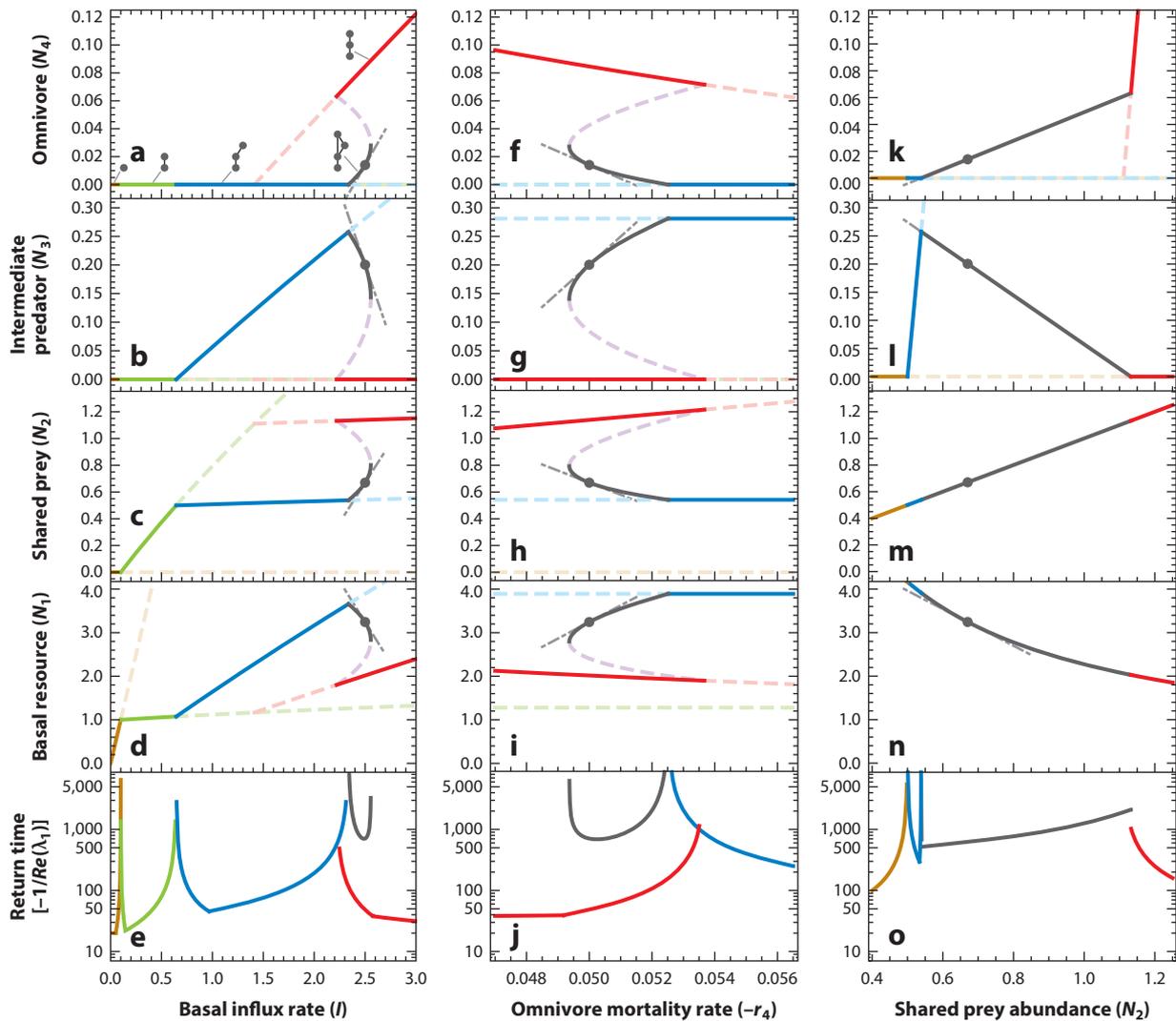
Supplemental Material

Figure 3

The true and approximated response of the four-species omnivory system (**Figure 1**) to press perturbations of (*a–d*) the basal species' influx rate (e.g., ecosystem productivity), (*f–i*) the omnivore's per capita mortality rate (e.g., fisheries harvest), and (*k–n*) the shared prey's abundance (e.g., manipulative experiment). Both stable (*solid line*) and unstable (*dashed line*) steady states are shown. Elements of the Net Effects matrix, $-\mathbf{A}^{-1}$, reflect the tangent slopes to such press perturbations of population growth rates (panels *a–d*) when $\mathbf{A}$ refers to the Community matrix and of per capita growth rates (panels *f–i*) when $\mathbf{A}$ refers to the Interaction matrix. Elements of the Normalized Net Effects matrix, $\check{\mathbf{A}}^{-1}$, approximate the responses to press manipulations of species abundances (panels *k–n*). Predictions using the approximations implicit in $\mathbf{A}$ assume that perturbations are sufficiently small so as not to affect transitions between alternative or consecutive stable states, as occurs when species go extinct. (*e, j, o*) Such critical transitions may be anticipated by changes in generic indicators such as a system's characteristic return time to steady state following pulse perturbations $[-1/Re(\lambda_1)]$. See **Supplemental Figure 1** for underlying equations and parameter values; panels *a–d* are as in case C of Takimoto et al. (2007).

▶ Supplemental Material

Consider again the matrix equation $\mathbf{A}\vec{N}^* = \vec{K}$ describing the relationship between the Alpha matrix, steady-state species abundances, and the carrying capacities of the species. Rearranging to $\vec{N}^* = \mathbf{A}^{-1}\vec{K}$ indicates that if we selectively change species j's carrying capacity ($K_j = r_j/a_{jj}$) by a small amount, we should expect to change species i's abundance by an amount proportional to $\alpha_{ij}^{(-1)}$, with species j's own abundance changing by an amount proportional to $\alpha_{jj}^{(-1)}$ (Bender et al. 1984, Levine 1976). Intuitively, the Alpha matrix thereby contains the necessary information to understand a community's response to an abundance-based press perturbation as well. The direction and magnitude of species i's response to a specific change in species j's abundance should be $\alpha_{ij}^{(-1)}/\alpha_{jj}^{(-1)}$ times the magnitude of species j's affected abundance change. Levine (1976) referred to the ratios of $\alpha_{ij}^{(-1)}/\alpha_{jj}^{(-1)}$ as normalized coefficients.

The Community and Interaction matrices hold the same information as the Alpha matrix because relative changes in species abundances can be obtained from the ratios of responses to any perturbation p_j:

$$\frac{\partial N_i^*}{\partial N_j^*} = \frac{\alpha_{ij}^{(-1)}}{\alpha_{jj}^{(-1)}} = \frac{\partial N_i^*/\partial p_j}{\partial N_j^*/\partial p_j} = \frac{\partial F_i(\vec{N}^*)/\partial p_j}{\partial F_j(\vec{N}^*)/\partial p_j} = \frac{\partial f_i(\vec{N}^*)/\partial p_j}{\partial f_j(\vec{N}^*)/\partial p_j} = \frac{a_{ij}^{(-1)}}{a_{jj}^{(-1)}}. \tag{17}$$

That is, the relative response of species i's abundance to a sustained change in j's abundance is equivalent not only to the ratio of the ij and jj elements of the Alpha Net Effects matrix, but also to the relative response of their population and per capita growth rates (respectively defining the Community and Interaction matrices) to the perturbation. In fact, normalizing the Net Effects matrices of the Alpha matrix and the Community matrix reduces both to the normalized Net Effects matrix of the Interaction matrix. This normalized matrix, which we denote by $\check{\mathbf{A}}^{-1}$ and suggest referring to as the Normalized Net Effects matrix, is composed of relative direct per capita interaction strengths. Its elements are net per capita interaction strengths (cf. Novak & Wootton 2010, Paine 1992). Each corresponds to a ratio of the j to i outgoing interspecific and j to j returning intraspecific net effects that are caused by the perturbation (Higashi & Nakajima 1995, Nakajima & Higashi 1995).

To a first-order approximation, the expected change in species i's abundance following the onset of a chronic alteration of species j's abundance is therefore

$$\Delta N_i^* \approx \frac{a_{ij}^{(-1)}}{a_{jj}^{(-1)}}\Delta N_j^* = \check{a}_{ij}\Delta N_j^*, \tag{18}$$

with the a_{ij} per capita interaction strengths defined by Equation 9 at steady state. The accuracy of this approximation will be highest the more linearly species' growth rates respond to changes in their abundance or life-history attributes and the smaller the perturbation is (**Figure 3k–o**). The Normalized Net Effects matrix is essentially equivalent to Lawlor's (1979) experimentally inspired Gamma matrix in all ways but their opposing sign structure. Lawlor (1979) defined negative γ_{ij} elements to indicate net mutualistic effects.

5. PUTTING THEORY INTO PRACTICE

The Normalized Net Effects matrix underscores how the non-normalized Net Effects matrices of the Alpha, Interaction, and Community matrices differ only in that their elements are scaled to the net effects of differing forms of growth rate perturbations. All three matrices offer an avenue for understanding community dynamics. The Normalized Net Effects matrix further shows that per capita interaction strengths underlie all characterizations of species' net effects, just as they

underlie all other characterizations of direct interactions strengths (Laska & Wootton 1998), including the Community and Alpha matrices. We therefore recommend that empiricists continue to pursue the estimation of direct per capita interaction strengths and, for interspecific interactions, refer to summaries of the alternative methods available for doing so (Berlow et al. 2004, Vázquez et al. 2015, Wootton & Emmerson 2005). Many of these methods require further development to extend them beyond the typical assumption of constant and linear functional forms and the use of isolated species pairs in order to enable statistical inferences on the parameters of more realistic functional dependencies in species-rich communities (Novak & Wootton 2008). Such refocusing on parameters rather than per capita interaction strengths per se will clarify distinctions among differing uses of the term interaction strength (cf. Berlow et al. 2004, Wootton & Emmerson 2005), will aid in avoiding the strict equilibrium assumptions implicit in many estimation approaches (Novak & Wootton 2010, Wootton & Emmerson 2005), and will permit the field to move beyond current sensitivity analyses to more probabilistic descriptions of interaction strengths and predictions than are currently possible (Petchey et al. 2015, Wolf et al. 2015).

Many additional challenges exist to understanding the dynamics of real ecological systems, such that humility and adaptive strategies will always be necessary (Doak et al. 2008, Petchey et al. 2015). The mechanisms governing rates of adaptive behavior (e.g., prey-switching) and the occurrence of hydra effects, for example, are of particular interest (Abrams 2009, Valdovinos et al. 2010). Implementing the theory of press perturbations poses at least two more general challenges. The first is that, in addition to estimating all interspecific interactions, it is just as important to estimate species' self-effects, which constitute the diagonal of **A**. These have received little empirical or theoretical attention. The second concerns the perturbation magnitude within which the approximations of Equations 16–18 will be quantitatively or even qualitatively correct. Theoreticians have been prone to state rigorously that perturbations must be infinitely or sufficiently small, but this provides little to no practicable guidance because most experiments, management actions, and other natural and anthropogenic disturbances involve large perturbations.

5.1. The Diagonal Elements

In applications of theory it has become standard to specify negative density dependence in all species by setting the diagonal elements of **A** to -1 or a general constant $-d$ (e.g., Allesina & Tang 2015, Novak et al. 2011) (**Figure 1**). May (1972) referred to this as setting the timescale of a community's dynamics. Others have assigned an arbitrary fraction of the basal species' self-effect to nonbasal species (e.g., Emmerson & Raffaelli 2004, Yodzis 1988b). The assumption of negative self-effects for all species has become typical in qualitative modeling as well (e.g., Dambacher et al. 2015). The biological and mathematical restrictions that such uniform assignments implicitly impose have been recognized for many years in the context of pulse perturbations (Haydon 1994, James et al. 2015, Jorgensen et al. 2000, Taylor 1988).

Increasing the magnitude of negative self-effects increases a system's asymptotic stability by diagonal dominance (Logofet 1993). Indeed, the magnitude of the diagonal elements required to stabilize otherwise empirically informed matrices has been used to gauge community stability (Neutel et al. 2007). Because the sum of a matrix's diagonal elements (its trace) equals the sum of its eigenvalues (Searle 1966) and a positive trace implies instability, increasing the proportion of species experiencing negative self-effects also increases stability (De Angelis 1975, Yodzis 1981). This occurs in qualitatively specified systems too, in which a necessary condition for stability is that no species has positive self-effects and that some species have negative self-effects (Logofet 1993).

The nature of the diagonal elements is relevant to press perturbations as well. For example, stable matrices are nonsingular ($|\det(\mathbf{A})| \neq 0$), which is a necessary condition for the inverse of $\mathbf{A}$ to exist. Assuming negative self-effects for all species in qualitative modeling therefore increases the likelihood that predictions of species responses can even be produced. Nevertheless, assumptions concerning the magnitude and prevalence of negative self-effects will alter predictions of community responses. As revealed by the Normalized Net Effects matrix, the more negative the diagonal elements are, the smaller species responses will be (Nakajima 1992). This may be understood more generally by noting that a matrix's determinant (which modulates all species' responses) is equal to the product of its eigenvalues (Searle 1966). Thus, the more negative the eigenvalues, the smaller the overall response will be. Further still, increasing the prevalence of nonzero diagonal elements can have even larger effects, altering predictions fundamentally by changing the relative number of counteracting feedback loops that exist between species.

These observations indicate the need for careful consideration of what the diagonal elements actually represent in a given community of species. Unfortunately, species' self-effects have received appreciable attention only in the debate over population regulation, which has focused primarily on single species (but see Haydon 1994, James et al. 2015, Taylor 1988). Of particular relevance in the multispecies context is the interpretation of the diagonal elements for nonbasal species and species with nonlinear interactions.

In regards to the diagonal elements of nonbasal species, recall that in the Interaction matrix of the Lotka-Volterra model (closed to migration) the diagonal elements reflect the intraspecific damping effects of self-limitation. In the Community matrix, this is only true at steady state. Because we have already accounted for exploitative competition by modeling their prey explicitly, one might argue that the consumers' diagonal element should be zero (Pimm & Lawton 1978) unless there is intraspecific interference (Yodzis 1981). This seems reasonable given that our resolution of species diets is often better for higher trophic levels (Paine 1988). Nevertheless, because higher-level consumers typically obtain resources across larger spatial scales than other species (Paine 1988), their nonlocal resources may remain unconsidered when one is reconstructing an interaction web for a focal community. Without the explicit inclusion of such subsidies, a consumer's diagonal element should be negative. Indeed, in more generally specified open systems, immigration and emigration respectively increase and decrease self-damping effects (Levins & Schultz 1996, Puccia & Levins 1991). Both empiricists and theoreticians should therefore be explicit in defining the spatial extent of their community. In many situations, quantifying incoming and outgoing fluxes may be just as important as quantifying interspecific interactions (Polis et al. 1997). Further theory and empirical data are needed to guide such considerations (Holyoak et al. 2005).

Species with nonlinear interactions complicate matters further because their diagonal elements also contain interspecific effects (De Angelis 1975, Haydon 1994). These can switch the sign of the diagonal elements depending on their form and strength and the abundances at which they are assessed (**Figure 2**; Equation 11). Although some empirical work suggests that inherently nonlinear pairwise interactions may be effectively linear within the typical short-term range over which species abundances vary in multispecies contexts (Wootton & Emmerson 2005; also see **Figures 3** and **2**), additional work is needed to generalize when and how interspecific interactions become important (James et al. 2015, Neutel & Thorne 2015). The issue is similar to the manner in which the relative importance of apparent competition and apparent mutualism to the long-term abundances of two prey species that share a predator (see Equation 11) depends on the degree to which the predator's numerical response is limited (Abrams & Matsuda 1996). Developments in the quasi-polynomial formalism, whereby some nonlinear systems may be transformed into dynamically equivalent Lotka-Volterra form, may offer a tool for gaining much-needed insights (Hernández-Bermejo & Fairén 1997).

5.2. Sufficiently Small Perturbations

The linearization of functional dependencies underlying the construction of a Jacobian matrix is fundamental to the power and generality of local stability analysis in the context of pulse perturbations. The dominant eigenvalue, λ_1, which may subsequently be determined near steady state, reflects the rate at which the system's slowest components will eventually return to steady state and is therefore itself an approximation to the system's true dynamical response (Neubert & Caswell 1997, Nolting & Abbott 2016). Its relevance is local in that too large a perturbation may send the system into a different basin of attraction that has a different community state and dynamical properties (Lewontin 1969). Only in some cases are local inferences global and thus robust to perturbation magnitude. The approximations for press perturbations are similarly local.

Local linearization does not, however, relegate applications of press perturbation theory to irrelevance in real-world applications. The four-species intraguild predation system (**Figure 1**) illustrates a number of the reasons why. First, although the accuracy of quantitative approximations will undoubtedly decline with increasing perturbation magnitude in real-world nonlinear systems, the type of press perturbation that is experienced will matter: Whereas some communities will have poorly approximated nonlinear responses to some perturbation types (e.g., to growth rates; **Figure 3a–d,f–i**), they may also respond more linearly to other perturbation types (e.g., to abundances; **Figure 3k,l**). Different community states will themselves differ in this regard, as illustrated by the contrast of the four-species coexistence state with either of the three-species states in all panels of **Figure 3**. Furthermore, even within a given community, some species will respond more linearly than others to different perturbation types or points of impact in their community (e.g., contrast **Figure 3k–n**). Recent extensions of so-called generalized modeling techniques offer a compelling approach for identifying these systems and species while circumventing the need to assume specific forms for species' functional dependencies (Aufderheide et al. 2013, Yeakel et al. 2011).

Second, qualitative predictions of a community's response derived from quantitative matrices will be correct over a greater range of perturbation magnitudes than the respective quantitative predictions, even in nonlinear systems in which quantitative predictions are poor (**Figure 3**). Often such qualitative predictions are sufficient for understanding experimental outcomes and informing management actions (Dambacher et al. 2002). In this context it is worth noting that the qualitative predictions of poorly estimated quantitatively specified matrices will, on average, be correct more often than those of qualitatively specified matrices (Novak et al. 2011). In fact, recent work suggests that qualitative predictions may be surprisingly insensitive to orders-of-magnitude levels of uncertainty when empirically informed allometric constraints on interaction strengths are considered, particularly in complex systems (Iles & Novak 2016). This corresponds to similar recent findings in the context of pulse perturbations (Barabás & Allesina 2015).

Regardless of whether quantitative or qualitative predictions are sought, the full domain within which these methods are relevant will extend only to perturbation magnitudes that do not cause a system to traverse a bifurcation boundary that separates basins of attraction. Such transitions can include abrupt tipping-point transitions between alternative stable states (e.g., the four-species to three-species omnivore-dominated transitions in **Figure 3a–d,f–i**), transitions between successive stable states (e.g., the two-species to three-species transition in **Figure 3a–d**), or transitions between fixed-point and limit-cycle dynamics (**Supplemental Figure 3**). Identifying the limits of these domains is challenging even in theory (Nolting & Abbott 2016). Fortunately, rapidly maturing theory with tantalizing empirical support is demonstrating the potential of combining high-frequency monitoring with early-warning indicators to recognize the impending occurrence of such transitions before the magnitude of a press perturbation is further increased (Boettiger & Hastings 2013, Dakos et al. 2015). These include changes in generic measures of a community's

▶ Supplemental Material

spatial and temporal autocorrelations, which are indicative of the community's rate of return to steady state following small, continually occurring pulse perturbations from the surrounding environment (**Figure 3***e,j,o*).

Nonetheless, the point at which species interactions become too nonlinear and perturbations too large for useful predictions to be made remains an open question for both empirical studies and empirically informed theory to address. Although the nonlinear and idiosyncratic characteristics of nature's dynamics have long been emphasized (Lawton 1999), and ecological surprises are widespread (Doak et al. 2008), many real communities are continuously subjected to perturbations across wide-ranging spatial and temporal scales without transitioning between different states. What is clear is that the consequences of outright species additions or removals, as are typical in manipulative experiments (e.g., Paine 1992), many natural experiments (e.g., Watson & Estes 2011), and many theoretical investigations (e.g., Berlow et al. 2009), will be poorly approximated by the press perturbations predictions of any Net Effects matrix. That is, elements of the so-called Removal matrix containing the pairwise effects of species removals on each other's equilibrium abundances (Laska & Wootton 1998) should rarely be expected to correspond to the elements of a Net Effects matrix. Changes in community composition not only alter a community's network topology and emergent feedback loops but also affect the transition of bifurcation points when secondary extinctions ensue (**Figure 3**). Other approaches are more suitable for investigating such perturbations (e.g., Allesina & Pascual 2009, Gao et al. 2016, Ovaskainen 2003).

6. CONCLUSIONS

The frequency with which the methods of community matrix theory are employed will likely increase as the network structure of natural communities becomes further resolved and the availability of data on interaction strengths increases. Many of the developments in our understanding of the factors that contribute to community stability and persistence need consideration in the framework of press perturbations (Ives & Carpenter 2007). By illustrating how the alternative characterizations of interaction strengths as encapsulated by the Community matrix, the Interaction matrix, the Alpha matrix, and their corresponding Net Effects matrices are related to one another, we have attempted to clarify how their interpretations differ. Despite these important differences, they each offer utility. The future use of more distinctly defined terms by both theoreticians and empiricists will increase clarity and prevent miscommunication, particularly as the much-needed integration of real-world data with theory continues. Our discussion highlights many of the considerations that will be involved in this effort, but arguably, the primary challenges of prediction are empirical rather than theoretical in their nature. Of particular note is the substantial challenge of understanding the behavior of communities in the vicinities of tipping points. Community ecology is clearly in a prime position to address many important issues facing society and the environment, whether in regards to informing conservation science or the sustainable extraction of Earth's resources. Perturbation experiments—be they in silica, intentional, or unintended consequences of society's actions—can contribute to this goal by providing important insights into how real-world systems behave.

SUMMARY POINTS

1. The Interaction matrix, the Community matrix, and the Alpha matrix each have formal definitions as (mathematical) Jacobian matrices.

2. Their alternative interaction strength characterizations each reflect linear approximations to the pairwise functional relationships that underlie species interactions.

3. Their Net Effects matrices provide insight into a community's response to different types of press perturbations of species growth rates.

4. The Normalized Net Effects matrix underlies each of the three Net Effects matrices and reflects a community's response to press perturbations of species abundances.

FUTURE ISSUES

1. Methods for the estimation of interspecific interactions require a refocusing on characterizing the functional relationships between species and the uncertainty of parameter estimates, rather than the description of static interaction strengths.

2. Theoretical and empirical work is needed to inform the estimation of intraspecific and interspecific feedbacks through which species affect their own growth rates.

3. Empirical work and empirically informed theory are needed to provide practical guidance for how community and network structure, species' attributes, and the nature of their functional relationships influence the perturbation magnitude within which both quantitative and qualitative matrix predictions remain useful.

DISCLOSURE STATEMENT

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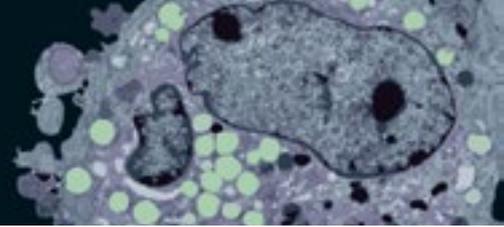
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