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Predicting species responses to perturbations: What is the community matrix?

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3 **Predicting species responses to perturbations: What is the community matrix?**

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24 *Author contributions:* Our article stems from a recent NCEAS working group in which all
25 authors (with the exception of JY) participated (*Conservation Planning for Ecosystem*
26 *Functioning: Testing Predictions of Ecological Effectiveness for Marine Predators*). DD, JE,
27 ME, UJ, MN, TT and TW conceived the study and outlined the manuscript; DD, MN, TT, TW
28 and JY derived key mathematical insights and relationships; MN performed the simulations; all
29 authors contributed to interpreting the results; and all authors contributed to writing the
30 manuscript and its appendices.

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Running Title: *What is the community matrix?*

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3 35 ABSTRACT: The community matrix is among ecology's most important mathematical
4 abstractions. From its encapsulation of all the pairwise interactions between the species of a
5 community one can deduce the consequences of all direct and indirect effects of disturbances
6 that propagate through the network of their interactions. Despite its importance, the term
7
8 37 community matrix has been applied to matrices having distinctly different interpretations of their
9 elements. This has hindered its application as a tool for understanding the structure and
10 dynamics of communities, and for predicting species-specific responses to targeted perturbations
11 in ecosystem-based management and conservation. Here we clarify the distinctions between the
12 community matrix (as originally defined), the interaction matrix and the Jacobian matrix which
13 have frequently been considered synonymous. Despite differences in their representation of
14 species interaction strengths, we illustrate how all three matrices can be used to predict a
15 community's species-specific responses to the sustained addition or extraction of species. We
16 illustrate how these predictions are of relative response and discuss the empirical effort that is
17 needed to convert these predictions to estimates of the post-perturbation community structure.
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3 53 The community matrix is among ecology's most important mathematical abstractions. From
4 54 its encapsulation of all the pairwise interactions between the species of a community one can
5 55 deduce the consequences of all the direct and indirect effects of disturbances that propagate
6 56 through the network of their interactions. The community matrix has thus been central to
7 57 understanding the mechanisms that influence the invasibility and stability of the complex,
8 58 species-rich systems of nature (May 1972; McCann 2000). More recently, a resurgence of
9 59 interest in the community matrix has been part of an effort to holistically predict how individual
10 60 species will respond to perturbations in their community, particularly in the context of
11 61 conservation and ecosystem-based management (e.g., Dambacher *et al.* 2009; Montoya *et al.*
12 62 2009; Ortiz & Wolff 2004; Ramsey & Veltman 2005).

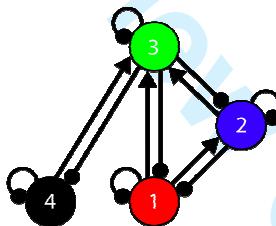
13
14 63 Despite its importance the term 'community matrix' has been used for different
15 64 representations of species interaction strengths that each have distinct derivations and
16 65 interpretations. In particular, the term has been used to denote not only the original formulation
17 66 by Levins (1968), but also the interaction matrix and the Jacobian (which we define explicitly
18 67 below). This has resulted in decades worth of confusion (e.g., Clark & Hallam 1982). While all
19 68 three matrices describe the effects that species in a community have on another, they
20 69 nevertheless have sometimes subtle, but important, distinctions. These distinctions are of
21 70 particular relevance in parameterizing these matrices with empirical data and thus in their
22 71 practical uses to understand real communities (Laska & Wootton 1998).

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24 72 Here we clarify these distinctions by contrasting the derivation of the community matrix (as
25 73 originally defined) with those of the interaction and the Jacobian matrices. Despite differences
26 74 in the way they represent species interaction strengths, we illustrate how all three matrices can be
27 75 used to predict the relative direction and magnitude by which species abundances will respond to

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3 76 sustained perturbations in their community. More specifically, we illustrate how the predictions
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5 77 of the three matrices differ only in their scaling, such that predictions of species responses
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7 78 derived from the original community matrix and the Jacobian can simplify to the predictions
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9 79 derived from the interaction matrix. We conclude by discussing the difficulties of converting the
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12 80 resulting predictions of relative species responses to the more useful and typically sought-after
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15 81 predictions of new, post-perturbation community structure.

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18 82 ***Using the community matrix to predict species responses to perturbations***

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20 83 To motivate subsequent discussion, we begin by illustrating in general terms how the
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23 84 community matrix can provide predictions of species responses to perturbations when the
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26 85 network structure of species interactions is known, either with or without knowledge of the
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29 86 strengths of these interactions.



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37 87 **Figure 1.** An interaction network of four species depicted in signed digraph form. Arrow heads indicate
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60 88 a positive effect of prey on predator, circles indicate a negative effect of predator on prey, or on self.

Consider a simple four-species system in which an omnivorous predator (sp. #3) preys upon three species: an intermediate predator (sp. #2) with whom it competes for a shared prey (sp. #1), and an alternative prey species (sp. #4) on which the intermediate predator does not feed (Fig. 1). All species are assumed to experience self-limitation. Other interactions, such as interference competition and mutualisms (Travis & Post 1979) and interaction modifications (Dambacher & Ramos-Jiliberto 2007) could also be incorporated, given that the resulting system is structurally stable. All the direct pairwise interactions between the species can be organized into a matrix

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3 97 which we denote by \mathbf{A} ,

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$$\mathbf{A} = \begin{bmatrix} \alpha_{11} & \alpha_{12} & \alpha_{13} & 0 \\ \alpha_{21} & \alpha_{22} & \alpha_{23} & 0 \\ \alpha_{31} & \alpha_{32} & \alpha_{33} & \alpha_{34} \\ 0 & 0 & \alpha_{43} & \alpha_{44} \end{bmatrix} \quad (1)$$

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12 99 This matrix is read as the direct effect of the species in column j on the species of row i . For
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14 example, the omnivore has a top-down negative effect on the shared prey ($\alpha_{13} < 0$) and receives
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16 a positive bottom-up effect from it ($\alpha_{31} > 0$).
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20 102 Although Levins (1968) coined the term ‘community matrix’ to refer to such a representation
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22 of an interaction network, the interpretation of what the α_{ij} elements represent has varied among
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24 subsequent authors, including Levins himself (e.g., Levins 1975). The term community matrix
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26 has thus been used synonymously with both the interaction matrix and the Jacobian. Neither is
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28 entirely correct, a point which we will discuss extensively below. We will continue to refer to \mathbf{A}
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30 as the community matrix, noting that the interpretation of the α_{ij} elements is largely irrelevant
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32 when the matrix is specified qualitatively (but see *The diagonal elements of the interaction*
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34 *matrix below*).
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39 110 *Predictions with the Quantitative Community Matrix*

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41 111 When all elements of \mathbf{A} are known, predictions for how equilibrial species abundances will be
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43 changed by a perturbation to a target species can be made quantitatively by calculating the
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45 negative of the inverse of the community matrix, $-\mathbf{A}^{-1}$ (Bender *et al.* 1984). This matrix has also
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47 been referred to as the net effects matrix, the predictions matrix, the sensitivity matrix, and the
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49 matrix of community effects. Each element of $-\mathbf{A}^{-1}$ specifies the expected direction and relative
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51 magnitude by which the equilibrium abundance of species i will respond to a unit increase in the
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53 growth rate of species j (a press perturbation, Bender *et al.* 1984; see also SOM, Higashi &
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3 118 Nakajima 1995; Nakajima 1992; Yodzis 1988b). Such a perturbation is not a one time change
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5 119 (pulse or removal) in species j 's abundance as is typically done in field experiments (but see
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7 120 Flake 1980). If no non-perturbed species goes extinct, then $-\mathbf{A}^{-1}$ summarizes the net changes in
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9 121 the equilibrium abundance of each species i resulting from all the direct and indirect interactions
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11 122 that cause both positive and negative feedback between it and species j .
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15 123 For example, if the direct pairwise interaction strengths of our four species system were
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$$\mathbf{A} = \begin{bmatrix} -1 & -2 & -0.2 & 0 \\ 50 & -1 & -50 & 0 \\ 1 & 5 & -1 & 10 \\ 0 & 0 & -2 & -1 \end{bmatrix}, \quad (2)$$

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20 124 then the predicted net effects of independent perturbations to each species (across the columns)
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23 125 would be
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$$-\mathbf{A}^{-1} = \begin{bmatrix} 0.12 & -0.02 & 0.04 & 0.43 \\ 0.43 & 0.01 & -0.03 & -0.26 \\ 0.11 & 0.001 & 0.04 & 0.44 \\ -0.22 & -0.003 & -0.09 & 0.13 \end{bmatrix}. \quad (3)$$

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30 126 In qualitative terms, the interpretation of $-\mathbf{A}^{-1}$ is as follows: For example, a sustained input to the
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33 127 omnivore's alternative prey (4th column) is predicted to cause a net increase in the equilibrium
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35 abundance of the shared prey (4th column, 1st row), the omnivore (4th column, 3rd row) and of
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37 128 itself (4th column, 4th row), and a net decrease in the abundance of the intermediate predator (4th
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39 129 column, 2nd row). A sustained removal would have the opposite effects.
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50 130 In making these predictions we assume that perturbations are small, that pre- and post-
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50 131 perturbed systems are at nearby stationary equilibria (Case 2000), and that species interactions
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50 132 are sufficiently linearized (Yodzis 1995) and thereby adequately described by constants
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50 133 (Hernandez 2009). The columns of $-\mathbf{A}^{-1}$ can be combined (added or subtracted) to predict the
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50 134 joint effects of perturbing two or more species simultaneously (Nakajima 1992). Methods for
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3 138 gaining insight into the temporal propagation of indirect effects between equilibria (Higashi &
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5 139 Nakajima 1995; Takimoto *et al.* 2009; Yodzis 1988b; Yodzis 1995) and in systems with bounded
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7 140 non-equilibrium dynamics (Dambacher *et al.* 2009; Puccia & Levins 1985; Puccia & Levins
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9 141 1991) have also been developed, but will not be discussed further here.
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14 142 *Predictions with the Qualitative Community Matrix*
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16 143 Community-wide knowledge of interaction strengths is typically not available, and only the
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18 144 existence and sign of the interactions has been inferred. The community matrix of our example
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20 145 is thereby specified qualitatively as
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$$\circ\mathbf{A} = \begin{bmatrix} -1 & -1 & -1 & 0 \\ 1 & -1 & -1 & 0 \\ 1 & 1 & -1 & 1 \\ 0 & 0 & -1 & -1 \end{bmatrix}$$
 (4)
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30 147 (we denote the matrix by $\circ\mathbf{A}$ when it is specified qualitatively). In what he originally termed
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32 148 loop analysis, Levins (1974) developed an algorithm for computing predictions of species
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34 149 responses from $\circ\mathbf{A}$ (see also Mason 1953) which was in practice limited to small matrices (Pilette
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36 150 *et al.* 1987). Dambacher *et al.* (2002) pointed out the correspondence of qualitative and
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38 151 quantitative prediction matrices, showing the classical adjoint of a matrix to be scaled to its
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40 152 inverse by its determinant (see also Levine 1976). Because the classical adjoint of a matrix
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42 153 retains the same sign structure as its inverse, this permits insights into the predictions of larger
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44 154 qualitatively-specified systems. However, $\circ\mathbf{A}$ must be nonsingular (non-degenerate) and must
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46 155 have a non-zero determinant for predictions to be made. A necessary, though not sufficient,
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48 156 requirement for this is that no two species may share the same set of interactions (i.e., the same
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50 157 competitors, predators, prey, and self-effects, etc.). (In the case of \mathbf{A} , no two species may share
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52 158 the same set of α values, which is far less likely to occur.)
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3 159 The adjoint of our four-species example community is
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$$6 \quad \text{adj}(-{}^\circ \mathbf{A}) = -{}^\circ \mathbf{A}^{-1} \cdot \det(-{}^\circ \mathbf{A}) = \begin{bmatrix} 3 & -3 & 0 & 0 \\ 1 & 3 & -2 & -2 \\ 2 & 0 & 2 & 2 \\ -2 & 0 & -2 & 4 \end{bmatrix} \quad (5)$$

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12 161 Thus in qualitative terms a sustained input to the omnivore's alternative prey (4th column) is
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14 162 predicted to cause a net increase in the equilibrium abundance of the omnivore (4th column, 3rd
15 row) and of itself (4th column, 4th row), a net decrease in the abundance of the intermediate
16 predator (4th column, 2nd row), and no net change in the abundance of the shared prey (4th
17 column, 1st row). The response of the shared prey to an input to the omnivore's alternative prey
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19 164 is indeterminate (Yodzis 1988b) because it is affected by two counteracting feedback loops
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21 165 summing to zero: one having a negative effect via the increased abundance of the omnivore, and
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23 166 a second having a positive effect via the decreased abundance of the intermediate predator (i.e.,
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25 167 $\alpha_{12} \alpha_{23} \alpha_{44} - \alpha_{13} \alpha_{22} \alpha_{44} = 0$ when all $\alpha_{ij} = -1$ or 1, see SOM). In such situations where the
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27 168 number of incoming positive and negative feedback loops is equal, the direction of a species'
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29 170 response depends on the interaction strengths (Dambacher *et al.* 2002; Novak *et al.* 2011; Yodzis
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31 171 1988b). (This, for example, accounts for difference between the predicted responses of the
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33 172 shared prey to a perturbation to the omnivore's alternative prey in our quantitative versus our
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35 173 qualitative predictions; cf. eqns 3 and 5.) The columns of the qualitatively-specified adjoint can
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37 174 also be combined to predict the effects of perturbing multiple species simultaneously
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39 175 (Dambacher *et al.* 2002).

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What is the community matrix?

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178 We turn to the interpretation of the α_{ij} elements of \mathbf{A} . Rather than beginning with the
179 community matrix itself, we first discuss the derivation of the interaction and Jacobian matrices

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3 180 because these may also be defined for the original community matrix.
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7 181 *The interaction matrix*
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10 182 A number of authors have referred to the interaction matrix as being synonymous with the
11 community matrix (e.g., Attayde & Hansson 2001; Berg *et al.* 2011; Jansen & Kokkoris 2003;
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13 184 Laska & Wootton 1998; Roberts & Stone 2004). Consider a community of S interacting species
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15 185 in which the i^{th} species exhibits a per capita growth rate described by
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$$\frac{1}{N_i} \frac{dN_i}{dt} = f_i(N_1, N_2, \dots, N_S) \quad i = 1 \text{ to } S. \quad (6)$$

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22 187 That is, the per capita rate of change of the species i 's abundance is some function of its own
23 abundance and that of other species in the community (not necessarily all S). Typically we
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25 188 assume that the community is closed to immigration or emigration, that the strengths of the
26 pairwise direct interactions are constant and linear with respect to species densities, and that
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28 189 there are no interaction modifications (sensu Wootton 1994). More often than not we do so by
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30 190 replacing $f_i(N_1, N_2, \dots, N_S)$ with a generalized version of a Lotka-Volterra model written as
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$$\begin{aligned} \frac{1}{N_i} \frac{dN_i}{dt} &= r_i + \sum_{j=1}^S a_{ij} N_j \\ 38 &= r_i + a_{ii} N_i + \sum_{j \neq i}^S a_{ij} N_j \end{aligned} \quad (7)$$

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45 194 (e.g., Pimm & Lawton 1978). Thus, species i 's observed per capita growth rate, $\frac{1}{N_i} \frac{dN_i}{dt}$, is a
46 function of its intrinsic per capita growth rate (r_i), its own self-effects ($a_{ii} < 0$), its interactions
47 with other species ($a_{ij} < 0$ and $a_{ji} > 0$ for a prey- i consumer- j pair; a_{ij} and $a_{ji} < 0$ for competitors;
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52 199 The per capita growth rate r is the net effect of a population's per capita birth and death rates in
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3 200 the absence of all other explicitly considered species. Thus for species whose resources are
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5 201 considered implicitly we assume $r > 0$, while for species whose resources are considered
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7 202 explicitly (e.g., consumers) we let $r < 0$ because we have already accounted for their prey-
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10 203 dependent birth rates in the $\sum a_{ji}N_j$ terms. A consumer's r therefore reflects its intrinsic per capita
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12 204 death rate.

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15 205 As emphasized by Yodzis (1988a), conclusions drawn regarding species dynamics in the
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17 206 context of the community matrix need not rest on an assumption of an underlying Lotka-Volterra
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19 207 model. Any alternative continuous differentiable model can suffice (e.g., Nakajima 1992;
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21 208 Yodzis 2000), although if nonlinearities exist, predictions will only be accurate when the new
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23 209 equilibrium of the perturbed community is close to the prior equilibrium (SOM, Bender *et al.*
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25 209 1984; Case 2000; Yodzis 1988b).

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29 211 The a_{ii} and a_{ij} parameters of this model (eqn 7) are, respectively, the diagonal and off-
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31 212 diagonal elements of the interaction matrix (Travis & Post 1979). For later contrast to the
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33 213 original community matrix, note that the a_{ij} parameters of eqn 7 are not scaled to the r_i . Thus the
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35 214 interaction matrix \mathbf{A}_I of our four-species example community is

$$36 \quad \mathbf{A}_I = \begin{bmatrix} a_{11} & a_{12} & a_{13} & 0 \\ a_{21} & a_{22} & a_{23} & 0 \\ a_{31} & a_{32} & a_{33} & a_{34} \\ 0 & 0 & a_{43} & a_{44} \end{bmatrix}. \quad (8)$$

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39 215 There are several ways to summarize what the a_{ij} elements of the interaction matrix mean:
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43 216 • Each a_{ij} reflects the direct effect that an individual of species j has on species i 's per capita
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45 217 growth rate; they are per capita interaction strengths (Laska & Wootton 1998).
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50 219 • Each a_{ij} reflects the direct effect that an individual of species j has on an individual of species
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52 220 *i* per (instantaneous) unit of time (Novak & Wootton 2010).
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55 221 • With only species i and j present, species i 's population-level growth rate is changed by

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3 222 $a_{ij}N_iN_j$ amount in the presence of species j relative to when j is absent.
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5 223 • A small change in the abundance of j has $a_{ij}N_i$ effect on the population growth rate of species
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7 224 i .
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9 225 In the absence of all other species in a community of competitors (resources considered
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11 implicitly), species i would eventually attain its carrying capacity $K_i = r_i/a_{ii}$ at equilibrium
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13 226 (Vandermeer 1975). For predator-prey interactions we typically consider the bottom-up per
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15 capita effect of prey i on predator j to be scaled to the predator's top-down per capita effect by
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17 227 the predator's efficiency at converting numbers of consumed prey individuals into numbers of
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19 228 predator individuals, $a_{ji} = -e_{ji}a_{ij}$. That is, we typically assume a constant linear numeric response
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21 229 (but see Lawton *et al.* 1975).

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23 232 Ecologists have come to formally define the a_{ij} elements of the interaction matrix as the
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25 partial derivative of the per capita growth rate of species i (eqn 6) with respect to the abundance
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27 of species j , the abundance of all other species held constant (Berlow *et al.* 2004; Christianou &
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29 234 Kokkoris 2008; Hernandez 2009; Laska & Wootton 1998; Travis & Post 1979):
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$$\begin{aligned} a_{ij} &= \frac{\partial [f_i(N_1, N_2, \dots, N_S)]}{\partial N_j} \\ &= \frac{\partial \left(\frac{1}{N_i} \frac{dN_i}{dt} \right)}{\partial N_j} \end{aligned} \quad . \quad (9)$$

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42 236 With this definition it can be seen that per capita interaction strengths need not be restricted
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44 to single values; they may themselves be functions – linear or nonlinear – of species abundances
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60 237 and other variables (e.g., Novak & Wootton 2008, 2010). Nonlinear interactions nonetheless
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60 complicate the simplistic extrapolation of per capita effects from a linear model. For example, in
a 2-species predator-prey interaction with a nonlinear functional response the predator's top-
down per capita effect might be described by a Type II response,

$$a_{ij} = -\frac{c}{1 + chN_i} \quad (10)$$

(Holling 1959), where parameter c is the per capita attack rate constant that describes the rate at which j 's feeding rate on i approaches a saturation point set by the handling time. In such a scenario, according to eqn 9, the interaction matrix is

$$\begin{bmatrix} a_{ii} + \frac{c^2 h N_j}{(1+c h N_i)^2} & -\frac{c}{1+c h N_i} \\ \frac{c}{(1+c h N_i)^2} & a_{jj} \end{bmatrix}. \quad (11)$$

248 The prey's per capita effect on itself thus becomes positive when the magnitude of a_{ii} is less than
249 $\frac{c^2 h N_j}{(1 - ch N_i)^2}$, which depends on species abundances and how far from linearity the predator's
250 functional response is.

The Jacobian

252 Numerous authors have also implicitly or explicitly referred to the Jacobian as being
253 synonymous with the community matrix; this has become the more typical use of the term (e.g.,
254 Dambacher *et al.* 2002; de Ruiter *et al.* 1995; Edelstein-Keshet 2005; Levins 1975; May 1972;
255 Montoya *et al.* 2009; Moore *et al.* 1993; Puccia & Levins 1991; Schmitz 1997; Solé &
256 Bascompte 2006; Stone & Roberts 1991; Travis & Post 1979; Yodzis 1995; Yodzis 1998).
257 Although May (1972) refers to a Jacobian with the term ‘interaction matrix’, this paper and May
258 (1973) appear to have been the origin of the reference to the community matrix as the Jacobian.

Unlike the interaction matrix, the Jacobian is derived using a species' population-level growth rate,

$$\frac{dN_i}{dt} = N_i f_i(N_1, N_2, \dots, N_S) \quad i = 1 \text{ to } S. \quad (12)$$

262 Note that, because $f_i(N_1, N_2, \dots, N_S)$ also contains N_i , eqn 12 is often written as

263 $\frac{dN_i}{dt} = f_i(N_1, N_2, \dots, N_S)$, just like the per capita growth rate (eqn. 6), which can cause

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3 264 confusion. In the generalized version of the Lotka-Volterra model (eqn 7),
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$$\begin{aligned} \frac{dN_i}{dt} &= N_i \left(r_i + \sum_{j=1}^S a_{ij} N_j \right) \\ &= r_i N_i + a_{ii} N_i N_i + \sum_{j \neq i}^S a_{ij} N_i N_j . \end{aligned} \quad (13)$$

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15 266 Formally, elements of the Jacobian, to which we will refer by \mathbf{J} , represent the partial derivatives
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17 of species i 's population-level growth rate with respect to the abundance of species j , all other
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19 species held constant (Berlow *et al.* 2004; Christianou & Kokkoris 2008; Hernandez 2009; Laska
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21 & Wootton 1998; Travis & Post 1979). That is,
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$$\begin{aligned} J_{ij} &= \frac{\partial[N_i f_i(N_1, N_2, \dots, N_S)]}{\partial N_j} \\ &= \frac{\partial(\frac{dN_i}{dt})}{\partial N_j} \\ &= \begin{cases} a_{ij} N_i & \text{for } i \neq j \\ f_i(N_1, N_2, \dots, N_S) + a_{ii} N_i & \text{for } i = j \end{cases} \end{aligned} \quad (14)$$

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35 271 (e.g., de Ruiter *et al.* 1995; Pimm & Lawton 1977, 1978). Note that, at equilibrium, $J_{ii} = a_{ii} N_i^*$
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37 272 because $r_i = \sum_{j=1}^S a_{ij} N_j^*$, such that $f_i(N_1, N_2, \dots, N_S) = 0$ (Case 2000; Hernandez 2009).
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40 273 Although the Jacobian is typically evaluated at equilibrium, this is not a necessary condition for
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42 its use (Berlow *et al.* 2004). Only at the equilibrium do the diagonal elements represent only
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44 intraspecific self-limitation effects, though this is itself only true when species interactions are
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46 linear (Haydon 1994, and see below). In matrix form the Jacobian of our example community is
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$$\begin{aligned} \mathbf{J} &= \begin{bmatrix} J_{11} & J_{12} & J_{13} & 0 \\ J_{21} & J_{22} & J_{23} & 0 \\ J_{31} & J_{32} & J_{33} & J_{34} \\ 0 & 0 & J_{43} & J_{44} \end{bmatrix} \\ &= \begin{bmatrix} r_1 + 2a_{11}N_1 + a_{12}N_2 + a_{13}N_3 & a_{12}N_1 & a_{13}N_1 & 0 \\ r_2 + a_{21}N_2 & a_{21}N_1 + 2a_{22}N_2 + a_{23}N_3 & a_{23}N_2 & 0 \\ a_{31}N_3 & a_{32}N_3 & 0 & a_{34}N_3 \\ 0 & 0 & a_{43}N_4 & r_4 + a_{43}N_3 + 2a_{44}N_4 \end{bmatrix} . \end{aligned}$$

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(15)

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There are several ways to summarize what the J_{ij} elements of the Jacobian mean:

279 • Each J_{ij} reflects the effect that an individual of species j has on species i 's population-level
 280 growth rate.

281 • Each J_{ij} reflects the effect that an individual of species j has on the population of species i .

282 • With only species i and j present, the i^{th} species' population-level growth rate is thus changed
 283 by amount $a_{ij}N_iN_j$ in the presence of species j relative to when j is absent, as described for the
 284 interaction matrix.

285 Potential confusion has arisen because elements of the Jacobian have also been referred to as per
 286 capita interaction strengths (e.g., de Ruiter *et al.* 1995) and per capita effects (Yodzis 1981;
 287 Yodzis 1988a).

288 As for the interaction matrix, nonlinear species interactions complicate the simplistic
 289 extrapolation of Jacobian elements from the linear case. For example, for the 2-species predator-
 290 prey interaction with a Type II functional response (eqn 10), the Jacobian is

$$291 \left[\begin{array}{cc} r_i + 2a_{ii}N_i + \frac{c^2hN_iN_j}{(1+chN_i)^2} - \frac{cN_j}{1+chN_i} & -\frac{cN_i}{1+chN_i} \\ \frac{ecN_j}{(1+chN_i)^2} & r_j + \frac{ecN_i}{1+chN_i} + 2a_{jj}N_j \end{array} \right]. \quad (16)$$

292 Here the prey's self-effect may be negative or positive depending on species abundances, how
 293 far from linearity the predator's functional response is, and the strength of the prey's self-
 294 limitation.

295 *The original community matrix*

296 So which of these matrices – the interaction matrix or the Jacobian – is the “community
 297 matrix”? Technically, neither is.

298 The term community matrix was coined to refer to a system of competing species (resources

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3 300 considered implicitly) whose empirically-inspired estimates of pairwise direct species interaction
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5 301 strengths were derived from measures of niche overlap (Davidson 1980; Levins 1968; May
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7 302 1975; May & Arthur 1972). Levins (1968) based his derivation on the Lotka-Volterra
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9 303 competition model (Lotka 1932; Volterra 1926) used by Gause (1934). This model can be
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11 304 expanded to obtain the generalized Lotka-Volterra model for any type of interaction (eqn 7) as
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13 305 follows:
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$$\begin{aligned}
 \frac{1}{N_i} \frac{dN_i}{dt} &= f_i(N_1, N_2, \dots, N_S) \\
 &= \frac{r_i(K_i - N_i - \sum_{j \neq i}^S \alpha_{ij} N_j)}{K_i} \\
 &= r_i \left(1 - \frac{N_i}{K_i} - \sum_{j \neq i}^S \frac{\alpha_{ij} N_j}{K_i} \right) = r_i \left(1 - \sum_{j=1}^S \frac{\alpha_{ij} N_j}{K_i} \right) \\
 &= r_i - \frac{r_i N_i}{K_i} - \frac{r_i}{K_i} \sum_{j \neq i}^S \alpha_{ij} N_j \\
 &= r_i - a_{ii} N_i - a_{ii} \sum_{j \neq i}^S \alpha_{ij} N_j \\
 &= r_i - a_{ii} N_i - \sum_{j \neq i}^S a_{ij} N_j \\
 &= r_i - \sum_{j=1}^S a_{ij} N_j \text{ with } a_{ij} > 0 \text{ and } a_{ji} < 0 \\
 &= r_i + \sum_{j=1}^S a_{ij} N_j \text{ with } a_{ij} < 0 \text{ and } a_{ji} > 0
 \end{aligned} \tag{17}$$

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47 306 The 2nd line is the formulation used by Levins (1968, pg. 52). The 3rd line contains the
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49 307 formulation used by Bender et al. (1984) where they used the letter c_i to represent r_i / K_i . Note
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51 308 that in the last four lines a switch is made by substituting $\alpha_{ii} = a_{ii}/a_{ii} = 1$ and $\alpha_{ij} = a_{ij}/a_{ii}$ using K_i
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53 309 = r_i/a_{ii} (Schaffer 1981; Seifert & Seifert 1976; Vandermeer 1975). The original community
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55 310 matrix is composed of these α competition coefficients which Levins (1968, p.51) interpreted as
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57 311 matrix is composed of these α competition coefficients which Levins (1968, p.51) interpreted as
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3 312 “the reduction in the rate of increase of [species i] caused by an individual of [species j]
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5 313 compared to the effect of an individual of [species i]”. That is, the interspecific effect of j on i is
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7 314 expressed as a fraction of species i ’s intraspecific effect (Vandermeer 1975).
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10 315 Levins’ derivation of the community matrix converted the Lotka-Volterra competition model
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12 316 to matrix form at equilibrium as follows:
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$$\begin{aligned}
 \frac{dN_i}{dt} &= \frac{r_i N_i (K_i - N_i - \sum_{j \neq i}^S \alpha_{ij} N_j)}{K_i} \\
 0 &= r_i N_i^* - \frac{r_i}{K_i} N_i^* N_i^* - \frac{r_i}{K_i} \sum_{j \neq i}^S \alpha_{ij} N_i^* N_j^* \\
 0 &= r_i N_i^* - \frac{r_i}{K_i} \sum_{j=1}^S \alpha_{ij} N_i^* N_j^* \\
 \frac{r_i}{K_i} \sum_{j=1}^S \alpha_{ij} N_i^* N_j^* &= r_i N_i^* \\
 \sum_{j=1}^S \alpha_{ij} N_i^* N_j^* &= N_i^* K_i \\
 \sum_{j=1}^S \alpha_{ij} N_j^* &= K_i
 \end{aligned}$$

317 $\mathbf{AN} = \mathbf{K}$, (18)

318 where

$$\mathbf{A} = \begin{bmatrix} \alpha_{11} & \alpha_{12} & \dots & \alpha_{1S} \\ \alpha_{21} & \ddots & \ddots & \ddots \\ \ddots & \ddots & \ddots & \ddots \\ \alpha_{S1} & \ddots & \ddots & \alpha_{SS} \end{bmatrix}, \quad \mathbf{N} = \begin{bmatrix} N_1^* \\ N_2^* \\ \vdots \\ N_S^* \end{bmatrix} \quad \text{and} \quad \mathbf{K} = \begin{bmatrix} K_1 \\ K_2 \\ \vdots \\ K_S \end{bmatrix}.$$

319 (19)

49 320 Levins (1968, pg. 53) referred to this \mathbf{A} matrix as the community matrix. He illustrated a matrix
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51 321 with diagonal elements $\alpha_{ii} = 1$ because, in terms of the competitive overlap of species niches, a
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53 322 species overlaps completely with itself. The off-diagonal α_{ij} elements of \mathbf{A} represent
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55 323 interspecific niche overlap. A sign reversal of the elements is needed to reflect the negative
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3 324 direct effects that competing species have on one another. In its original usage the community
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5 325 matrix was thus synonymous with both the alpha matrix (e.g., Lawlor 1979) and the competition
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7 326 matrix (e.g., Levine 1976; May 1975; May & Arthur 1972; Riebesell 1974), but see Vandermeer
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9 327 (1970). Vandermeer (1975) also presented what could be defined as the “beta matrix” with
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11 328 elements $\beta_{ii} = a_{ii}/a_{jj}$ and $\beta_{ij} = a_{ij}/a_{jj}$ representing the strength of intra- and interspecific
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13 interactions relative to the strength of the intraspecific interaction of the species affecting the
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15 329 competition.

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21 331 *What's the difference?*

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24 332 What is the distinction between the interaction strength measures of the original community
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26 333 matrix and those of the interaction and Jacobian matrices? The difference is only that, in
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28 334 contrast to the Lotka-Volterra model from which the interaction matrix and Jacobian were
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30 335 obtained (eqn 7), the α_{ij} interaction coefficients of the model used by Levins to define the
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32 336 community matrix (eqn 18) are scaled to the a_{ii} self-effects and the r_i intrinsic growth rates.
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35 337 Indeed, one can derive an interaction matrix and a Jacobian for this and any other differentiable
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37 338 model. Their elements, however, require different interpretations. This is shown by reapplying
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39 339 their formal definitions (eqns 9 and 14) to the model used by Levins (eqn 18) to obtain
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$$42 \quad \mathbf{A_I} = \begin{bmatrix} \frac{r_1\alpha_{11}}{K_1} & \frac{r_1\alpha_{12}}{K_1} & \cdot & \cdot & \frac{r_1\alpha_{1S}}{K_1} \\ \frac{r_2\alpha_{21}}{K_2} & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \frac{r_S\alpha_{S1}}{K_S} & \cdot & \cdot & \cdot & \frac{r_S\alpha_{SS}}{K_S} \end{bmatrix} \quad (20)$$

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$$\mathbf{J} = \begin{bmatrix} \frac{r_1(K_1 - 2\alpha_{11}N_1 - \sum \alpha_{1j}N_j)}{K_1} & -\frac{r_1\alpha_{12}N_1}{K_1} & \cdot & \cdot & -\frac{r_1\alpha_{1S}N_1}{K_1} \\ -\frac{r_2\alpha_{21}N_2}{K_2} & \frac{r_2(K_2 - 2\alpha_{22}N_2 - \sum \alpha_{2j}N_j)}{K_2} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ -\frac{r_S\alpha_{S1}N_S}{K_S} & \cdot & \cdot & \cdot & \frac{r_S(K_S - 2\alpha_{SS}N_S - \sum \alpha_{Sj}N_j)}{K_S} \end{bmatrix} \quad (21)$$

Interaction strengths as quantified by the α_{ij} of the original community matrix are thus not equivalent to those of the interaction matrix (eqn 8) or the Jacobian (eqn 15) obtained from the generalized Lotka-Volterra model (eqn 7) but are directly related to them.

Press perturbations revisited

In the previous section we have shown how the elements of the interaction, Jacobian, and the original community matrices represent different empirical measures of direct species interaction strengths. Each matrix is therefore composed of a different values. Its inverse consequently produces different predictions of a communities net responses to perturbations. To illustrate, we return to our example four-species community, letting the parameters of eqns 7 and 13 be as follows: $r_1 = r_4 = 0.1$, $r_2 = r_3 = -0.01$, $a_{11} = a_{44} = -0.5$, $a_{22} = a_{33} = -0.01$, $a_{12} = -1$, $a_{13} = -0.1$, $a_{23} = -0.5$, $a_{43} = -1$, $a_{21} = 0.5$, $a_{31} = 0.01$, $a_{32} = 0.05$, $a_{34} = 0.1$, and $a_{14} = a_{41} = a_{24} = a_{42} = 0$. Applying eqns 9 and 14 gives

$$\mathbf{A_I} = \begin{bmatrix} -0.5 & -1 & -0.1 & 0 \\ 0.5 & -0.01 & -0.5 & 0 \\ 0.01 & 0.05 & -0.01 & 0.1 \\ 0 & 0 & -1 & -0.5 \end{bmatrix} \quad (22)$$

and

$$\mathbf{J} = \begin{bmatrix} -4.24 \times 10^{-2} & -8.49 \times 10^{-2} & -8.49 \times 10^{-3} & 0 \\ 2.56 \times 10^{-2} & -5.12 \times 10^{-4} & -2.56 \times 10^{-2} & 0 \\ 6.38 \times 10^{-4} & 3.19 \times 10^{-3} & -6.38 \times 10^{-4} & 6.38 \times 10^{-3} \\ 0 & 0 & -7.23 \times 10^{-2} & -3.62 \times 10^{-2} \end{bmatrix} \Big|_{N^*}, \quad (23)$$

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3 359 and, substituting $\alpha_{ii} = a_{ii}/a_{ii} = 1$ and $\alpha_{ij} = a_{ij}/a_{ii}$, gives
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$$6 \quad \mathbf{A} = \begin{bmatrix} 1 & 2 & 0.2 & 0 \\ 7 -50 & 1 & 50 & 0 \\ 8 -1 & -5 & 1 & -10 \\ 9 0 & 0 & 2 & 1 \end{bmatrix} \quad (24)$$

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12 361 (Note that the sign structure of $-\mathbf{A}$ corresponds to the more intuitive interpretation of the
13 community's predator-prey interactions (cf. eqn 2)). The corresponding predictions of net
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15 362 effects are
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$$19 \quad -\mathbf{A}_{\mathbf{I}}^{-1} = \begin{bmatrix} 0.23 & -1.85 & 4.30 & 0.86 \\ 20 0.86 & 0.91 & -2.58 & -0.52 \\ 21 0.22 & 0.13 & 4.35 & 0.87 \\ 22 -0.43 & -0.26 & -8.70 & 0.26 \end{bmatrix} \quad (25)$$

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41 368 Roberts & Stone (2004) refer to $-\mathbf{A}_{\mathbf{I}}^{-1}$ as the effective interaction matrix. Nakajima (1992) refers
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44 369 to $-\mathbf{J}^{-1}$ as the sensitivity matrix.

$$26 \quad -\mathbf{J}^{-1} = \begin{bmatrix} 2.75 & -36.20 & 67.34 & 11.89 \\ 27 10.15 & 17.85 & -40.49 & -7.15 \\ 28 2.55 & 2.53 & 68.15 & 12.04 \\ 29 -5.10 & -5.05 & -136.30 & 3.59 \end{bmatrix} \Big|_{N^*}, \quad (26)$$

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$$35 \quad -\mathbf{A}^{-1} = \begin{bmatrix} -0.12 & 0.02 & -0.04 & -0.43 \\ 36 -0.43 & -0.01 & 0.03 & 0.26 \\ 37 -0.11 & -0.001 & -0.04 & -0.44 \\ 38 0.22 & 0.003 & 0.09 & -0.13 \end{bmatrix} \quad (27)$$

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46 370 So which is the correct matrix to use in predicting the net effects of press perturbations?
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49 371 That is, how should we best quantify interaction strengths? The answer depends on which of
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51 two subtly different types of press perturbations is imposed, or, more specifically, on the type of
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53 prediction that is sought: While the elements of $-\mathbf{J}^{-1}$ reflect the change in species i 's abundance
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56 373 due to a unit increase in species j 's population-level growth rate (Higashi & Nakajima 1995), the
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3 375 elements of $-\mathbf{A}_I^{-1}$ reflect the change in species i 's abundance due to a unit increase in species j 's
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5 376 per capita growth rate. (And since \mathbf{A} is a rescaling of \mathbf{A}_I , $-\mathbf{A}^{-1}$ is a rescaling of $-\mathbf{A}_I^{-1}$, see below).
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8 377 That is, each matrix provides predictions of a different type of press change to species j 's growth
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10 378 rate.

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13 379 Nevertheless, for predicting post-perturbation community structure given an change (positive
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15 or negative) in the actual abundance of species j (as opposed to its per capita or population-level
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17 growth rate) these differences don't matter; any of the three matrices can be used because their
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19 381 predictions differ only by a matter of scaling. The relative ranking of their predictions is the
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21 382 same. To illustrate this we begin by returning to Bender *et al.*(1984). Confusion arises because
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23 383 Bender *et al.*(1984) used the letter a to represent α interaction strengths. We will continue
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25 384 following the classic usage (i.e. $\alpha_{ij} = a_{ij}/a_{ii}$).
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30 386 Consider again the matrix equation $\mathbf{AN}=\mathbf{K}$ describing the relationship between the original
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32 (competition-based) community matrix (\mathbf{A}), each species' equilibrium abundance (\mathbf{N}), and their
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34 carrying capacities (\mathbf{K}). This can be rewritten as $\mathbf{N}=\mathbf{A}^{-1}\mathbf{K}$, where \mathbf{A}^{-1} is the inverse of \mathbf{A} .
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37 389 Because a press perturbation that increases species j 's growth rate has a direct negative effect on
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39 its competing species one must impose a sign reversal on \mathbf{A} to convert measures of niche overlap
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41 391 to species effects (Bender *et al.* 1984; Case 2000). The equation $\mathbf{N}=\mathbf{A}^{-1}\mathbf{K}$ suggests that if we
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43 392 selectively change species j 's carrying capacity by a small amount we should expect to see the
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45 393 equilibrium abundance of species i change by an amount proportional to $\alpha_{ij}^{(-1)}$, i.e., the ij^{th}
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47 394 element of \mathbf{A}^{-1} (Bender *et al.* 1984; Levine 1976). (For predictions of response direction we take
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49 395 the negative of \mathbf{A}^{-1} , see SOM.)
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54 396 To affect such a change in species j 's carrying capacity one might alter its population-level
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56 397 growth rate by amount P_j . That is

$$\frac{dN_i}{dt} = \begin{cases} N_i f_i(N_1, N_2, \dots, N_S) + P_j & \text{for } i = j \\ N_i f_i(N_1, N_2, \dots, N_S) & \text{for } i \neq j \end{cases} \quad (28)$$

(Case 2000; Higashi & Nakajima 1995; Solé & Bascompte 2006; Yodzis 1988b), equivalent to adding a constant P number of species j individuals to the community per unit time. The connection to j 's carrying capacity is seen more clearly by expressing the effect that perturbation P_j has on the elements of $\mathbf{A_I}$. Recalling that $K_j = 1/a_{jj}$, doing so shows the new j^{th} element of $\mathbf{A_I}$ to be $a_{jj} - P_j/N_j^2$, with all the other elements of $\mathbf{A_I}$ remaining unchanged. Thus imposing perturbation P_j on species j is not equivalent to affecting its per capita growth rate (which would be equivalent to $dN_i/dt = N_j f_i(N_1, N_2, \dots, N_l) + p_j N_i$ for $i = j$.)

406 However, Bender et al. (1984) recognized that estimating species abundances is far easier
 407 than estimating changes in their carrying capacities. They showed that predictions of relative
 408 abundance changes can also be made using A^{-1} and N , rather than A^{-1} and K , because

$$\frac{\partial N_i^* f_i(N_1^*, N_2^*, \dots, N_S^*) / \partial P_j}{\partial N_j^* f_j(N_1^*, N_2^*, \dots, N_S^*) / \partial P_j} = \frac{\partial N_i^*(P_j) / \partial P_j}{\partial N_j^*(P_j) / \partial P_j} = \frac{\alpha_{ij}^{(-1)}}{\alpha_{jj}^{(-1)}} = \lim_{P_j \rightarrow 0} \frac{\Delta N_i^*}{\Delta N_j^*} \quad (29)$$

(Bender *et al.* 1984; Case 2000; Higashi & Nakajima 1995; Nakajima & Higashi 1995). That is, the ratio of the partial derivatives of species i 's and species j 's population growth rates with respect to perturbation P_j is equivalent to the ratio of their respective elements in \mathbf{A}^{-1} . This, in turn, is approximated by the ratio of the changes in their equilibrium abundance. The predicted equilibrium abundance of species i following a press perturbation to species j is therefore (Case 2000)

$$N_i^{*\text{new}} = N_i^{*\text{old}} + \frac{\alpha_{ij}^{(-1)}}{\alpha_{jj}^{(-1)}} \Delta N_j^*. \quad (30)$$

417 That is, the predicted post-perturbation abundance of species i will equal its pre-perturbation

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3 abundance plus a fraction $\frac{\alpha_{ij}^{(-1)}}{\alpha_{jj}^{(-1)}}$ of the amount that the perturbed species j is itself affected by the
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5 perturbation.
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10 420 *Scaling the matrix of net effects*
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13 421 How might we use the other matrices to make the same predictions of post-perturbation
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15 community structure given a change in species j 's equilibrium abundance? As just described,
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17 predicting net changes in species abundances resulting from a press perturbation on species j
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19 requires knowledge of the net effect elements of \mathbf{A}^{-1} . The chains of interactions that contribute
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21 to each element of \mathbf{A}^{-1} for a given interaction web can be difficult to decipher even though matrix
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23 methods make it relatively simple to calculate these symbolically (Dambacher *et al.* 2002). For
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25 example, for a two-species community where
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$$\mathbf{A} = \begin{bmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{bmatrix}, \quad (31)$$

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33 429 we obtain
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36 430
$$-\mathbf{A}^{-1} = \begin{bmatrix} \frac{\alpha_{22}}{\alpha_{12}\alpha_{21}-\alpha_{11}\alpha_{22}} & \frac{\alpha_{12}}{-\alpha_{12}\alpha_{21}+\alpha_{11}\alpha_{22}} \\ \frac{\alpha_{21}}{\alpha_{12}\alpha_{21}-\alpha_{11}\alpha_{22}} & \frac{\alpha_{11}}{\alpha_{12}\alpha_{21}-\alpha_{11}\alpha_{22}} \end{bmatrix}. \quad (32)$$

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40 431 By contrast, the elements of \mathbf{A}^{-1} are already quite complex for our four-species community (see
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42 SOM). Perturbing the shared prey, for example, causes a change in the intermediate predator
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44 proportional to
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$$\alpha_{21}^{(-1)} = \frac{\text{adj}(-\mathbf{A})_{21}}{\det(\mathbf{A})} = \frac{\alpha_{21}\alpha_{33}\alpha_{44} - \alpha_{21}\alpha_{34}\alpha_{43} - \alpha_{23}\alpha_{31}\alpha_{44}}{\det(\mathbf{A})} \quad (33)$$

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$$\det(\mathbf{A}) = \alpha_{13}(-\alpha_{22}\alpha_{31} + \alpha_{21}\alpha_{32})\alpha_{44} + \alpha_{12}(\alpha_{23}\alpha_{31}\alpha_{44} + \alpha_{21}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})) - \alpha_{11}(\alpha_{23}\alpha_{32}\alpha_{44} + \alpha_{22}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})). \quad (34)$$

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3 437 Nonetheless, observe that eqn 30 uses the ratio of the net effects between species i and j (the
4 outgoing effects, $\alpha_{ij}^{(-1)}$) and the net effects returning to species j itself, $\alpha_{jj}^{(-1)}$ (Higashi &
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6 Nakajima 1995; Nakajima & Higashi 1995). We refer to a matrix of these ratios as the scaled
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8 inverse of the community matrix. This matrix may be calculated as
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13 441 $\mathbf{A}_{\text{scaled}}^{-1} = \mathbf{A}^{-1} \oslash [\text{diag}(\mathbf{A}^{-1}) \otimes \text{diag}(\mathbf{I})^T]^T$, (35)

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16 442 where \oslash indicates element-wise Hadamard division, \otimes indicates a Kronecker product, \mathbf{I} is an
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18 identity matrix with the dimensions of \mathbf{A} , and $\text{diag}(\mathbf{I})^T$ indicates the transpose of its diagonal (see
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21 SOM). Each element of the j^{th} column of \mathbf{A}^{-1} is thereby divided by element $\alpha_{jj}^{(-1)}$. That is
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$$\mathbf{A}_{\text{scaled}}^{-1} = \begin{bmatrix} \frac{\alpha_{11}^{(-1)}}{\alpha_{11}^{(-1)}} & \frac{\alpha_{12}^{(-1)}}{\alpha_{11}^{(-1)}} & \dots & \frac{\alpha_{1S}^{(-1)}}{\alpha_{11}^{(-1)}} \\ \frac{\alpha_{21}^{(-1)}}{\alpha_{11}^{(-1)}} & \frac{\alpha_{22}^{(-1)}}{\alpha_{11}^{(-1)}} & \dots & \frac{\alpha_{2S}^{(-1)}}{\alpha_{11}^{(-1)}} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\alpha_{S1}^{(-1)}}{\alpha_{11}^{(-1)}} & \dots & \dots & \frac{\alpha_{SS}^{(-1)}}{\alpha_{11}^{(-1)}} \end{bmatrix} = \begin{bmatrix} 1 & \frac{\alpha_{12}^{(-1)}}{\alpha_{22}^{(-1)}} & \dots & \frac{\alpha_{1S}^{(-1)}}{\alpha_{SS}^{(-1)}} \\ \frac{\alpha_{21}^{(-1)}}{\alpha_{11}^{(-1)}} & 1 & \dots & \dots \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\alpha_{S1}^{(-1)}}{\alpha_{11}^{(-1)}} & \dots & \dots & 1 \end{bmatrix}. (36)$$

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34 446 Levine (1976) refers to such ratios as normalized coefficients (Davidson 1980; Lawlor 1979).

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46 447 The fact that we make use of the ratios of outgoing versus returning net effects in the scaled
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50 inverse of the community matrix means that most of the terms contributing to the elements of the
449 unscaled inverse of the community matrix, including the determinant, cancel out. Scaling also
450 affects an automatic sign reversal in each element as needed; taking the negative of \mathbf{A}^{-1} is no
451 longer necessary. In the two species community this means a simplification to

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50 452
$$\mathbf{A}_{\text{scaled}}^{-1} = \begin{bmatrix} 1 & -\frac{\alpha_{12}}{\alpha_{11}} \\ -\frac{\alpha_{21}}{\alpha_{22}} & 1 \end{bmatrix} = \begin{bmatrix} 1 & -\alpha_{12} \\ -\alpha_{21} & 1 \end{bmatrix}, (37)$$

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50 because by definition $\alpha_{ii}=1$. Thus, as per intuition, relative to the change in the equilibrium
52 abundance of species 1, a press perturbation causing a one-individual increase in the equilibrium
53 abundance of species 1 will cause the equilibrium abundance of species 2 to be reduced by α_{21} .

1
2
3 456 In the four-species system of our example community, perturbing the shared prey causes a
4
5 457 change in the abundance of the intermediate predator proportional to
6
7

$$\alpha_{21 \text{ scaled}}^{(-1)} = \frac{\alpha_{21}^{(-1)}}{\alpha_{11}^{(-1)}} = \frac{\alpha_{21} (\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44}) + \alpha_{23}\alpha_{31}\alpha_{44}}{\alpha_{22} (\alpha_{33}\alpha_{44} - \alpha_{34}\alpha_{43}) - \alpha_{23}\alpha_{32}\alpha_{44}} \quad (38)$$

8 12 459 (see SOM).
9 13
10 14 460 Applying this procedure of eqn 35 to the inverse of the interaction and Jacobian matrices
11 15
12 16 461 shows that all three matrices – the original community matrix, the interaction matrix, and the
13 17
14 18 462 Jacobian – reduce to equivalent matrices when their inverses are scaled to their diagonals. The
15 19
16 20 463 inverse of each produces a matrix of predictions of relative species responses that are relative
17 21
18 22 464 within, not across, each of their columns. Thus, while matrices $\mathbf{-A}^{-1}$, $\mathbf{-A_I}^{-1}$ and $\mathbf{-J}^{-1}$ differ in that
19 23
20 24 465 they are relative to different net self-effects of the perturbed species affected by different types of
21 25
22 26 466 perturbations, all three can be used to predict the net effects that a press perturbation will have on
23 27
24 28 467 the community, relative to the net effects expressed in the abundance of the perturbed species
25 30
26 31 468 itself. In a two-species community, for example, since $\alpha_{ij} = a_{ij}/a_{ii}$,
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$$\begin{aligned} \mathbf{A}_{\text{scaled}}^{-1} &= \begin{bmatrix} 1 & -\alpha_{12} \\ -\alpha_{21} & 1 \end{bmatrix} \\ &= \begin{bmatrix} 1 & -\frac{\alpha_{12}}{\alpha_{11}} \\ -\frac{\alpha_{21}}{\alpha_{22}} & 1 \end{bmatrix} = \mathbf{A_I}^{-1}_{\text{scaled}} \end{aligned} \quad (39)$$

43 44 470 Similarly,
45
46

$$\begin{aligned} \mathbf{J}_{\text{scaled}}^{-1} &= \begin{bmatrix} 1 & \frac{\alpha_{12}N_1}{-2\alpha_{11}N_1 - \alpha_{12}N_2 - r_1} \\ \frac{\alpha_{21}N_2}{-\alpha_{21}N_1 - 2\alpha_{22}N_2 - r_2} & 1 \end{bmatrix} \\ &= \left[\begin{bmatrix} 1 & -\frac{\alpha_{12}}{\alpha_{11}} \\ -\frac{\alpha_{21}}{\alpha_{22}} & 1 \end{bmatrix} \right]_{N^*} = \mathbf{A_I}^{-1}_{\text{scaled}} \end{aligned} \quad (40)$$

53 54 472 For our quantified four-species community,
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$$\mathbf{A}_{\mathbf{I}_{\text{scaled}}}^{-1} = \mathbf{A}_{\text{scaled}}^{-1} = \mathbf{J}_{\text{scaled}}^{-1} = \begin{bmatrix} 1 & -2.03 & 0.99 & 3.31 \\ 3.69 & 1 & -0.59 & -1.99 \\ 0.93 & 0.14 & 1 & 3.35 \\ -1.85 & -0.28 & -2.00 & 1 \end{bmatrix}. \quad (41)$$

That is, a positive perturbation to the shared prey (column 1) is predicted to affect a 3.69-fold increase in the intermediate predator, a 0.93-fold increase in the omnivore, and a 1.85-fold decrease in the omnivore's alternative prey, relative to the change in the shared prey's own abundance (Fig. 2).

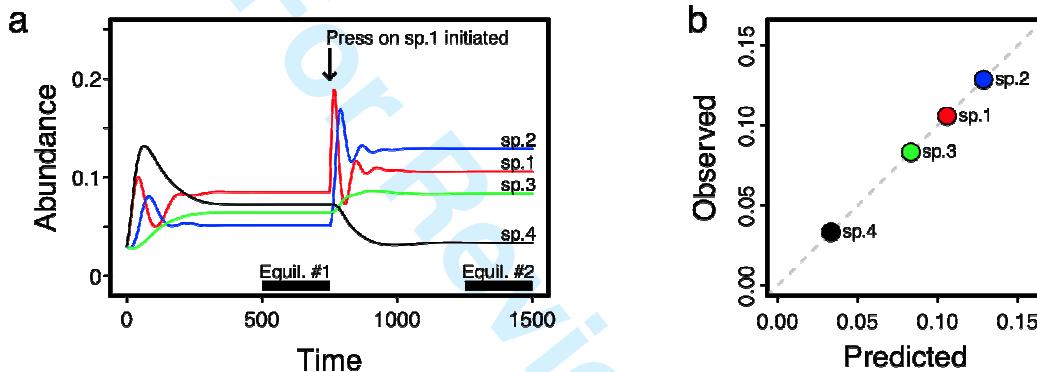


Figure 2. (a) Species dynamics of the four-species example community (Fig. 1) before and after the initiation of a press-perturbation to the shared-prey (species 1). Regions of pre- and post-perturbation equilibrium abundances are indicated. (b) One-to-one correspondence between the observed post-perturbation equilibrium abundances and those predicted by eqn 42 using the scaled inverse of the interaction matrix. Note that the post-perturbation abundance of species 1 is not itself predicted, but rather is needed for predicting the post-perturbation abundances of the other species. Dynamics simulated using eqn 13, with parameters as described in the main text, corresponding to eqns 22-24. The press-perturbation to species 1 was imposed at time = 750 by increasing r_1 to 0.19.

To convert these predictions of relative change to predictions of post-perturbation community structure we need to multiply each column of $\mathbf{A}_{\text{scaled}}^{-1}$ by the amount that the perturbed species' equilibrium abundance is changed (eqn 30). To do so in matrix form, thereby predicting the post-perturbation community structures caused by S independent perturbations simultaneously, we write

$$\mathbf{N}_{\text{new}} = [\mathbf{N}_{\text{old}} \otimes \text{diag}(\mathbf{I})^T] + \mathbf{A}_{\text{scaled}}^{-1} \circ [\mathbf{D} \otimes \text{diag}(\mathbf{I})^T]^T \quad (42)$$

where $\mathbf{N}_{\text{old}} = [N_1^{*\text{old}}, N_2^{*\text{old}}, \dots, N_S^{*\text{old}}]$, \circ indicates the element-wise Hadamard product (see

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3 494 SOM), and $\mathbf{D} = [\Delta N_1^*, \Delta N_2^*, \dots, \Delta N_S^*]$. The elements of vector \mathbf{D} are the differences of each
4 perturbed j^{th} species' pre- and post-perturbation equilibrium abundance
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6 495 $(\Delta N_j^* = N_j^{*\text{new}} - N_j^{*\text{old}})$ and equal zero if targeting the respective species is not of interest or
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8 496 the change in its abundance is unknown (see SOM and discussion below).
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13 498 The scaled inverse of any of the three matrices, which we might succinctly call the scaled net
14 effects matrix, is thus essentially equivalent to Lawlor's (1979) experimentally inspired gamma
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16 499 matrix, Γ , although Lawlor left the diagonal γ_{jj} elements undefined because in his derivation of Γ
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18 500 the experimenter holds species j 's abundance constant.
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22 502 A consequence of the equivalence of the scaled inverse of all three matrices is that press
23 perturbations need not be limited to changing the perturbed species' population-level growth rate
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25 503 (as in eqn 28) if the intent is to predict post-perturbation community structure given an observed
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27 504 change in the perturbed species' abundance. Such predictions may also be made for press
28 perturbations that change a species' growth rate by means of the per capita birth or death rates
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30 505 (e.g., r_j ; Fig. 2), the self-effect rate (e.g., a_{jj}), or the interspecific interaction strengths (e.g., a_{ij} , so
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32 506 long as the reciprocal a_{ji} is not also affected) (Higashi & Nakajima 1995; Nakajima 1992).
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509 ***Putting theory into practice: What should empiricists measure?***

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43 510 We have shown that scaling the off-diagonal elements of the inverse community matrix and
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45 511 of the inverse Jacobian by their diagonal elements reduces their predictions of net effects on
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47 512 community structure to the predictions made by the scaled inverse of the interaction matrix.
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50 513 Estimates of per capita interaction strengths thereby underlie not only the other measures of
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52 514 direct pairwise interaction strengths (Laska & Wootton 1998) but their net effects as well. We
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54 515 therefore recommend that empiricists continue to quantify interaction strengths on a per capita
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56 basis and refer to recent summaries of alternative methods aimed at doing so for interspecific
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3 517 interactions (Berlow *et al.* 2004; Novak 2010; Novak & Wootton 2008; Wootton & Emmerson
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5 518 2005).

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7 519 The approach of the scaled net effects matrix nevertheless leave us with at least two potential
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9 520 quandaries when it comes to predicting the post-perturbation abundances. In addition to having
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11 521 to estimate all pairwise direct interspecific interaction strengths, we also need to (*i*) know the
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13 522 change in the equilibrium abundance of the perturbed species (ΔN_j^*) in order to convert
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15 523 predictions of relative changes to absolute changes in species abundances, and (*ii*) have
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17 524 measured the diagonal elements of the interaction matrix (each species' effect on its own per
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19 525 capita growth rate). The first of these is problematic since we might like to predict the response
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21 526 of the perturbed species itself, without having to perform the actual perturbation. The second is
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23 527 problematic because self-effects are arguably even more difficult to estimate than interspecific
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25 528 interactions. We discuss each of these issues in turn.

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27 529 Unlike the focus of our discussion on using interaction strength estimates to predict species
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29 530 responses to an anticipated perturbation, the intent of Bender *et al.* (1984) was to use
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31 531 perturbation experiments to estimate the interaction strengths themselves. In reversing this
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33 532 process, Case (2000) ostensibly solved the first of our stated problems by having the
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35 533 experimenter remove all of species j , thereby making ΔN_j^* equal to the pre-disturbance $N_j^{*\text{old}}$.
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37 534 This approach suffers from potential limitations: First, as Bender *et al.* (1984) pointed out,
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39 535 perturbations may not affect subsequent extinctions; the math breaks down when $N_i^{*\text{new}} < 0$ (Fig.
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41 536 3b). Species removals therefore preclude predicting the effects of prey species having specialist
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43 537 predators, for example. Second, species removal will change the topology of a non-competitive
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45 538 interaction web to affect consequent changes in the indirect effects even without the occurrence
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47 539 of secondary extinctions (see discussion of the removal matrix, \mathbf{R} , by Laska & Wootton 1998;

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3 540 Wootton & Emmerson 2005). Third, such perturbations are unlikely to be “sufficiently small” to
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5 541 adequately represent non-linear systems by linear approximations (Fig. 3c, see SOM). Finally,
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7 542 the approach of removing a species is of little use for predicting the effects of press perturbations
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9 543 that do not lead to complete extinction, such as sustainable fishing pressure or the incomplete
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11 544 eradication of a targeted invasive. Two solutions are readily apparent, each with pros and cons.
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15 545 The first solution is to predict the post-perturbation abundance of the perturbed species
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17 546 following a pre-designed alteration of its growth rate (per capita or population-level) akin to
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19 547 setting a catch rate in a fisheries context. Unfortunately, in addition to estimating all per capita
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21 548 interaction strengths and pre-perturbation abundances, this approach requires us to have also
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23 549 estimated all intrinsic per capita growth rates (e.g., the r_i of a Lotka-Volterra model). In other
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25 550 words, we must obtain estimates for all the parameters of the model representing the community
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27 551 of interest. The scaled net effects matrix is thereby only a shortcut to simulating or obtaining an
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29 552 analytical solution of the equilibria for the entire model. It is possible that development of semi-
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31 553 parametric (Wood 2001) and generalized modeling techniques (Yeakel *et al.* 2011) in the context
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33 554 of community matrix theory will offer a means to reduce these empirical limitations in the future.
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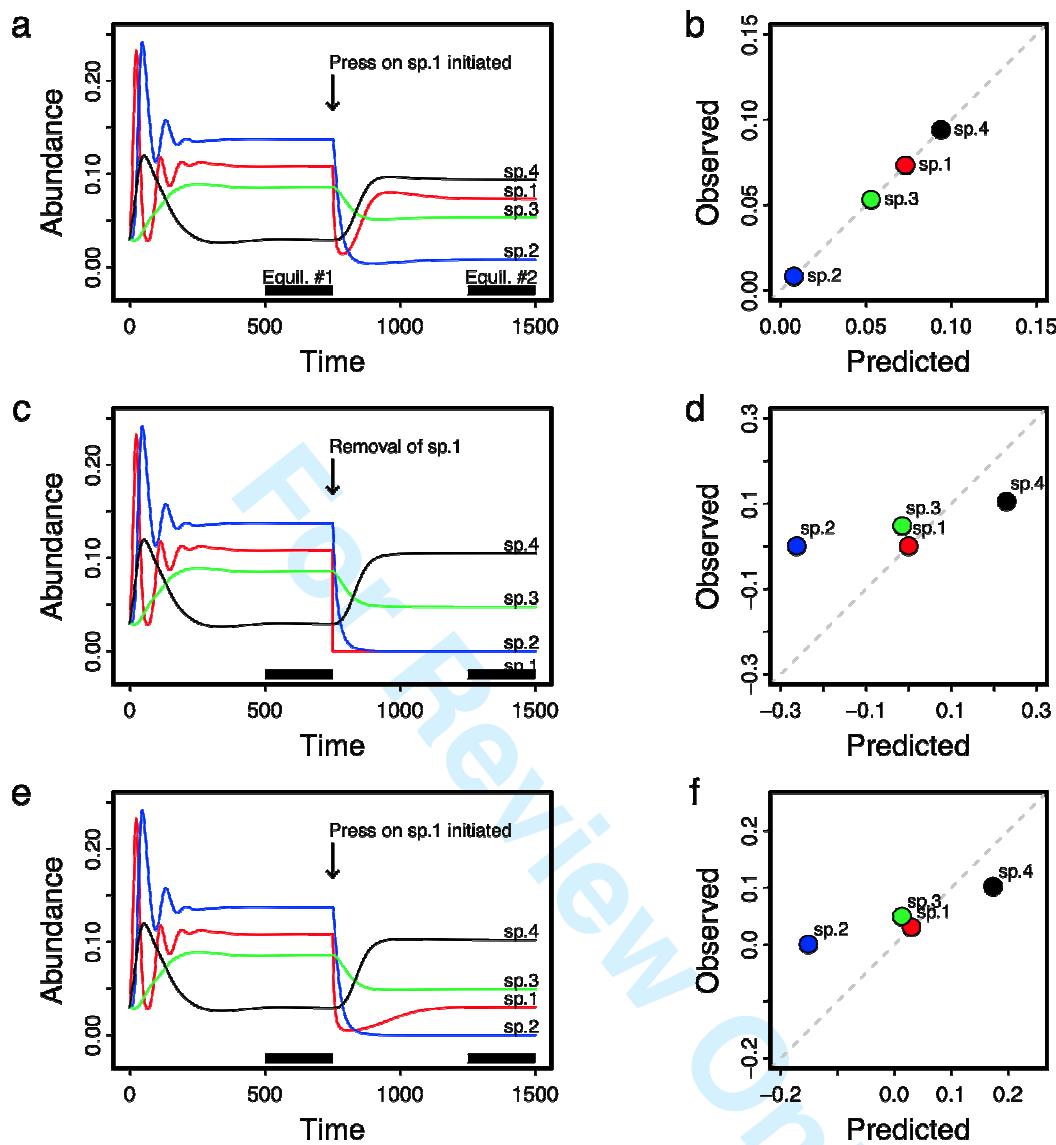


Figure 3. Left column: Species dynamics of the four-species interaction web (Fig. 1) before and after the initiation of three different perturbations to the shared-prey (species 1). Right column: Associated correspondence between the observed post-perturbation equilibrium abundances and those predicted by eqn 42 using the scaled-inverse of the interaction matrix. All pre-perturbation parameters and starting abundances as in Fig. 2 except r_1 which is here set to 0.2. (a-b) A press reduction in r_1 to 0.05 (as opposed to the increase illustrated in Fig. 2.). (c-d) A complete removal of species 1, parameters unchanged. (e-f) A more extreme reduction in r_1 to 0.02 affecting the effective extinction of the intermediate predator ($N_2 < 1 \times 10^9$). Note that the abundance of species 1 is not itself predicted.

The second solution is to predetermine an abundance for the perturbed species and adjust the magnitude of the perturbation accordingly until a stable target abundance is achieved (Bender *et al.* 1984). In a fisheries context this would be akin to an adaptive management strategy. The

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3 567 scaled net effects matrix and pre-perturbation abundances could then be used to forecast the post-
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5 568 perturbation abundances of the non-perturbed species under alternative perturbed-species
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7 569 abundance scenarios. This avoids having to measure all intrinsic growth rates at the price of
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9 570 needing an adaptive strategy in the implementation of the perturbation. This may be the more
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11 571 accessible approach. Nevertheless, given the counter-intuitive changes in abundance that may
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13 572 result, particularly when interaction strengths vary or are estimated imprecisely (Novak *et al.*
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15 573 2011; Roberts & Stone 2004; Yodzis 1988b), such an adaptive strategy may be far from simple
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17 574 (Doak *et al.* 2008). Further work is needed to understand how empirical network topologies and
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19 575 the topological position of strong and weak interactions may influence our predictive limits
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22 576 (Novak *et al.* 2011).

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28 577 *The diagonal elements*

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30 578 The second problem – the measurement of the diagonal elements of either the Jacobian or the
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32 579 interaction matrix – is more fundamental. In most theoretical investigations of non-competitive
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34 580 communities it is standard to assume full self-limitation in all basal species; species without
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36 581 explicitly-included resources are assumed to be regulated by implicit factors. The diagonal
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38 582 elements are thus typically set to -1 (e.g., Christianou & Ebenman 2005; Emmerson & Raffaelli
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40 583 2004; Yodzis 1988b). May (1972; 1973) refers to this as setting the time-scale of the
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42 584 community's dynamics; each species in isolation thereby contributes a damping time of -1 to
43
44 585 which off-diagonal elements are assumed scaled (see eqn 16 and Haydon 1994 for a critique).
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47 586 Non-basal species are typically assigned some small fraction of the basal species' self-effect
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49 587 (e.g., Christianou & Ebenman 2005; Emmerson & Raffaelli 2004; Yodzis 1988b). In qualitative
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52 588 modeling it is typical to impose negative self-effects on all species (e.g., Dambacher *et al.* 2002).

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3 589 Increasing the strength of negative self-effects leads to increased stability (by diagonal
4 dominance, Logofet 1993). Indeed, the magnitude of diagonal elements in the Jacobian has been
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6 590 used to gauge stability (Neutel *et al.* 2002; Neutel *et al.* 2007). Because the sum of a matrix's
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8 591 diagonal elements (its trace) equals the sum of its eigenvalues, and a positive trace implies
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10 592 instability (Allesina & Pascual 2008; Haydon 1994; May 1973), increasing the proportion of
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12 593 species experiencing self-limitation also increases stability (De Angelis 1975; Saunders 1978;
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14 594 Yodzis 1981). The presence of negative self-effects also increases structural stability when a
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16 595 community is specified qualitatively. Indeed, a necessary condition for structural stability is that
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18 596 ${}^{\circ}\mathbf{A}_{ii} \leq 0$ for all species and that some ${}^{\circ}\mathbf{A}_{ii} < 0$ (Allesina & Pascual 2008; Logofet 1993).
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20 597 Structurally stable matrices are non-singular. Because this is a necessary condition for inverting
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22 598 \mathbf{A} (and for calculating the adjoint of ${}^{\circ}\mathbf{A}$) assuming negative self-effects among all species
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24 599 increases the likelihood that predictions of species responses to press perturbations can be
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26 600 produced.
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42 603 **Figure 4.** The interaction web of Fig. 1, but with no self-limitation for the two consumer species.
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45 604 The nature of the diagonal elements is relevant to our discussion because assumptions
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47 concerning the presence of negative self-effects can alter our predictions of community
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49 responses. For example, in our four-species community we specified negative self-effects in all
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51 species (Fig. 1). Removing the self-effects of the two consumers (Fig. 4) changes the predictions
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53 for how the shared prey species (1st row) will respond to a press perturbation of the omnivore (1st
54 row, 3rd column) or of the omnivore's alternative prey (1st row, 4th column):
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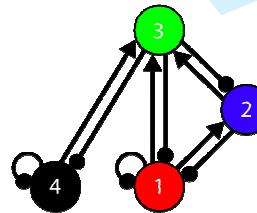


Figure 4. The interaction web of Fig. 1, but with no self-limitation for the two consumer species.

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609 The nature of the diagonal elements is relevant to our discussion because assumptions
concerning the presence of negative self-effects can alter our predictions of community
responses. For example, in our four-species community we specified negative self-effects in all
species (Fig. 1). Removing the self-effects of the two consumers (Fig. 4) changes the predictions
for how the shared prey species (1st row) will respond to a press perturbation of the omnivore (1st
row, 3rd column) or of the omnivore's alternative prey (1st row, 4th column):

$$\circ \mathbf{A} = \begin{bmatrix} -1 & -1 & -1 & 0 \\ 1 & 0 & -1 & 0 \\ 1 & 1 & 0 & 1 \\ 0 & 0 & -1 & -1 \end{bmatrix} \quad \text{adj}(-\circ \mathbf{A}) = \begin{bmatrix} 1 & -2 & 1 & 1 \\ 0 & 2 & -2 & -2 \\ 1 & 0 & 1 & 1 \\ -1 & 0 & -1 & 1 \end{bmatrix}. \quad (43)$$

That is, whereas our previous predictions were indeterminate (eqn 5), the shared prey is now predicted to respond to these perturbations by increasing. Such changes can occur in quantitatively-specified matrices as well. Generally, the more negative the a_{ii} , the smaller the relative species responses will be (Nakajima 1992).

These observations suggest that serious consideration of what the diagonal elements represent is needed when making predictions. The issues of assessing self-limitation effects in general terms have received considerable attention in the debate over population regulation (e.g., Krebs 2002; Turchin 1999). Rather than rehash these issues we will discuss only two of particular relevance in the context of multispecies interactions: the interpretation of the diagonal elements for (i) consumer species and (ii) for species with nonlinear interactions.

In regards to the diagonal elements of consumer species, recall that in the interaction matrix of the Lotka-Volterra model (closed to immigration or emigration) the diagonal elements reflect the intraspecific damping effects of self-limitation (eqn 8). In the Jacobian this is only true at equilibrium (eqn 14). Because we have already accounted for intraspecific exploitative competition by modeling their prey explicitly, one might argue that a consumer's a_{ii} should therefore 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 consumer levels (Dunne *et al.* 2004; Havens 1992; Paine 1988). Nevertheless, higher-level consumers may obtain resources across larger spatial scales than other species (McCann *et al.* 2005; Paine 1988); their non-local resources may remain unconsidered. Without the explicit inclusion of such subsidies a population's mortality rate would be underestimated, its diagonal

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3 632 element in the interaction matrix should be < 0 (e.g., let P of eqn 28 represent a density-
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5 633 independent input of non-dynamic allochthonous resources.) Indeed, in more generally-specified
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7 634 open systems, immigration and emigration respectively increase and decrease self-damping
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9 635 effects (Puccia & Levins 1991). Empiricists should be particularly careful and explicit in
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11 636 defining the spatial extent of their community. In some situations quantifying immigration and
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13 637 emigration rates may be just as important as quantifying interaction strengths. Further theory is
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15 638 needed to help guide such considerations.

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20 639 Species with nonlinear interactions complicate matters further because their diagonal
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22 640 elements in the interaction matrix also contain interspecific effects (eqn 11). These effects do
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24 641 not cancel in the off-diagonals of the scaled net effects matrix. For example, with two species
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26 642 (eqn 10),

$$\begin{aligned} \mathbf{A}_{\text{I scaled}}^{-1} &= \begin{bmatrix} 1 & \frac{c(1+chN_1)}{a_{11}(1+chN_1)^2+c^2hN_2} \\ -\frac{ce}{a_{22}(1+chN_1)^2} & 1 \end{bmatrix} \\ &= \begin{bmatrix} 1 & -\frac{c}{\left(1+\frac{ch(a_{22}r_1-a_{11}r_2)}{a_{12}a_{21}-a_{11}a_{22}}\right)\left(-a_{11}+\frac{c^2h(a_{12}a_{21}-a_{11}a_{22})(a_{21}r_1-a_{11}r_2)}{(a_{22}(-a_{11}+chr_1)+a_{12}(a_{21}-chr_2))^2}\right)} \\ -\frac{ce}{a_{22}\left(1+\frac{ch(a_{22}r_1-a_{12}r_2)}{a_{12}a_{21}-a_{11}a_{22}}\right)^2} & 1 \end{bmatrix} \Big|_{N^*}. \end{aligned}$$

(44)

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38 644 Nonlinear interactions can switch the sign of predicted perturbation effects because the diagonal
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40 645 elements of the interaction matrix can be either positive or negative depending on species
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42 646 abundances and the form and strength of interspecific density-dependence. Thus, even in
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44 647 qualitative modeling, how to specify self-effects need not be obvious when nonlinear interaction
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46 648 are likely. Although some empirical work has suggested that pairwise predator-prey interactions
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48 649 in multispecies communities may be effectively linear despite their inherent nonlinearity (Novak
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50 650 2010; Wootton & Emmerson 2005), additional research is needed to generalize when and how
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52 651 the nonlinear nature of interactions may influence our predictive ability in the context of
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54 652 the nonlinear nature of interactions may influence our predictive ability in the context of

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3 653 community matrix methods. How nonlinear is too nonlinear for accurate predictions is an open
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5 654 question.
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Conclusions

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11 656 The frequency with which the methods of the community matrix are employed will likely
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13 657 increase as the network structure of natural communities becomes further resolved and the
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15 658 availability of empirical data on the strengths of species interactions increases. By illustrating
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17 659 how the alternative measures of species interaction strengths encapsulated by the Jacobian,
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19 660 interaction, and original community matrices are related to one another, we have attempted to
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21 661 clarify how the empirical interpretations of these matrices and their predictions differ. Despite
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23 662 their important biological distinctions, all are scaled variants of each other. Each matrix offers
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25 663 utility in predicting species responses to press perturbations. Our discussion has highlighted a
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27 664 number of considerations necessary for parameterizing the matrices with empirical (or
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29 665 empirically-inspired) data – focusing particularly on the characterization of their diagonal
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31 666 elements – and for converting their predictions of relative species changes to the more sought-
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33 667 after predictions of post-perturbation community structure. Many of these considerations are
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35 668 equally germane to the more common investigation of community responses to pulse
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37 669 perturbations by analysis of the Jacobian (e.g., May 1972).

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39 670 To conclude, we note that we do not wish to completely dissuade the use of the term
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41 671 ‘community matrix’ as a general means of denoting the structure and strengths of the direct
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43 672 pairwise interactions between species. We do, however, urge theoreticians in particular to be
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45 673 more explicit regarding the empirical interpretation of their matrix’s elements. The use of the
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47 674 more distinctly defined terms of the interaction and Jacobian matrices will increase clarity and
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49 675 prevent miscommunication. Furthermore, the term community matrix should not be limited to
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3 676 denoting a specific underlying model because both the Jacobian and the interaction matrix may
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5 677 be calculated for any differentiable model, be it Lotka-Volterra or otherwise. Theoreticians and
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7 678 empiricists alike should therefore be appropriately explicit about the model that they presume to
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9 679 characterize the dynamics of their study system. Distinctions are particularly important as
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11 680 empiricists continue the much needed integration of real world data into the mix. Community
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13 681 ecology is clearly in prime position to address many important issues facing society and the
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15 682 environment, be it in regards to informing conservation science or the sustainable extraction of
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17 683 the earth's resources (May 2009; Memmott 2009; Sutherland *et al.* 2009). Perturbation
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19 684 experiments – be they real experiments, computer-based, or the consequences of society's
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21 685 actions – will provide important insights into how real world systems could respond.
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Supporting Information

875 Additional Supporting Information may be found in the online version of this article:

876 **S1. How the negative of the inverse community matrix reflects the net effects of press**

877 **perturbations.**

878 **S2. Symbolic inverse and scaled inverse matrices of the four species example**

879 **community.**

880 **S3. Code to calculate the scaled net effects matrix and post-perturbation community**

881 **structure in R, Mathematica, and Matlab.**

For Review Only

S1. How the negative of the inverse community matrix reflects the net effects of press perturbations.

For completeness, we illustrate below how the negative of the inverse of the community matrix reflects the net effects of press perturbations. More specifically, we illustrate how the negative of the inverse of the Jacobian reflects the net effects of perturbing the species' population-level growth rates. (The derivations for the original community matrix and the interaction matrix are equivalent.) We first focus on species i and j (species i being the focal affected species and species j being the species whose population growth rate is perturbed) and then generalize to include possible perturbations of all species by reformulating our expressions to vector-matrix form. Abbreviated derivations have been presented by Yodzis (1988b), Stone (1990), Nakajima (1992), Case (2000), Solé and Bascompte (2006), and others.

We begin with

$$\frac{dN_i}{dt} = N_i f_i(N_1, N_2, \dots, N_S) \quad i = 1 \text{ to } S, \quad (\text{S1.1})$$

such that at equilibrium, before the initiation of a focal perturbation,

$$\frac{dN_i}{dt} = N_i^{*\text{old}} f_i(N_1^{*\text{old}}, N_2^{*\text{old}}, \dots, N_S^{*\text{old}}) = 0 \quad (\text{S1.2})$$

(where N_i^{old} refer to pre-perturbation equilibrium abundances). We now initiate a press

perturbation that adds P_j individuals of species j to the community,

$$\frac{dN_i}{dt} = \begin{cases} N_i f_i(N_1, N_2, \dots, N_S) + P_j & \text{for } i = j \\ N_i f_i(N_1, N_2, \dots, N_S) & \text{for } i \neq j \end{cases} \quad (\text{S1.3})$$

We can write eqn S1.3 more compactly using Kronecker's delta as

$$\frac{dN_i}{dt} = N_i f_i(N_1, N_2, \dots, N_S) + \delta_{ij} P_j \quad (\text{S1.4})$$

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3 904 where

$$905 \quad \delta_{ij} = \begin{cases} 1 & \text{for } i = j \\ 0 & \text{for } i \neq j \end{cases} \quad (\text{S1.5})$$

10 906 (here and subsequently the $i = 1$ to S is implied). If a new $N_i^{*\text{new}}$ post-perturbation equilibrium
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12 907 exists, then it must be that

$$15 908 \quad \frac{dN_i}{dt} = N_i^{*\text{new}} f_i(N_1^{*\text{new}}, N_2^{*\text{new}}, \dots, N_S^{*\text{new}}) + \delta_{ij} P_j = 0. \quad (\text{S1.6})$$

18 909 More explicitly, it must be that species abundances have responded to the perturbation such that

$$21 910 \quad \frac{dN_i}{dt} = (N_i^{*\text{old}} + \Delta N_i^*) f_i(N_1^{*\text{old}} + \Delta N_1^*, N_2^{*\text{old}} + \Delta N_2^*, \dots, N_S^{*\text{old}} + \Delta N_S^*) + \delta_{ij} P_j = 0, \quad (\text{S1.7})$$

24 911 where ΔN^* is the difference between a species' post- and pre-perturbation abundance

27 912 ($\Delta N_i^* = N_i^{*\text{new}} - N_i^{*\text{old}}$). The steady state condition will therefore occur when

$$29 913 \quad N_i^{*\text{new}} f_i(N_1^{*\text{new}}, N_2^{*\text{new}}, \dots, N_S^{*\text{new}}) = -\delta_{ij} P_j. \quad (\text{S1.8})$$

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34 915 We now ask how $N_i^{*\text{new}}$ will be affected by the addition of P_j . (For subsequent notational
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36 916 simplicity we will refer to $N^{*\text{new}}$ using N^* .) We do so by differentiating eqn S1.8 with respect to
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38 917 P_j . Effectively we are asking how ΔN_i^* will respond to a small change in P_j .

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44 919 Readers might recall from calculus that one can express how the value of a function
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46 920 dependent on a single variable x , call it $g(x)$, will be affected by a change in that variable using
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48 921 delta notation:

$$51 922 \quad \lim_{\Delta x \rightarrow 0} \frac{g(x + \Delta x) - g(x)}{(x + \Delta x) - x} = \frac{d(g(x))}{dx}. \quad (\text{S1.9})$$

55 923 Furthermore, recall that the total differential of any such differentiable function can be expressed
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57 924 using a Taylor expansion. That is, for the single variable function $g(x)$ where

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3 925 $d(g(x)) = g(x + dx) - g(x),$ (S1.10)

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5 926 we can rewrite
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$$\begin{aligned} g(x + dx) &= \sum_{n=0}^{\infty} \frac{g^{(n)}(x)}{n!} dx^n \\ &= g(x) + \frac{g'(x)dx}{1!} + \underbrace{\frac{g''(x)dx^2}{2!} + \dots}_{h.o.t.} \\ &= g(x) + g'(x)dx + h.o.t \\ &= g(x) + \frac{\partial g(x)}{\partial x} dx + h.o.t \end{aligned} .$$
 (S1.11)

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21 928 When dx is sufficiently small, then all the higher-order terms of this exact equation (all terms of
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23 $n > 1$) will rapidly become vanishingly small. We therefore expect an equation without these
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25 930 higher-order terms,

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$$\begin{aligned} d(g(x)) &\approx g(x) + \frac{\partial g(x)}{\partial x} dx - g(x) \\ &\approx \frac{\partial g(x)}{\partial x} dx \end{aligned} ,$$
 (S1.12)

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34 932 to be a good (first-order) approximation to S1.10. Note that the higher-order terms will only
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36 exist if $g(x)$ is nonlinear with respect to x ; eqn. S1.12 remains exact if $g(x)$ is a linear function of
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38 934 x because higher derivatives of a linear function equal zero.

41 935 One can extend this reasoning to functions dependent upon multiple variables as well. We
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43 936 therefore express the differentiation of eqn S1.8 with respect to P_j as

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46 937 $d(N_i^* f_i(N_1^*, N_2^*, \dots, N_S^*)) = -\delta_{ij} dP_j.$ (S1.13)

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49 938 The Taylor expansion of a function dependent on multiple variables is more involved than in the
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51 939 single variable case, but by ignoring all higher-order terms we arrive at the analogous
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53 940 approximation

$$\begin{aligned}
 d(N_i^* f_i(N_1^*, \dots, N_S^*)) &= \sum_{k=1}^S \frac{\partial(N_i^* f_i(N_1^*, \dots, N_S^*))}{\partial N_k} dN_k + h.o.t \\
 &\approx \sum_{k=1}^S \frac{\partial(N_i^* f_i(N_1^*, \dots, N_S^*))}{\partial N_k} dN_k
 \end{aligned}, \quad (\text{S1.14})$$

where we introduce k to indicate that the summation is performed across all $k = 1$ to S species, including our focal species i and j .

Notice that eqn S1.14 contains within it a summation of elements that correspond to the definition of the Jacobian matrix elements (eqn 14 of main text). That is

$$\sum_{k=1}^S \frac{\partial(N_i^* f_i(N_1^*, \dots, N_S^*))}{\partial N_k} = \sum_{k=1}^S J_{ik}, \quad (\text{S1.15})$$

which is the sum of the i^{th} row of the Jacobian. For each i^{th} species, we can therefore rewrite eqn S1.13 as

$$\sum_{k=1}^S J_{ik} dN_k \approx -\delta_{ij} dP_j. \quad (\text{S1.16})$$

By considering only the first-order approximation, we write

$$\sum_{k=1}^S J_{ik} dN_k = -\delta_{ij} dP_j. \quad (\text{S1.17})$$

We thereby introduce the assumption that pre- and post-perturbation equilibria are close enough to each other that any existing nonlinearities in species interactions are unimportant (i.e. the dN_k are very small or the nonlinearities are very weak), or that such nonlinearities do not exist in the first place (as is the case in the generalized Lotka-Volterra model of eqn 7, see main text).

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To express the effects of $j = 1$ to S possible perturbations on all $i = 1$ to S affected species, we reformulate eqn S1.17 into matrix-vector form

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$$\mathbf{J} d\mathbf{N} = -\mathbf{I} d\mathbf{P}, \quad (\text{S1.18})$$

960 where

$$d\mathbf{N} = \begin{bmatrix} dN_1 \\ dN_2 \\ \vdots \\ dN_S \end{bmatrix} \quad \text{and} \quad d\mathbf{P} = \begin{bmatrix} dP_1 \\ dP_2 \\ \vdots \\ dP_S \end{bmatrix}$$

962 and Kronecker's delta has been replaced by the identity matrix \mathbf{I} , (i.e. $(\mathbf{I})_{ij} = \delta_{ij}$). Finally, we use
 963 the property of the identity matrix – that it equals any square matrix times its own inverse (i.e. \mathbf{I}
 964 $= \mathbf{J} \mathbf{J}^{-1}$) – to rearrange eqn S1.18 as

$$965 \quad \frac{d\mathbf{N}}{d\mathbf{P}} = -(\mathbf{J}^{-1}). \quad (\text{S1.19})$$

966 Thus, with i denoting a matrix row and j denoting a matrix column, a press perturbation to any j^{th}
 967 species' population growth rate affects a change in any i^{th} species equilibrium population size
 968 (approximately) equal to the negative of the ij^{th} element of the inverse of the Jacobian.

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970 Note that, had we begun this derivation using descriptions of the per capita growth rate of
 971 species i (eqn 6 of main text) as opposed to its population-level growth rate (eqn. S1.1, or eqn. 12
 972 of main text), we would have arrived at a corresponding derivation of the negative of the inverse
 973 of the interaction matrix $-\mathbf{A}_{\mathbf{I}}^{-1}$. And similarly so for the original community matrix, as its
 974 elements are rescaled from the per capita interaction strengths of the interaction matrix (see main
 975 text).

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3 **S2. Symbolic inverse and scaled inverse matrices of the four species example community.**

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5 976 The inverse of the four species example community (Fig. 1) is

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$$\mathbf{A}^{-1} = \begin{bmatrix} \alpha_{11}^{(-1)} & \alpha_{12}^{(-1)} & \alpha_{13}^{(-1)} & \alpha_{14}^{(-1)} \\ \alpha_{21}^{(-1)} & \alpha_{22}^{(-1)} & \alpha_{23}^{(-1)} & \alpha_{24}^{(-1)} \\ \alpha_{31}^{(-1)} & \alpha_{32}^{(-1)} & \alpha_{33}^{(-1)} & \alpha_{34}^{(-1)} \\ \alpha_{41}^{(-1)} & \alpha_{42}^{(-1)} & \alpha_{43}^{(-1)} & \alpha_{44}^{(-1)} \end{bmatrix}$$

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15 979 where

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$$\alpha_{11}^{(-1)} = \frac{\alpha_{23}\alpha_{32}\alpha_{44} + \alpha_{22}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})}{\det(\mathbf{A})}$$

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$$\alpha_{21}^{(-1)} = \frac{-\alpha_{23}\alpha_{31}\alpha_{44} + \alpha_{21}(-\alpha_{34}\alpha_{43} + \alpha_{33}\alpha_{44})}{\det(\mathbf{A})}$$

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23
24
$$\alpha_{31}^{(-1)} = \frac{(\alpha_{22}\alpha_{31} - \alpha_{21}\alpha_{32})\alpha_{44}}{\det(\mathbf{A})} \quad \alpha_{41}^{(-1)} = \frac{(-\alpha_{22}\alpha_{31} + \alpha_{21}\alpha_{32})\alpha_{43}}{\det(\mathbf{A})}$$

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$$\alpha_{12}^{(-1)} = \frac{-\alpha_{13}\alpha_{32}\alpha_{44} + \alpha_{12}(-\alpha_{34}\alpha_{43} + \alpha_{33}\alpha_{44})}{\det(\mathbf{A})}$$

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30
$$\alpha_{22}^{(-1)} = \frac{\alpha_{13}\alpha_{31}\alpha_{44} + \alpha_{11}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})}{\det(\mathbf{A})}$$

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33
$$\alpha_{32}^{(-1)} = \frac{(-\alpha_{12}\alpha_{31} + \alpha_{11}\alpha_{32})\alpha_{44}}{\det(\mathbf{A})} \quad \alpha_{42}^{(-1)} = \frac{(\alpha_{12}\alpha_{31} - \alpha_{11}\alpha_{32})\alpha_{43}}{\det(\mathbf{A})}$$

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$$\alpha_{13}^{(-1)} = \frac{(\alpha_{13}\alpha_{22} - \alpha_{12}\alpha_{23})\alpha_{44}}{\det(\mathbf{A})} \quad \alpha_{23}^{(-1)} = \frac{(-\alpha_{13}\alpha_{21} + \alpha_{11}\alpha_{23})\alpha_{44}}{\det(\mathbf{A})}$$

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$$\alpha_{33}^{(-1)} = \frac{(\alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22})\alpha_{44}}{\det(\mathbf{A})} \quad \alpha_{43}^{(-1)} = \frac{(-\alpha_{12}\alpha_{21} + \alpha_{11}\alpha_{22})\alpha_{43}}{\det(\mathbf{A})}$$

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$$\alpha_{14}^{(-1)} = \frac{(-\alpha_{13}\alpha_{22} + \alpha_{12}\alpha_{23})\alpha_{34}}{\det(\mathbf{A})} \quad \alpha_{24}^{(-1)} = \frac{(\alpha_{13}\alpha_{21} - \alpha_{11}\alpha_{23})\alpha_{34}}{\det(\mathbf{A})}$$

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$$\alpha_{34}^{(-1)} = \frac{(-\alpha_{12}\alpha_{21} + \alpha_{11}\alpha_{22})\alpha_{34}}{\det(\mathbf{A})}$$

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$$\alpha_{44}^{(-1)} = \frac{\alpha_{13}(\alpha_{22}\alpha_{31} - \alpha_{21}\alpha_{32}) + \alpha_{12}(-\alpha_{23}\alpha_{31} + \alpha_{21}\alpha_{33}) + \alpha_{11}(\alpha_{23}\alpha_{32} - \alpha_{22}\alpha_{33})}{\det(\mathbf{A})}$$

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60 991 and

$$\det(\mathbf{A}) = \alpha_{13}(-\alpha_{22}\alpha_{31} + \alpha_{21}\alpha_{32})\alpha_{44} \\ + \alpha_{12}(\alpha_{23}\alpha_{31}\alpha_{44} + \alpha_{21}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})) \\ - \alpha_{11}(\alpha_{23}\alpha_{32}\alpha_{44} + \alpha_{22}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})).$$

993 Scaling \mathbf{A}^{-1} by its diagonal gives the scaled inverse of the community matrix:

$$\mathbf{A}_{\text{scaled}}^{-1} = \begin{bmatrix} 1 & \alpha_{12(s)}^{(-1)} & \alpha_{13(s)}^{(-1)} & \alpha_{14(s)}^{(-1)} \\ \alpha_{21(s)}^{(-1)} & 1 & \alpha_{23(s)}^{(-1)} & \alpha_{24(s)}^{(-1)} \\ \alpha_{31(s)}^{(-1)} & \alpha_{32(s)}^{(-1)} & 1 & \alpha_{34(s)}^{(-1)} \\ \alpha_{41(s)}^{(-1)} & \alpha_{42(s)}^{(-1)} & \alpha_{43(s)}^{(-1)} & 1 \end{bmatrix}$$

995 where

$$\alpha_{21(s)}^{(-1)} = \frac{\alpha_{23}\alpha_{31}\alpha_{44} + \alpha_{21}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})}{-\alpha_{23}\alpha_{32}\alpha_{44} + \alpha_{22}(-\alpha_{34}\alpha_{43} + \alpha_{33}\alpha_{44})}$$

$$\alpha_{31(s)}^{(-1)} = \frac{(-\alpha_{22}\alpha_{31} + \alpha_{21}\alpha_{32})\alpha_{44}}{-\alpha_{23}\alpha_{32}\alpha_{44} + \alpha_{22}(-\alpha_{34}\alpha_{43} + \alpha_{33}\alpha_{44})}$$

$$\alpha_{41(s)}^{(-1)} = \frac{(\alpha_{22}\alpha_{31} - \alpha_{21}\alpha_{32})\alpha_{43}}{-\alpha_{23}\alpha_{32}\alpha_{44} + \alpha_{22}(-\alpha_{34}\alpha_{43} + \alpha_{33}\alpha_{44})}$$

$$\alpha_{32(s)}^{(-1)} = \frac{\alpha_{13}\alpha_{32}\alpha_{44} + \alpha_{12}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})}{-\alpha_{13}\alpha_{31}\alpha_{44} + \alpha_{11}(-\alpha_{34}\alpha_{43} + \alpha_{33}\alpha_{44})}$$

$$\alpha_{32(s)}^{(-1)} = \frac{(\alpha_{12}\alpha_{31} - \alpha_{11}\alpha_{32})\alpha_{44}}{-\alpha_{13}\alpha_{31}\alpha_{44} + \alpha_{11}(-\alpha_{34}\alpha_{43} + \alpha_{33}\alpha_{44})}$$

$$\alpha_{42(s)}^{(-1)} = \frac{(\alpha_{12}\alpha_{31} - \alpha_{11}\alpha_{32})\alpha_{43}}{\alpha_{13}\alpha_{31}\alpha_{44} + \alpha_{11}(\alpha_{34}\alpha_{43} - \alpha_{33}\alpha_{44})}$$

$$\alpha_{13(s)}^{(-1)} = \frac{\alpha_{13}\alpha_{22} - \alpha_{12}\alpha_{23}}{\alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22}} \quad \alpha_{23(s)}^{(-1)} = \frac{\alpha_{13}\alpha_{21} - \alpha_{11}\alpha_{23}}{-\alpha_{12}\alpha_{21} + \alpha_{11}\alpha_{22}} \quad \alpha_{43(s)}^{(-1)} = -\frac{\alpha_{43}}{\alpha_{44}}$$

$$\alpha_{14(s)}^{(-1)} = \frac{(\alpha_{13}\alpha_{22} - \alpha_{12}\alpha_{23})\alpha_{34}}{\alpha_{13}(-\alpha_{22}\alpha_{31} + \alpha_{21}\alpha_{32}) + \alpha_{12}(\alpha_{23}\alpha_{31} - \alpha_{21}\alpha_{33}) + \alpha_{11}(-\alpha_{23}\alpha_{32} + \alpha_{22}\alpha_{33})}$$

$$\alpha_{24(s)}^{(-1)} = \frac{(-\alpha_{13}\alpha_{21} + \alpha_{11}\alpha_{23})\alpha_{34}}{\alpha_{13}(-\alpha_{22}\alpha_{31} + \alpha_{21}\alpha_{32}) + \alpha_{12}(\alpha_{23}\alpha_{31} - \alpha_{21}\alpha_{33}) + \alpha_{11}(-\alpha_{23}\alpha_{32} + \alpha_{22}\alpha_{33})}$$

$$\alpha_{34(s)}^{(-1)} = \frac{(\alpha_{12}\alpha_{21} - \alpha_{11}\alpha_{22})\alpha_{34}}{\alpha_{13}(-\alpha_{22}\alpha_{31} + \alpha_{21}\alpha_{32}) + \alpha_{12}(\alpha_{23}\alpha_{31} - \alpha_{21}\alpha_{33}) + \alpha_{11}(-\alpha_{23}\alpha_{32} + \alpha_{22}\alpha_{33})}$$

S3. Code for calculating the scaled net effects matrix and post-perturbation community structure in R, Mathematica, and Matlab.

The scaled net effect matrix is calculated as

$$\mathbf{A}_{\text{scaled}}^{-1} = \mathbf{A}^{-1} \oslash [\text{diag}(\mathbf{A}^{-1}) \otimes \text{diag}(\mathbf{I})^T]^T. \quad (\text{S1})$$

Kronecker multiplication by the transpose of the diagonal of the Identity matrix is necessary to

expand the vector of the diagonal of A^{-1} into a matrix with dimensions of A^{-1} . Note that

$$\mathbf{A}_{\text{I scaled}}^{-1} = \mathbf{A}_{\text{scaled}}^{-1} = \mathbf{J}_{\text{scaled}}^{-1} \quad (\text{S2})$$

and thus that A^{-1} can be replaced by either A_1^{-1} or J^{-1} .

In the R programming language, $-\mathbf{A}_{\text{scaled}}^{-1}$ is calculated by:

```
t(t(ginv(A))/diag(ginv(A)))
```

In Mathematica, by:

`Transpose[Transpose[Inverse[A]]]/Diagonal[Inverse[A]]]`

In Matlab, by:

```
inv(A) ./ (kron(diag(inv(A)), diag(eye(S))'))')
```

Given a vector of pre-perturbation community structure \mathbf{N}_{old} and a vector of how much each

1
2
3 1030 possible independent perturbations to each potential target species affects its abundance **D**,
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5 1031 predictions of post-perturbation community structure are made by:
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$$\mathbf{N}_{\text{pred}} = [\mathbf{N}_{\text{old}} \otimes \text{diag}(\mathbf{I})^T] + \mathbf{A}_{\text{scaled}}^{-1} \circ [\mathbf{D} \otimes \text{diag}(\mathbf{I})^T]^T$$
 (S3)
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13 1034 Let S be the number of species and $s\text{InvA}$ stand for $\mathbf{A}_{\text{scaled}}^{-1}$.
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16 1035
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18 1036 In R, \mathbf{N}_{pred} is calculated by:
19
20 1037 `kronecker(N_old,t(rep(1,S)))+sInvA*(t(kronecker(D,t(rep(1,S)))))`
21
22 1038
23
24
25 1039 In Mathematica, by:
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27 1040 `KroneckerProduct[Nold,Diagonal[IdentityMatrix[S]]] +`
28
29 1041 `sInvA*Transpose[KroneckerProduct[DD,Diagonal[IdentityMatrix[S]]]]`
30
31 1042 `//MatrixForm`
32
33 1043
34
35 1044 In Matlab, by:
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37 1045 `kron(N_old,diag(eye(S))')+sInvA.* (kron(D,diag(eye(S))'))'`
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