

# Identification of key players for the impact of perturbations in food webs

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It is a challenge to predict the response of a large, complex system to a perturbation. Recent attempts to predict the behavior of food webs has revealed that the more complex the system, the more precisely the elements of the system must be measured. As a result, the amount of effort needed to understand a system grows quickly with its complexity, making predictions difficult. Here, we show that not all elements must be measured equally. We then develop analytical tools that determine some parts of a system require more precise measurements, suggesting a more efficient allocation of effort to understanding complex systems is possible. We then develop an iterative technique to efficiently arrive at this solution. Then, in our assessment of model food webs, we find that it is most important to precisely measure the mortality and predation rates of large, generalist, top predators. Prioritizing the study of such species will make it easier to understand the response complex food webs to perturbations.

**Keywords:** Perturbations, Food Webs, Complex Systems, Generalized Models

## 1. Introduction

Predicting the result of environmental perturbations, such as the arrival of new species or habitat change, is a major goal in ecology [29, 1]. What makes this challenging is the complex interconnected nature of ecological systems. In any densely-connected system, a perturbation of one element can percolate across the network of interactions. This is particularly true for the complex food webs that form the backbones of most ecosystems [25, 26, 21]. Even perturbations acting only on a small subset of species may thus propagate through the network and lead to serious systemic changes [28, 2, 36, 21, 7].

A central factor determining the response to perturbations in food webs is the topology, the precise pattern of predator-prey interactions. It has been shown that topological properties affect local and global dynamical stability [23, 24, 22, 13, 4, 3] and other notions of robustness such as the likelihood of secondary extinctions [5]. However, in addition to knowledge of the topology, faithful prediction of the impact of perturbations requires information about underlying biomass flows and the control coefficients characterizing the nonlinearity of processes. Such parameters require extensive measurements and errors in their estimation quickly reduce the accuracy of predictions about how food webs respond to perturbations [35, 25].

Because precise information on biomass flows and control coefficients is typically limited, our ability to make precise predictions on the ultimate effect of perturbations is still strongly limited. For instance predictions for systems of more than 25 species are practically impossible, unless very detailed information is available [27].

Here, we ask if food-web dynamics are more sensitive to particular species or parameters. If we can identify such influential elements in advance, we should be able to make more precise predictions about dynamics with a given effort in parameterization. In this paper we investigate the predictability of responses to perturbations in a broad class of food web models. Our results show that the parameters of different species do not need to be measured with the same accuracy. We use analytical calculations and numerical demonstrations to show that it is possible to assign to each species a value that indicates the importance of precise knowledge about this species for the quality of the prediction. Furthermore, we demonstrate that this importance can be estimated reasonably well already from imprecise information.

The paper is structured as follows: We start in Sec. 2 by introducing a method for predicting the impact of perturbations in a broad class of food-web models. The method is illustrated in Sec. 3 with two examples. In Sec. 4, we then derive measures for species' influence on others and for their sensitivity to perturbations. Finally, in Sec. 5, we test these predictions in a series of numerical experiments. The numerical results illustrate a feasible strategy for field studies, where mathematical analysis and experimental measurements are used to iteratively improve predictions.

## 2. Impact Evaluation

Consider a biological system described by a set of state variables  $X_1, \dots, X_N$  denoting, for instance, the abundances of established species in a food web. The system is now subject to a perturbation that is characterized by another set of variables  $Y_1, \dots, Y_M$ , for instance denoting the abundances of newly arriving species.

We assume that in the absence of the perturbation the variables  $X_1, \dots, X_N$  are governed by a set of ordinary differential equations of the form

$$\frac{d}{dt}X_i = A_i(X_1, \dots, X_N, Y_1, \dots, Y_M), \quad (2.1)$$

where  $A_i$  is a function representing the *right-hand-side* of the differential equations. For instance, the generalized model for food webs [11] which we use below, describes the dynamics of the populations  $X_1, \dots, X_N$  by  $N$  differential equation of the form

$$\frac{d}{dt}X_i = G_i(\mathbf{X}) + S_i(X_i) - L_i(\mathbf{X}) - M_i(X_i), \quad (2.2)$$

where  $G_i$ ,  $L_i$ ,  $M_i$ , and  $S_i$  are unspecified functions describing respectively the gain by predation ( $G_i$ ), the loss by predation ( $L_i$ ), the loss due to natural mortality ( $M_i$ ), and the gain by primary production ( $S_i$ ) of the focal species.

Following Ref. [27] we consider the case where the unperturbed system resides in a stable equilibrium  $\mathbf{X}^*$  and where the perturbation is characterized by a small and constant  $\mathbf{Y}^*$ . For example, new species persisting at a low constant abundance in the ecosystem due to initially positive growth or constant influx.

Because the stationary abundance,  $X_i^*$ , of a given established species  $i$  is dependent on the new species  $\mathbf{Y}^*$ , we can regard it as a function  $X_i^* = X_i^*(\mathbf{Y}^*)$ . We

can then define the impact  $I_{i,j}$  of a perturbation variable  $Y_j^*$  on a resident species abundance  $X_i^*$  as the change of  $X_i^*$  per unit  $Y_j^*$ , i.e.

$$I_{i,j} = \left. \frac{\partial X_i^*}{\partial Y_j^*} \right|_0, \quad (2.3)$$

where we used  $|_0$  to indicate that the derivative is evaluated in the limit of vanishing densities of the arriving species  $Y_j^*$ . In other words, the entries of the impact matrix  $I_{i,j}$  state the loss of units of the established species  $i$  per unit of arriving species  $j$  that enters the system.

In simple models, the impact can be computed by first solving (2.1) for the stationary solution  $X_i^*(\mathbf{Y}^*)$  and subsequently computing the derivative in (2.3). However, in models with more than three species, the analytical computation of stationary solution becomes prohibitively difficult. Furthermore, in the present paper, we seek a general solution, that does depend on the functional forms in the model. However, with this degree of generality, the explicit computation of the stationary solution is not possible.

Computing the stationary solution can be avoided by recognizing that the stationary density of a resident species  $X_i^*$  can be considered as an implicit function that is defined as the solution of the stationarity condition  $0 = A_i(\mathbf{X}^*, \mathbf{Y}^*)$ . Using a corollary to the implicit function theorem [17], we can then write the impact matrix as

$$\mathbf{I} = -\mathbf{J}^{-1}\mathbf{K}, \quad (2.4)$$

where the superscript  $-1$  indicates the matrix inverse. The matrix  $\mathbf{J}$  is the so-called Jacobian, which is defined as the derivatives of  $A_i$  with respect to the abundances of established species, i.e.  $J_{i,j} = \partial A_i / \partial X_j|_*$ . And, the matrix  $\mathbf{K}$  is a  $N \times M$  defined by  $K_{i,j} = \partial A_i / \partial Y_j|_*$ , where  $|_*$  indicates that the derivative is evaluated in the equilibrium under consideration. The matrix  $\mathbf{K}$  thus captures the direct impact of an arriving species on an established species, which is quantified by the reduction in production (or respectively increase in mortality) of the established species per unit of the arriving species.

In summary, (2.4) establishes a relationship between the direct proximal impact of the arriving species  $\mathbf{K}$ , the indirect ultimate impact  $\mathbf{I}$  and internal interactions among the established species  $\mathbf{J}$ . As a note of caution, we remark that this relationship holds up to linear order. The impact-approximation therefore remains valid only as long as the perturbation caused is reasonably small.

Explicitly, (2.4) means that we can obtain the ultimate impact matrix as a function of the Jacobian of the established community and the matrix of the direct perturbations. For instance, consider a perturbation due to a single new species of abundance  $Y_1^*$  arriving in a system of established species. Because there is only a single arriving species, the matrix  $\mathbf{K}$  is a vector in this case. For each established species  $i$ , the entry  $K_i$  denotes the change to its biomass intake and loss rates that is directly caused by the new species, e.g. by feeding or competition. The impact vector  $\mathbf{I}$  then describes the response of each species to this change induced by  $\mathbf{K}$  as the perturbation propagates through the network.

In the equations above, we refer to the steady state of the system, which seems to imply that information about this state is required. However, relationship (2.4)

remains valid independently of the specific steady state under consideration. When we evaluate the matrices, the steady state appears only in the Jacobian which contains elements of the form  $J_{i,j} = \partial/\partial X_j(dX_i/dt)|_*$ . For instance, in the generalized food web model, this leads to expressions such as  $\partial G_i/\partial X_i|_*$ . Because we cannot evaluate this expression without further assumptions, it is an unknown quantity. However, we note that for any specific system the expression is simply a number. In other words, this means that the unknown derivatives appearing in the Jacobian constitute unknown parameters of the model.

So far, we have recognized that the unknown derivatives can be formally treated as unknown parameters of the model. However, as such, these parameters are hard to interpret and are thus not suitable for an ecological discussion of the results. We solve this problem by using a slightly different parametrization, which is obtained either by a special normalization procedure [11] or directly by the identity

$$\left. \frac{\partial G_i}{\partial X_i} \right|_* = \frac{G_i^*}{X_i^*} \left. \frac{\partial \log G_i}{\partial \log X_i} \right|_*, \quad (2.5)$$

which is true for  $G_i^*, X_i^* > 0$  (a condition that is generally met by definition; see Ref. [18] for the special case of  $X_i^* = 0$ ).

The expression on the right-hand-side of (2.5) is a product of two factors that have a direct interpretation in most applications. The first factor is a per-capita rate. Such rates have the dimension of inverse time and can be directly interpreted as characteristic turnover rates, in this case, as the per-capita growth rate of the members of species  $i$  by predation on other species.

The second factor in (2.5) is a logarithmic derivative. Such derivatives are also called elasticities and have been proposed originally in economic theory [16] and subsequently in metabolic control theory [6] and ecology [34, 31]. They can be estimated well from observational data and interpreted straightforwardly. For every power-law,  $f(x) = Ax^p$ , the logarithmic derivative is  $\partial \log f/\partial \log x = p$ , independently of  $A$  or  $x$ . Thus, for instance, any linear function has an elasticity of one regardless of the slope. For functions that are not power-laws the elasticity still provides an intuitive non-linear measure of the sensitivity in the steady state. For instance, for the well-known Holling type-II functional response the corresponding elasticity is 1 if evaluated in the linear regime and 0 at saturation.

In summary, the identity (2.5) allows breaking the partial derivative of the process in the steady state into two constant factors, describing the per-capita rate and the sensitivity of the process, respectively. These factors are, therefore, well-defined ecological parameters in their own right, which can be understood and discussed even if the steady state of the system is unknown. For food webs, this parametrization leads to the Jacobian matrix expressions given in App. Appendix A[11]. According to (2.4), the Jacobian that is thus parameterized can then be used to relate a perturbation to its eventual impact. In the following, we use this approach to discuss the prediction of the impact of perturbations on food webs. We have so far focused specifically on the arrival of new species. Let us however remark that the applicability of (2.4) is not limited to this case, but remains valid for all perturbations that can be quantified by a set of variables  $\mathbf{Y}^*$ .

We note that the approach to impact taken in this paper is closely related to [27]. Our main methodological contribution is to apply this approach to generalized models. The main advantage of generalized modeling used here is its high

Name	Interpretation	Value(s)
<b>Scale parameters</b> - defining the biomass flows in the steady state.		
$\alpha_i$	Rate of biomass turnover in species $i$	(0,1]
$\beta_{i,j}$	Contribution of predation by $i$ to loss rate of species $j$	[0,1]
$\chi_{i,j}$	Contribution of species $i$ to the prey of species $j$	[0,1]
$\rho_i$	Fraction of growth in species $i$ gained by predation	0 (producers) 1 (consumers)
$\tilde{\rho}_i$	Fraction of growth in species $i$ gained by primary production	$1 - \rho_i$
$\sigma_i$	Fraction of mortality in species $i$ resulting from predation	0 (top pred.) (0,1] (others)
$\tilde{\sigma}_i$	Fraction of mortality in species $i$ not resulting from predation	$1 - \sigma_i$
<b>Elasticities</b> - Sensitivities of interactions to state variables.		
$\gamma_i$	Sensitivity of predation in species $i$ to $i$ 's prey density	[0.5,1.5]
$\lambda_{i,j}$	Exponent of prey switching	1 (passive)
$\mu_i$	Exponent of closure in species $i$	[1,2]
$\phi_i$	Sensitivity of primary production in species $i$ to the density of species $i$	[0,1]
$\psi_i$	Sensitivity of predation in species $i$ to the density of predators	[0.5,1.5]

Table 1. *Generalized model parameters as defined in Ref. [11].*

numerical efficiency, which enables a detailed and statistically sound numerical exploration. For the practical application to real world food webs, generalized models offer additional advantages. In contrast to half-maximum concentrations and maximal growth rates used in conventional models, all parameters of the generalized model are defined in the state observed in nature. The parameters can therefore be measured directly without requiring a fitting procedure. Furthermore, the parameters are defined in such a way that their estimation from noisy data converges maximally fast [16, 20]. In practice this should lead to a higher accuracy.

The formulation of the generalized model is straight-forward. Using the results of [11] even large models with tens of species can be set up in few hours. Using the equations derived here, the impact of different species can then be computed in seconds, using a simple algorithm [?]. Once the model has been set up, integration of new data requires entering new numerical values. In principle this allows the impact computation and importance to be carried out in the field by non-expert users on a small laptop.

### 3. Examples

For illustration, we consider two examples, a simple predator-prey system and the 10-species food web shown in Fig. 1. While the predator-prey system is analytically tractable, the second example requires numerical calculations.

As a first example, we consider a class of predator-prey models in which a grazer of abundance  $X_1$  consumes a producer of abundance  $X_2$ . A detailed treatment and discussion of the stability of this system in terms of the generalized model parameters can be found in Refs. [9, 11].

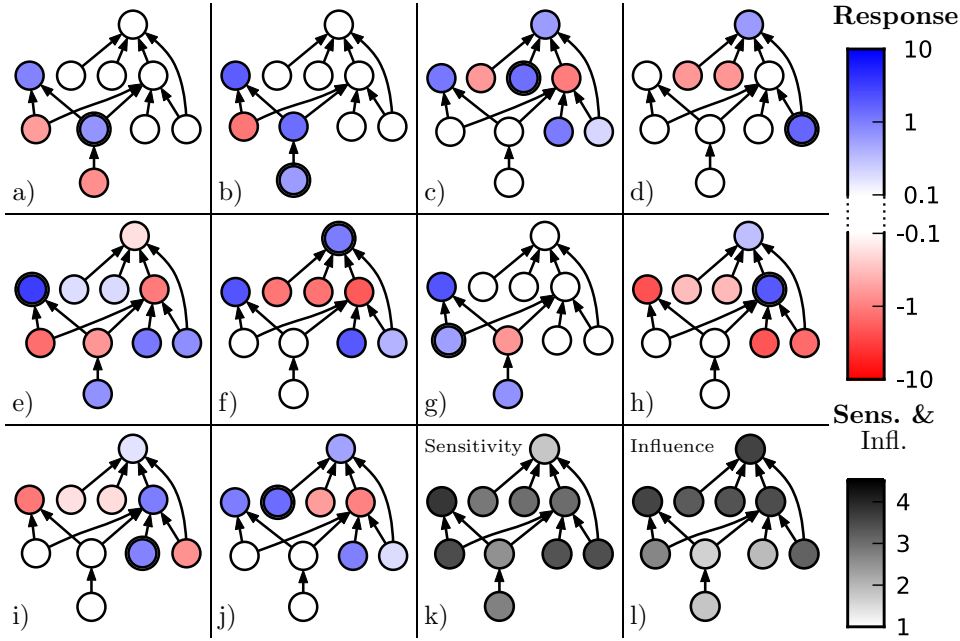


Figure 1. Responses of a food web for perturbations of different species. Shown are species (circles) and predator-prey relationships (arrows, in the direction of the biomass flow). In a-j), the species printed as a larger circle is affected by a perturbation that increases this species' biomass intake and thus leads to an increase of its abundance. The color code denotes the response of the system to this perturbation. The perturbation of each species  $i$  is normalized to the species turnover rate  $\alpha_i$ , i.e.  $K_i = \alpha_i$ . In particular, the effect on the perturbed species is always positive, but the amount the abundance changes is determined by the surrounding system. In k) and l) the grey-scale denotes the sensitivity and the influence of each species respectively, approximating its propensity to experience or cause large impact (details are given in Sec. 4, or see App. Appendix C for their definitions (C 3) and (C 2)).

The Jacobian matrix of this system near the steady state is

$$\mathbf{J} = \begin{pmatrix} \alpha_1(\psi - \mu) & \alpha_1\gamma \\ -\alpha_2\sigma\psi & \alpha_2(\phi - \sigma\gamma - \bar{\sigma}\mu) \end{pmatrix} \quad (3.1)$$

where  $\alpha_i$  represents each species turnover rate and  $\sigma$  the relative loss of the producer due to predation (instead of natural mortality). Furthermore,  $\phi$  denotes the elasticity (i.e. sensitivity) of primary production to the producer abundance,  $\gamma$  the elasticity of predation to primary producer abundance,  $\psi$  the elasticity of predation to predator abundance, and  $\mu$  the elasticity of natural mortality to a species' own abundance.

We now consider the impact of the arrival of a new grazer in the established producer-grazer system. It can be assumed that this new grazer has a direct negative effect on the primary producer but no direct effect on the established grazer, such that the perturbation matrix  $\mathbf{K}$  contains the entries  $K_{1,1} = 0$  and  $K_{2,1} < 0$ . As shown in detail in App. Appendix B, the impact on the established grazer is

$$I_1 = \frac{\alpha_1}{\det \mathbf{J}} \gamma K_2, \quad (3.2)$$

and the impact on the producer is

$$I_2 = \frac{\alpha_1}{\det \mathbf{J}}(\mu - \psi)K_2, \quad (3.3)$$

where  $\det \mathbf{J} \geq 0$  represents the determinant of the Jacobian matrix.

We see that generally the impact on the established grazer is negative. This result is intuitive as the established grazer is now in exploitative competition with the arriving grazer. Of particular interest is the case where the established predator suffers from linear loss ( $\mu = 1$ ) and has an effect on the producer that scales linearly with the grazer abundance ( $\psi = 1$ , i.e. there is no interference between the grazers). In this limit,  $\det \mathbf{J}$  approaches 0. In the impact on the producer  $I_2$  this is compensated by the factor  $\psi - \mu$ , which also vanishes [12], whereas the impact  $I_1$  on the established grazer approaches infinity. This is a manifestation of the well-known competitive exclusion principle, which precludes the coexistence of the grazers in this case [15, 10]. The infinite value indicates that the impact of the arriving grazer is disproportionately strong, because it leads to a loss of stability. Also in larger systems such infinite values of the impact occur whenever the arrival of a new species causes a bifurcation, in which the local stability is lost.

The assessment of impact in a larger food web can be carried out analogously, but requires numerical computations in which the generalized parameters are set to specific values. In the following, we consider generalized models described in detail in Ref. [13]: The topology of a model food web is generated using the niche model [32]. For this topology we then draw the generalized parameters uniformly and independently from the ranges given in Tab. 1.

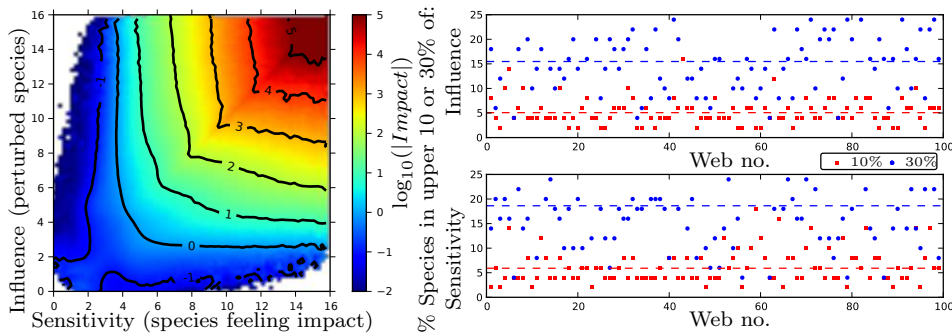


Figure 2. Sensitivity and Influence of species in model food webs. Left: The average absolute impact on a species with given sensitivity if a species of given influence is perturbed. Right: Percentage of species in a food web with an Influence (upper graph) or sensitivity (lower graph) within the highest 10 or 30% of the range for each food web. The average percentage is given by the dashed lines. For example, for the influence, only 18% of all species lie in the upper 30% of the distribution. Therefore, the number of very influential or sensitive species is low. Other Parameters: System size  $N = 50$ , connectance  $C = 0.04$ .

A specific example of a food web in this family of models is shown in Fig. 1. The figure shows the response of the food web to the perturbation of a focal species. Some focal species have greater impacts on the food web than others. For instance, in Fig. 1e) most species respond to the perturbation of the focal species while in Fig. 1a), few species respond to the perturbation of a different focal species.

#### 4. Sensitive and Influential Species

Now we identify two types of species that are particularly important for perturbations. *Sensitive species* are easily perturbed by disturbances propagating through the web, and *influential species* have a strong effect on other species, when perturbed. In this section, we use intuitive reasoning to derive measures for the sensitivity and influence of each species. A more formal derivation is given in App. Appendix C.

Close to a steady state, the dynamical properties of a system are characterized by its dynamical modes which are characterized in terms of the eigenvectors and eigenvalues of the Jacobian matrix. For a given matrix there are generally two different sets of eigenvectors, which are called right and left eigenvectors [33]. For each eigenvalue  $\lambda_k$  of the matrix there is a corresponding right eigenvector  $\mathbf{v}^{(k)}$  and left eigenvector  $\mathbf{w}^{(k)}$ .

A common picture, is to visualize dynamical modes as vibrations traveling through a drum when it is struck. Here the different modes correspond to different notes that are played on the drum. The right eigenvectors characterize the pattern of vibration when a specific note is played. Specifically, the elements of the right eigenvector describe how strongly the respective area of the drum vibrates in that note. The same is true for the food web. In a stable steady state that is hit by a short (pulse) perturbation the right eigenvectors govern how the system returns to the steady state after the perturbation.

Drummers know how to play different notes by striking different parts of the drum. This is captured by left eigenvectors. Specifically, the elements of the left eigenvector for a given dynamical mode describe how strongly the specific mode is excited when the drum is struck in a given area. Similarly, in the food web, the left eigenvectors characterize the strength of a specific dynamical response when a given species is perturbed.

Intuitively, one can think of each dynamical mode as a possible response of the system to a perturbation. More precisely, the right eigenvector denotes the impact of response (which species “feel the vibrations”), while the corresponding left eigenvector denotes the type of perturbation that can trigger a particular response (which species needs to be perturbed to “play a given note”). For instance, consider the pair of a right eigenvector  $\mathbf{v} = (1, 2)$  and a left eigenvector  $\mathbf{w} = (1, 0)$ . If a perturbation affects only the first species, the direction of the system’s response due this dynamical mode is in the direction  $(1, 2)$ ; i.e., the second species changes twice as much as the first.

The strength of a mode’s response is determined by its *excitability*. As explained in more detail in App. Appendix C, the excitability of each mode is inversely proportional to the magnitude of the corresponding eigenvalue  $1/|\lambda_k|$ . Intuitively, the eigenvalue of a dynamical mode indicates a system’s resistance to a particular perturbation. The impact of such a perturbation is, therefore, inversely proportional to this resistance.

The potential impact that a species feels due to a given dynamical mode is given by the product of the mode’s excitability and the component of the right eigenvector on this species. The potential impact from all modes is the sum over the contributions from the individual modes. We define the *sensitivity* of a species, denoted  $\mathbf{Se}$ , as the logarithm of this potential impact, where the logarithm brings



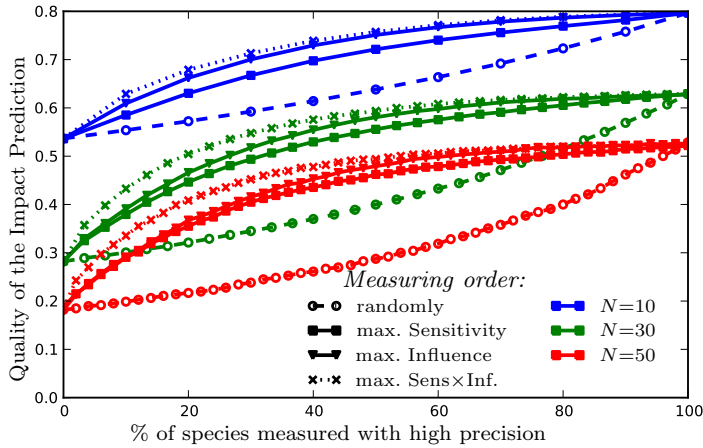


Figure 3. Prediction quality when species are measured successively with higher precision. Starting on the left, all food web species are known with low precision. Advancing to the right the measurement error is reduced for one species at a time until all nodes have been measured with high precision. The different curves refer to different strategies for selecting the next species for improving precision. For the dashed line (empty symbols), the next species is selected randomly. For the solid curves, we first evaluate the sensitivity or influence of each species based on current knowledge and then select the species with the highest value. For the dotted curves we select the species with the highest product of influence and sensitivity ( $Se_i In_i$ ). Error-carrying parameters of each node:  $\alpha, \mu, \psi, \phi, \gamma, \sigma, \beta, \chi$ . Other Parameters: Initial error of each parameter 10%, final error 2%, connectance  $C = 0.04$ .

the numerical values into a more manageable range. For a more formal derivation, see App. Appendix C.

The potential impact that a species causes by exciting a given dynamical mode is given by the product of the mode's excitability and the component of the left eigenvector on this species. The potential impact caused through all nodes is the sum over the excitations of the individual modes. Analogously to the sensitivity, we define the *influence*, denoted  $\mathbf{In}$ , as the logarithm of this potential excitation. For a more formal derivation, see App. Appendix C.

For the example food web in Fig. 1, the sensitivity and influence of each node in the food web are shown in panels k) and l). Comparison with the impact for this food web confirms that sensitive nodes are often affected by the perturbations happening elsewhere and that direct perturbation of influential nodes has a strong effect on the network.

The close relationship between the sensitivity, the influence, and the impact is also confirmed in Fig. 2. On average, the impact of a perturbation on a species increases strongly with its sensitivity, and with the influence of the directly perturbed species. Further, the right-hand graphs in Fig. 2 show the percentage of species in a series of sample food webs that have a sensitivity or influence within the highest 10% or 30% of the respective range for this food web. The average values for these percentages are significantly below the 10% and 30% thereby indicating that for each food web the number of very influential and very sensitive species is small.

In summary, knowledge of the Jacobian of a specific food web enables us to pre-

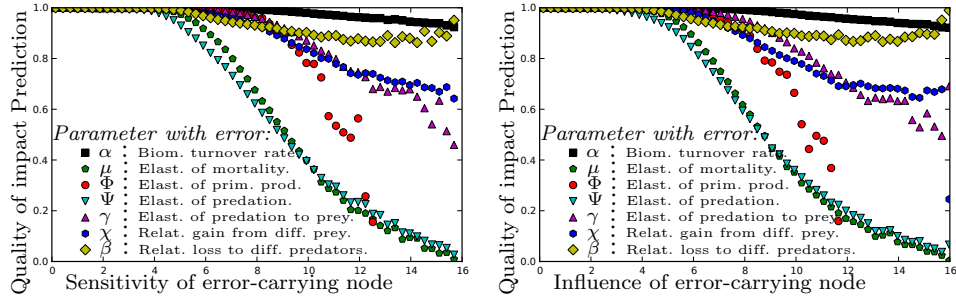


Figure 4. Average quality of an impact prediction in the presence of measurement errors. The average quality of an impact prediction if one node with the specified sensitivity (left) or influence (right) in a food web is subject to a measurement error. The different datasets refer to errors in different parameters (c.f. Tab. 1). Other parameters are: System size  $N = 50$ , connectance  $C = 0.04$ , and the standard deviation of the relative measurement error 10%. For higher  $C$  the effect of  $\chi$  and  $\beta$  increases (not shown). Noise around high importance and sensitivity values is due to the the relatively rare occurrence of these values in the numerical experiments.

dict the impact of specific perturbations, and also allows us to gain a more general understanding of the species' sensitivity and influence with regard to perturbations of the network. The main challenge for impact assessment is thus to collect the necessary data for constructing the system's Jacobian. We show in the following, that high precision is required only for some species.

## 5. Who and What to Measure

Intuitively, to understand the dynamics of a system, one would need to understand the properties of the most influential and sensitive species. However, our notion of sensitivity and influence is itself derived from the Jacobian matrix. Therefore, we can't identify the species that we need information from without having information on those species. We propose two ways to address this dilemma. We start with an iterative strategy in which existing preliminary information is used to estimate the impact and sensitivity of species. This preliminary assessment is then used to obtain improved parameter estimates on seemingly important species. Once additional data on these species becomes available they can be used to further improve the estimates of the impact and sensitivity of species, refining the process. Thus a cycle is formed in which the necessary information for precise impact predictions is iteratively assembled.

We explore the quality of impact prediction in a series of numerical experiments. In each experiment, the task is to predict the impact of a random perturbation to a randomly generated food web that is generated according to the procedure described in Sec. 3. The food web generation determines values of the generalized parameters of the *true* Jacobian of the food web. In addition to this true Jacobian we generate an *estimated* Jacobian, in which we simulate measurement errors by drawing each generalized parameter from a log-normal distribution centered on the corresponding parameter value used in the true Jacobian. We then compute the true impact of the random perturbation,  $\mathbf{I}$  based on the true Jacobian, and the estimated impact  $\tilde{\mathbf{I}}$  based on the estimated Jacobian. The quality of this impact

estimation is then evaluated as the cosine of the angle between the true and the estimated impact vector, which is computed as

$$Q = \frac{\mathbf{I} \cdot \tilde{\mathbf{I}}}{\|\mathbf{I}\| \|\tilde{\mathbf{I}}\|}, \quad (5.1)$$

where  $\cdot$  denotes the scalar product and  $\|\mathbf{I}\|$  is the norm of the vector  $\mathbf{I}$ . The computation yields values between  $Q = 1$ , indicating an exact match of estimated and true impact, and  $Q = -1$ , indicating that the true impact for every species is the exact opposite of the prediction.

We now study a numerical implementation of the iterative strategy described above. We consider numerical experiments in which the knowledge of the Jacobian is initially poor, such that the generalized parameters are drawn from a lognormal distribution with a standard deviation of 10% of the true value. We furthermore assume that additional empirical work can be carried out on specific species that brings the error in all parameters of the respective species down to 2%. Our aim is to carry out the precise measurements in the order that leads to the most rapid increase in the quality of impact prediction.

For the purpose of demonstration we consider four different protocols: a) precise measurements are carried out in random order, b) species are measured in the order of decreasing influence, c) species are measured in the order of decreasing sensitivity, d) species are ordered according to the product of sensitivity and influence, starting with the highest. The choice of species to measure next is always based on the *estimated* Jacobian that is available at the time. Thus, only information is used that would also be available in the real world at the respective time.

The results shown in Fig. 3 demonstrate that estimating influence and sensitivity of the species prior to each measurement strongly increases the accuracy of predictions. This is particularly pronounced if measurements focus on the species with the highest product of sensitivity and influence. For instance after measuring 20% of all species according to this protocol, we attain a quality of prediction that is comparable to measuring 60% – 80% of all species, when species are chosen randomly. Using the estimation of influence and sensitivity to focus observational or experimental efforts can thus significantly reduce the amount of empirical work that is needed to achieve a given prediction quality.

In addition to the iterative approach, we explore what types of parameters and what types of species were most important to measure. To get an initial intuition of the importance of different parameters for impact prediction, we consider a situation where the estimated Jacobian is identical to the true Jacobian except for a single parameter that carries an error. Fig. 4 shows the quality of the estimated impact as a function of the influence and sensitivity of the species affected and the type of parameter varied. The figure furthermore shows the decrease in quality for sensitive and influential species depends on the parameter under consideration; precision in the elasticity of the mortality  $\mu$ , and of the elasticity of predation  $\psi$  with respect to predator abundance are the most important. Fig. 4 thus confirms our intuition that not all parameters need to be measured to the same level of accuracy.

To determine which species are most important to measure in the absence of knowledge about the Jacobian, we looked for simple correlations between sensitivity or influence and species properties (see below) in a set of  $10^6$  stable food webs. Each sample web consists of  $N = 50$  species and has a connectance of 0.04. They

were sampled as before by generating a niche model topology, then drawing the generalized parameters from uniform distributions in their ranges given in Tab. 1, and retaining only stable configurations. For a given web, consider that each of the species  $i$  has a property  $x_i$  and sensitivity or influence  $y_i$ . Then we denote the correlation coefficient between  $x$  and  $y$  as  $R = \sum_i (x_i - \bar{x})(y_i - \bar{y}) / \sqrt{\bar{x}^2 \bar{y}^2}$  where  $i$  runs over all species in a web, and where  $\bar{x}$  denotes the mean value of this property.

In the correlation analysis we considered the correlations (not causal effects) of sensitivity and influence with the following potential biological indicators:

- Generality, or the number of prey species of the focal species.
- Vulnerability, or the number of predators of the focal species.
- A binary value that is 1 if the focal species is a primary producer and 0 otherwise.
- The trophic level  $TL$ , which we calculate by solving a set of linear equations, such that  $TL_i = 1$  for primary producers and  $TL_i = 1 + \text{mean}(TL_{prey})$  for consumers, where  $\text{mean}(TL_{prey})$  denotes the mean trophic level of  $i$ 's prey species.
- The biomass turnover rate (generalized model parameter  $\alpha$ ), indicating the amount of biomass an individual consumes in comparison to its own mass.

The result of the correlation analysis, presented in Fig. 5, shows that high trophic positions and the related low biomass turnover rate correlate most strongly with sensitivity and influence. This result suggests that top predators and other large species, despite their typically small total biomass, play a disproportionate role in the systems' response to perturbations. Without specific information these are the species that should be targeted for initial parameterization (as opposed to our random selection of initial species earlier).

The sensitivity of a species is highly correlated with its generality, while its influence appears to be independent. Intuitively, this might mean that at a species with a large number of prey is likely affected if any of its prey species changes, while a perturbation of this species has little effect on each of the prey species. However, finding if our correlations are based on an causal relationship requires in-depth statistical research that leaves the scope of this work.

## 6. Conclusions

Previous work has suggested that without near perfect information on a range of parameters, it may be nearly intractable to predict the effects of perturbances to large, complex systems [27]. In this paper we proposed a method to predict the impact of perturbations on complex systems more efficiently. We used this method to investigate the relative importance of different species in food webs. Our results show that there are typically a small number of species that are highly important, because they react sensitively to perturbations, have a strong influence on others, or both.

While we have focused exclusively on food webs, we note that the same approach can likewise be applied to other networks of nonlinear interactions that are found for

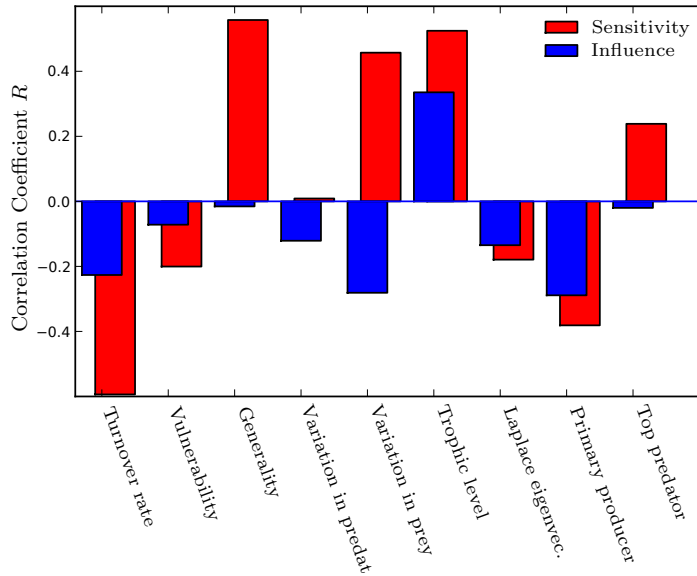


Figure 5. I WILL REMOVE THE EXTRA MESURES FROM THE GRAPH AS SOON AS THE IT-DEPARTMENT HAS “UN-IMPROVED” OUR FILESERVER... Correlation of various properties with the species’ sensitivity and influence. The pattern of correlations is consistent with large predators playing an important role for a system’s response to perturbations.

instance in metabolism [30] or gene regulation [8] and cellular population dynamics [37].

Our results suggest that the potential impact of environmental perturbations on food webs can be predicted with reasonable accuracy if the relevant parameters for a small number of important species in the web are known with reasonable accuracy. We have shown how to find these species iteratively, and how to pre-select potentially important species based on their biological properties. In addition, we have shown that some parameters are particularly important to measure accurately.

For real world food webs, identifying the important species itself requires some information on the system. However, we demonstrated in numerical experiments that an iterative approach is feasible where preliminary inaccurate information is used to estimate the importance of different species, which can then be used to guide further field work, leading to refined prediction. Computing the importance of species based on a generalized model[11] can be done in seconds, even for large systems with tens of species, by using a simple algorithm [? ].

Our correlation analysis suggests that it is most important to obtain precise parameter estimates for large, generalist consumers at top trophic levels. This analysis was not meant to determine which factors cause a species to be influential in a food web. Many of the biological traits we measured are highly correlated, and parsing out their independent effects was not a goal of our study. With caution, one could investigate hypotheses about biological traits that lead species to be more sensitive or influential in a food web, but that would require a different statistical approach than used here and is best the subject of future work.

## Appendix A. GM Jacobian matrix

In this appendix, we show the explicit expressions of the Jacobian matrix for general food webs of the form of (2.1) that was established in Ref. [11]. The diagonal and off-diagonal entries of the Jacobian depending on the generalized parameters in Tab. 1 are separately given by

$$\begin{aligned}
 J_{i,i} &= \alpha_i \left( \tilde{\rho}_i \Phi_i + \rho_i (\gamma_i \chi_{i,i} \lambda_{i,i} + \Psi_i) \right. \\
 &\quad \left. - \tilde{\sigma}_i \mu_i - \sigma \left( \sum_k \beta_{k,i} \lambda_{k,j} ((\gamma_k - 1) \chi_{k,i} + 1) \right) \right) \\
 J_{i,j} &= \alpha_i \left( \rho_i \gamma_i \chi_{i,j} \lambda_{i,j} \right. \\
 &\quad \left. - \sigma_i \left( \beta_{j,i} + \sum_k \beta_{k,i} \lambda_{k,j} ((\gamma_k - 1) \chi_{k,j}) \right) \right).
 \end{aligned}$$

Intuitively, the terms in the first line of each expression are due to the possible feeding of species  $i$  on species  $j$ , while those in the second line are due to loss of  $i$  by natural mortality ( $\sigma\mu$ ) or predation. The terms including  $\gamma - 1$  represent the indirect effects of apparent competition of  $i$  with other species  $j$  if they share a predator  $k$ . For a more detailed discussion, please refer to Ref. [11].

We note that  $\mathbf{J}$  characterizes the dynamics near any steady state. Stability of any particular steady state (corresponding to a particular set of generalized parameters) is ensured by checking that all eigenvalues of the Jacobian have negative real parts [19, 14].

## Appendix B. Predator-prey example

In this appendix we provide the explicit calculations of the impact of the simple system in which a grazer of biomass density  $X_1$  consumes a primary producer of biomass density  $X_2$ . The Jacobian matrix is in terms of generalized modelling parameters near the steady state

$$\mathbf{J} = \begin{pmatrix} \alpha_1(\psi_1 - \mu_1) & \alpha_1\gamma_1 \\ -\alpha_2\sigma_2\psi_1 & \alpha_2(\phi_2 - \sigma_2\gamma_2 - \tilde{\sigma}_2\mu_2) \end{pmatrix}. \quad (\text{B } 1)$$

A more detailed treatment and discussion of stability of this system in terms of the generalized modelling parameters can be found in Refs. [11, 9].

For calculating impact the impact of a perturbation, we require the inverse of the Jacobian

$$\mathbf{J}^{-1} = \frac{1}{\det \mathbf{J}} \begin{pmatrix} \alpha_2(\phi_2 - \sigma_2\gamma_2 - \tilde{\sigma}_2\mu_2) & -\alpha_1\gamma_1 \\ \alpha_2\sigma_2\psi_1 & \alpha_1(\psi_1 - \mu_1) \end{pmatrix}, \quad (\text{B } 2)$$

where

$$\det \mathbf{J} = \alpha_1\alpha_2(\phi_2 - \sigma_2\gamma_2 - \tilde{\sigma}_2\mu_2)(\psi_1 - \mu_1) \quad (\text{B } 3)$$

denotes the determinant of  $\mathbf{J}$ .

A new grazer that has a direct negative effect on the primary producer, but no direct effect on the established grazer, causes a perturbation  $\mathbf{K}$  with entries  $K_1 = 0, K_2 < 0$ . Now we use this vector  $\mathbf{K}$  in the impact equation (2.4) and obtain  $\mathbf{I} = -\mathbf{J}^{-1}(0, K_2)^T$ . The impact on the grazer is therefore

$$I_1 = \frac{\alpha_1}{\det \mathbf{J}} \gamma_1 K_2, \quad (\text{B } 4)$$

and the impact on the producer is

$$I_2 = \frac{\alpha_1}{\det \mathbf{J}} (\mu_1 - \psi_1) K_2. \quad (\text{B } 5)$$

### Appendix C. Derivation of Influence and Sensitivity

Here, we derive the definitions of influence and sensitivity for the food web species, that are motivated with intuitive arguments in the paper. For this, we formulate the Jacobian matrix as a sum of its dynamical modes. Then we use the impact-definition in (2.4) to identify the sensitive species as species for which the expected impact of randomly excited modes is largest, and to identify the influential species as species for which the expected excitation of dynamical modes is largest when they are perturbed.

Each dynamical mode of the Jacobian matrix consists of a left eigenvector, a right eigenvector and a corresponding eigenvalue. These eigenvectors of the Jacobian matrix are defined as  $\mathbf{J}v^{(k)} = \lambda_k v^{(k)}$  and  $\mathbf{w}^{(k)}\mathbf{J} = \mathbf{w}^{(k)}\lambda_k$ . Writing these eigenvectors as the columns of a matrix, e.g.  $\mathbf{V} = (\mathbf{v}^{(1)} \dots \mathbf{v}^{(N)})$ , results in the transformation matrices  $\mathbf{V}$  and  $\mathbf{W}$ . In terms of these matrix and of the diagonal matrix  $\mathbf{D}$  containing the eigenvalues of  $\mathbf{J}$  we can write  $\mathbf{J} = \mathbf{VDW}^T$ .

The inverse Jacobian matrix  $\mathbf{J}^{-1}$ , required for the impact calculation, has the same the same right and left eigenvectors  $\mathbf{v}^{(k)}$  and  $\mathbf{w}^{(k)}$  as the Jacobian matrix, corresponding to the eigenvalues  $1/\lambda_k$ . Therefore  $\mathbf{J}^{-1}$  can be written as  $\mathbf{J}^{-1} = \mathbf{VD}^{-1}\mathbf{W}^T$ .

Now we insert  $\mathbf{J}^{-1} = \mathbf{VD}^{-1}\mathbf{W}$  into the impact equation (2.4). For a given perturbation vector  $\mathbf{K}$  the impact is then

$$\mathbf{I} = \sum_k \mathbf{v}^{(k)} \frac{\mathbf{w}^{(k)} \cdot \mathbf{K}}{\lambda_k}, \quad (\text{C } 1)$$

where  $k$  runs over all eigenvalues and where  $\cdot$  denotes the scalar product. Impact is thus the sum over the dynamical modes of the Jacobian matrix.

Above, we compared dynamical modes to notes played on a drum. We see that for a given given mode  $k$  in (C 1) the contribution to the impact depends on three factors. First, the product  $\mathbf{w}^{(k)} \cdot \mathbf{K}$  determines which dynamical modes are excited by the perturbation. Second,  $\mathbf{v}^{(k)}$  determines which entries in  $\mathbf{I}$  are affected by this dynamical mode. And finally  $1/\lambda_k$  indicates how strongly the mode will be excited.

For the sensitivity of a species, we do not want to explicitly refer to any particular perturbation  $\mathbf{K}$ . In absence of additional information, we therefore consider the case of a perturbation affecting every dynamical mode  $k$  with identical probability. The sensitivity  $Se_i$  can thus be measured as the effects on node  $i$ ,

$$Se_i = \log \left( \sum_k \frac{|\mathbf{v}^{(k)}{}_i|}{|\lambda_k|} \right), \quad (\text{C } 2)$$

where  $|\mathbf{v}^{(\mathbf{k})}_i|$  denotes the absolute value of  $\mathbf{v}^{(\mathbf{k})}$  on node  $i$ , and where we used the logarithm to bring the numerical values into a more manageable range.

For the influence of a species, we evaluate the impact of a perturbation affecting only this specific species  $\mathbf{K}$ . In absence of additional information, the influence is then measured by the resulting excitation of all the dynamical modes

$$\text{In}_i = \log \left( \sum_k \frac{|\mathbf{v}^{(\mathbf{k})}_i|}{|\lambda_k|} \right). \quad (\text{C } 3)$$



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