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Combining bifurcation and sensitivity analysis for ecological models

Model analysis, and the allegory of the cave

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Abstract. Plato's well-known allegory of the cave describes an observer chained in a cave facing a blank wall on which shadows are projected of objects that are outside the cave. Only by breaking free from the chains can the observer submerge from the cave to see what the objects really look like. Ecological model features compare to the objects outside the cave in this allegory. By performing model analysis light is shed on these features, creating projections that researchers can see. Model analysis methodologies like bifurcation analysis and sensitivity analysis each focus on particular model features and thus allow researchers to uncover only part of the model behaviour. By combining methodologies for model analysis possibilities arise for unravelling more of the model's behaviour, allowing researchers to 'break free'. In this paper benefits and issues of combining model analysis methodologies are discussed using a case study. The case study involves three representations of the well-known Rosenzweig-MacArthur predator-prey model, namely the usual one where state variables and parameters have dimensions, a dimensionless representation, and a generalized representation. Based on the results we argue that researchers should combine bifurcation and sensitivity analysis methodologies when analyzing ecological models.

1 Introduction

Models consisting of ordinary differential equations (ODEs) are commonly applied to describe the dynamics of ecological food webs and eco-epidemic systems [1–14]. Different methodologies have been developed to analyse such models, in particular methodologies for bifurcation analysis and sensitivity analysis. *Bifurcation analysis* is aimed at analyzing the stability properties of steady states under parameter variation, i.e., it focuses on the asymptotic model behaviour [15–18]. This is in particular useful for studying bifurcations and manifolds that underlie emergent ecological

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phenomena such as tipping points and chaotic dynamics. *Sensitivity analysis* [19–23], using either local or global methods, is aimed at quantifying the contribution of changes in parameters to changes in model output. This may concern asymptotic model behaviour, but more often it deals with transient behaviour. Sensitivities may change as a function of time.

The application of one methodology for model analysis usually gives a limited view on the full possible model behaviour. One can compare this to Plato’s well-known allegory of the cave, in which an observer is chained to the wall inside the cave and can only see the reflections of objects placed outside the cave that are projected onto the wall by incoming light.

Bifurcation analysis focuses on asymptotic model behaviour, i.e., what the model does assuming time goes to infinity. It does not give information about the sensitivity of a model to certain parameters, but it is used to expose the qualitative aspects of the model behaviour. A complete bifurcation analysis with generic results can only be done for models with a limited number of state variables. Numerical bifurcation analysis using e.g., software like AUTO [24] can be performed for larger systems, but numerical values have to be chosen (generally not a restriction in applications) and the results are usually restricted to regions in parameter space.

Sensitivity analysis can be used to look at time-dynamical aspects, which is more suitable for applications that require estimations of model uncertainties, like parameter estimation and model identification, and for the selection of parameters that make a considerable contribution to ecological model output of interest, e.g., in cases when one is interested in how uncertainties in a large number of parameter estimates propagate to model output. Local sensitivities however are restricted to the analysis around specific parameter values, and become cumbersome when many parameters are under consideration [20]. To maximize sampling efficiency one may adopt methodologies for global sensitivity analysis [22, 23]. Such methodologies take a relatively small number of samples from a large region of parameter space.

Typically methodologies for sensitivity analysis make assumptions about the distributions of residuals from fitting the model to data and about the behaviour of model output. For (near) linear models such assumptions may often be applicable and relevant. Many ecological models, however, contain (strong) nonlinearities, and such statistical assumptions may no longer be valid. Sensitivities give no direct information about bifurcations that typically arise when nonlinearities are involved, and bifurcations are easily ‘missed’ when performing sensitivity analysis, thus ignoring the structure of the model behaviour. Moreover, the use of global, variance-based sensitivities can even lead to spurious results when not considering bifurcations, as simulation end points from regions with different qualitative behaviour may become aggregated into single, non-discriminatory statistics [25].

A combination of bifurcation analysis to expose the qualitative aspects of model behaviour with sensitivity analysis for the quantification of parameter uncertainties may help the modeller understand all aspects of model behaviour and thus improve the quality of the model analysis. This can be compared with an observer that is being unchained, and who is therefore able to walk around and look at objects from different angles. Model sensitivities may be interpreted differently when one is aware of the existence of bifurcations. Methodologies for sensitivity analysis can even provide clues about some types of bifurcations in models of ODEs and Agent-Based Models [25, 26], but only when used in a specific fashion. For example, model output at a certain end point plotted as function of different parameters can easily indicate *transcritical bifurcations*, which are commonly interpreted as an invasion criterion for species [12]. The same is the case for global sensitivities in which samples are considered in which all parameters are allowed to vary randomly except one that is evaluated step-wise [25]. A transcritical bifurcation may become apparent when the means for each

step-wise value of the one parameter decline strongly or converge to zero as a function of that one parameter. Moreover, the existence of clusters of end points away from these means may be an indication of limit cycle behaviour or even a global bifurcation. Such findings may be of interest, in particular when a model description is not explicitly available or when one is developing a model based on data.

In this paper we attempt to cut the chains of the observer and consider issues and possibilities that may arise by making a combination of methodologies for bifurcation and sensitivity analysis to study the dynamics of ODE models. This includes the application of dimension analysis that is often used to reduce the number of parameters while all generic features of the system can still be studied. In addition to local sensitivities *per se*, which have dimensions, one can also study dimensionless sensitivities such as *elasticities*, which may better indicate the importance of a parameter.

As a case study we consider the well-known predator-prey Rosenzweig-MacArthur model [1], henceforth abbreviated as RM model. This model has a specific form with the Holling type II functional response for the predator-prey interaction. We also consider a non-dimensional representation of this model, as well as a generalized version, introduced by Gross et al. [5,11], where the functional response is more general.

The paper is organized as follows. In Section 2 we introduce the used methodologies for local bifurcation and local sensitivity analysis. The case study is introduced in Section 3. The results of the case study analysis are presented in Section 4. Finally, in Section 5 the findings are discussed in a broader context.

2 Model analysis methodology

Let an autonomous system consisting of a set of ODEs read

$$\frac{dY_j(t)}{dt} = f_j(\mathbf{Y}(t), \mathbf{p}), \quad Y_j(0) = Y_j^0, \quad j = 1, 2, \dots, N_v \quad (1)$$

where t is time, $\mathbf{Y}(t)$ is the state vector with the output variables Y_j with $j = 1, 2, \dots, N_v$, with N_v the number of model state variables of the system, and $\mathbf{p}$ is the vector containing the model parameters p_i , $i = 1, 2, \dots, N_p$, where N_p is the number of model parameters. For purposes of analysis the model parameters can also be considered as independent variables, besides time t . Note that the methodologies described below are also applicable for non-autonomous systems, and hence the t can be dropped for convenience. For the remainder of this paper, nontrivial steady states of equation (1) are indicated as $\mathbf{Y}^*$. Symbols used here and elsewhere are explained briefly in Table 1.

2.1 Bifurcation analysis

Bifurcation analysis is aimed at the identification of points in parameter and state space where the stability properties of one or more steady states change (i.e., local bifurcations), as well as the continuation of curves of these points in parameter space [15–18]. Local bifurcations are indicated by one or more eigenvalues equal to zero, and can be found by evaluation of the Jacobian matrix evaluated at a steady state

$$\mathbf{J} = \left(\frac{\partial f_j}{\partial Y_m} \right), \quad m, j = 1, 2, \dots, N_v. \quad (2)$$

Table 1. List of symbols used in this paper with their meaning and the primary equation in which they appear.

Symbol	Meaning	equation
$f_j(\mathbf{Y}(t), \mathbf{p})$	Function	equation (1)
t	Time, non-dimensional	equation (1)
T	Dimensional time	equation (14)
$\mathbf{Y}(t)$	Vector of state variables	equation (1)
Y_j	State variable, indicated by j , non-dimensional	equation (1)
X_j	Dimensional state variable, indicated by j	equation (14)
x_j	Dimensionless state variable, indicated by j	equation (19)
j	Index for state variables, $j = 1, 2, \dots, N_v$	
m	Index for state variables, $m = 1, 2, \dots, N_v$	
N_v	Total number of state variables	
$\mathbf{p}$	Vector of parameters	equation (1)
p_i	Model parameter	
i	Index for parameters, $i = 1, 2, \dots, N_p$	
N_p	Total number of parameters	
s_{p_i}	Local sensitivity for parameter p_i	equation (5)
$\mathbf{J}$	Jacobian matrix	equation (2)
$\mathbf{J}_E$	Jacobian matrix of extended system	equation (13)
N_E	Size of $\mathbf{J}_E$	
$\mathbf{B}_i$	Sub-matrix in extended Jacobian $\mathbf{J}_E$	
$\mathbf{D}_{p_i}$	Parameter Jacobian matrix	equation (34)
*	Indicates evaluation at steady state	
$\text{Det}(\cdot)$	Determinant	equation (3)
$\text{Tr}(\cdot)$	Trace	equation (4)
TC	Value at which transcritical bifurcation occurs	equation (24)
H	Value at which Hopf bifurcation occurs	equation (24)
λ_j	Eigenvalue	
a_j	Amplitude of limit cycle	equation (25)
τ_0	Limit cycle period	
R	Intraspecific growth rate	equation (14)
$R(X_1)$	Intraspecific growth rate as function of X_1	equation (18)
A	Attack rate	equation (14)
$F(X_1)$	Functional response	equation (14), equation (18)
C	Conversion yield	equation (14)
E	Efficiency	equation (18)
M	Mortality rate	equation (14), equation (18)
k	Handling time	equation (14)
γ	Dimensionless yield	equation (15)
θ	Dimensionless handling time	equation (15)
h	Dimensionless mortality rate	equation (15)
$r(x)$	Dimensionless intraspecific growth rate	equation (20)
$g(x)$	Dimensionless growth function	equation (20)
e	Dimensionless efficiency	equation (20)
α_{x_j}	Normalization functions	equation (22)
q	Normalization function	equation (29)
σ	Sensitivity of production to prey density	equation (30)
ϕ	Sensitivity of functional response to prey density	equation (30)

Local bifurcations may be found algebraically with the help of symbolic packages like MAPLE [27], or, when this becomes intractable, with the numerical package AUTO [24]. In addition, systems of the type equation (1) may display *global bifurcations*, i.e., homo- or heteroclinic orbits that connect steady states to themselves or each other, respectively. Global bifurcations are not usually detected by evaluating local bifurcations, but can be found by solving *boundary value problems* [28]. We do not consider global bifurcations in this paper, but we refer to [25] for an example.

For different types of local bifurcations there are different conditions that have to be fulfilled [15–18]. In this paper we limit ourselves to two types that are often found in ecological models, namely the *transcritical bifurcation* and the *Hopf bifurcation*. When the model describes only two variables these bifurcations can easily be found algebraically by taking the determinant

$$\text{Det}(\mathbf{J}^*) = J_{1,1}J_{2,2} - J_{1,2}J_{2,1}, \quad (3)$$

and the trace

$$\text{Tr}(\mathbf{J}^*) = J_{1,1} + J_{2,2} = \lambda_1 + \lambda_2, \quad (4)$$

where $\mathbf{J}^*$ is the Jacobian evaluated at the nontrivial steady state. The *transcritical* bifurcation has an ecological interpretation of the invasion criterion of a species in a food chain or food web. This bifurcation is found in a model of two variables by taking $\text{Det}(J) = 0$. The *Hopf* bifurcation marks the onset of periodic cycling. It can be found in a model of two variables by taking $\text{Tr}(J) = 0$ while $\text{Det}(J) > 0$.

2.2 Sensitivity analysis

Local sensitivities are defined as

$$s_{p_i, Y_j}(t) = \frac{\partial Y_j}{\partial p_i}(t), \quad i = 1, 2, \dots, N_p, \quad j = 1, 2, \dots, N_v, \quad (5)$$

where N_p and N_v have been defined earlier. Local sensitivities can be determined for instance by approximation, e.g., by taking finite differences ($\Delta Y_j / \Delta p_i$), or better by what is known as the *direct differential method* [25, 29, 30]. In the latter case one expresses each sensitivity index s_{p_i, Y_j} as an additional state variable described by a set of differential equations. These equations are obtained by taking the time-derivative of each sensitivity index,

$$\frac{d}{dt}(s_{p_i, Y_j}) = \frac{d}{dt} \left(\frac{\partial Y_j}{\partial p_i} \right) = \frac{\partial}{\partial p_i} \left(\frac{dY_j}{dt} \right), \quad (6)$$

where it is assumed that change of the order of differentiation is allowed. Considering that $Y_j = Y_j(t, \mathbf{p})$, we use the chain rule for differentiation of the sensitivity indices with respect to time to get

$$\frac{d}{dt}(s_{p_i, Y_j}) = \frac{\partial f_j}{\partial p_i} + \sum_{m=1}^{N_v} \frac{\partial f_j}{\partial Y_m} s_{p_i, Y_m}, \quad i = 1, 2, \dots, N_p, \quad j = 1, 2, \dots, N_v, \quad (7)$$

with the summation running over all N_v state variables, or in matrix-valued form

$$\frac{d\mathbf{s}_{p_i, \mathbf{Y}}}{dt} = \frac{\partial \mathbf{f}^*}{\partial p_i} + \mathbf{J}^* \mathbf{s}_{p_i, \mathbf{Y}}, \quad i = 1, 2, \dots, N_p. \quad (8)$$

The $N_v \times N_p$ ODE's for the $N_v \times N_p$ sensitivity coefficients s_{p_i, Y_j} are solved numerically alongside the original N_v ODEs for the state variables Y_j to obtain the local sensitivity indices as a function of time. The extended system reads

$$\frac{dY_j}{dt} = f_j(\mathbf{Y}, \mathbf{p}), \quad j = 1, 2, \dots, N_v \quad (9a)$$

$$\frac{ds_{p_1, Y_j}}{dt} = \frac{\partial f_j}{\partial p_1} + \sum_{m=1}^{N_v} \frac{\partial f_j}{\partial Y_m} s_{p_1, Y_m}, \quad j = 1, 2, \dots, N_v \quad (9b)$$

$$\frac{ds_{p_2, Y_j}}{dt} = \frac{\partial f_j}{\partial p_2} + \sum_{m=1}^{N_v} \frac{\partial f_j}{\partial Y_m} s_{p_2, Y_m}, \quad j = 1, 2, \dots, N_v \quad (9c)$$

$$\vdots \quad (9d)$$

$$\frac{ds_{p_{N_p}, Y_j}}{dt} = \frac{\partial f_j}{\partial p_{N_p}} + \sum_{m=1}^{N_v} \frac{\partial f_j}{\partial Y_m} s_{p_{N_p}, Y_m}, \quad j = 1, 2, \dots, N_v. \quad (9e)$$

The size of the extended system is $N_E = (N_p + 1)N_v$. The subscript E indicates 'extended'.

The initial conditions read

$$Y_j(0) = Y_j^0, \quad j = 1, 2, \dots, N_v \quad (10a)$$

$$s_{p_1, Y_j}(0) = 0 \text{ or } 1, \quad j = 1, 2, \dots, N_v \quad (10b)$$

$$\vdots$$

$$s_{p_{N_p}, Y_j}(0) = 0 \text{ or } 1, \quad j = 1, 2, \dots, N_v. \quad (10c)$$

Since at $T = 0$ the state variables are given by their initial conditions, we have $s_{p_i, Y_j}(0) = 1$ for the sensitivity to the initial condition $Y_j(0) = Y_j^0$, and $s_{p_i, Y_j}(0) = 0$ for other parameters.

When evaluated for Y_j^* , $j = 1, 2, \dots, N_v$, we have for the extended system

$$\mathbf{0} = \frac{d}{dt} \left(\frac{\partial \mathbf{Y}^*}{\partial p_i} \right) = \frac{\partial \mathbf{f}^*}{\partial p_i} + \mathbf{J}^* \mathbf{s}_{p_i}^*, \quad \forall i. \quad (11)$$

The steady state of the sensitivity coefficients can then be calculated as follows

$$\mathbf{s}_{p_i}^* = -(\mathbf{J}^*)^{-1} \frac{\partial \mathbf{f}}{\partial p_i} \Big|_{\mathbf{f}=\mathbf{f}^*} = \frac{\partial \mathbf{Y}}{\partial p_i} \Big|_{\mathbf{Y}=\mathbf{Y}^*}, \quad \forall i, \quad (12)$$

where $(\mathbf{J}^*)^{-1}$ is the inverse of the Jacobian given in equation (2). Observe, that for the transcritical bifurcation $\text{Det}(\mathbf{J}^*) = 0$, and hence the inverse does not exist. If there is an algebraic solution of the steady state, it may be possible to obtain symbolic expressions for the local sensitivities equation (5) by differentiation of the steady state solution with respect to each of the parameters. This is convenient for the verification of numerical results by comparing the numerical values of long iterations (in practice comparable to $t \rightarrow \infty$) to the symbolic expressions evaluated at the correct parameter values.

The extended system equation (9) with size $N_E = N_v + N_p N_v$ to be integrated can be written in the form [29]

$$\mathbf{s}_E = \begin{pmatrix} \mathbf{Y} \\ \mathbf{s}_1 \\ \mathbf{s}_2 \\ \vdots \\ \mathbf{s}_{N_p-1} \\ \mathbf{s}_{N_p} \end{pmatrix}, \quad \mathbf{J}_E = \begin{pmatrix} \mathbf{J} & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{B}_1 & \mathbf{J} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{B}_2 & \mathbf{0} & \mathbf{J} & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{B}_{N_p-1} & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{J} & \mathbf{0} \\ \mathbf{B}_{N_p} & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{J} \end{pmatrix}, \quad (13)$$

where all sub-vectors have length N_v . The subscript E in matrix J_E indicates ‘extended’ again. The Jacobian $\mathbf{J}$ block sub-matrix has sizes $N_v \times N_v$ and is repeated $N_p + 1$ times on the diagonal of the matrix J_E . The sub-matrices $\mathbf{B}_i$ are the elements of the Jacobian matrix part belonging to the right-hand sides of equations (9b)–(9e) and have sizes $N_v \times N_v$ for $i = 1, \dots, N_p$. Only the non-diagonal sub-matrices $N_v \times N_v$ in their first block-column are non-zero. This means that for each parameter the sensitivity parameter vector $\mathbf{s}_j$ depends only on the N_v state variables $\mathbf{Y}_j$, and on other elements of sensitivity parameter vector $\mathbf{s}_j$ itself and not on the sensitivity parameter vectors of the other parameters. Hence, the matrix J_E is a lower-diagonal block matrix. As a result, the eigenvalues of $\mathbf{J}_E^*$ (i.e., Eq. (2) evaluated at the non-trivial steady state) are $N_p + 1$ multiples of the eigenvalues of the Jacobian $\mathbf{J}^*$ of the original system and therefore the stability properties of the original system and the extended system are the same.

As mentioned earlier, the existence of the inverse of the Jacobian matrix is guaranteed when none of the eigenvalues of the Jacobian matrix $\mathbf{J}$ evaluated at the steady state is zero or its determinant is zero. This holds for instance when the steady state is hyperbolic, when the steady state is attracting and stable but also when it is repelling and unstable. At a Hopf bifurcation point the existence of the inverse of the Jacobian matrix is guaranteed as well. Observe, that when the original system shows limit cycles, then the extended system can be decoupled. One then obtains the original state variable vector $\mathbf{Y}_j$ of the autonomous system and N_p forced independent sub-systems for $\mathbf{s}_{p_i, Y_j}$, $j = 1, \dots, N_v$ sensitivity vectors. In the coming analysis we will discuss in more detail what happens in the region where the unstable steady state and stable limit cycle occur.

3 Model description

3.1 Specific RM model

The RM model [1] is given as

$$\frac{dX_1}{dT} = RX_1(1 - X_1K^{-1}) - AF(X_1)X_2, \quad (14a)$$

$$\frac{dX_2}{dT} = (CAF(X_1) - M)X_2, \quad (14b)$$

where $F(X_1) = X_1(1 + AkX_1)^{-1}$ is the well-known Holling type II functional response, with X_j the state variables, k handling time, A the attack rate, C a conversion efficiency, M the predator removal rate (mortality, maintenance, and harvesting), and T is time. This model can be rescaled by using $t = TR$, $Y_1 = X_1/K$, and

$Y_2 = X_2/(CK)$. The non-dimensional model then reads

$$\frac{dY_1}{dt} = f_1(Y_j(t), p) = Y_1(1 - Y_1) - \gamma Y_1 Y_2(1 + \gamma\theta Y_1)^{-1}, \quad (15a)$$

$$\frac{dY_2}{dt} = f_2(Y_j(t), p) = \gamma(Y_1(1 + \gamma\theta Y_1)^{-1} - h)Y_2, \quad (15b)$$

where $\gamma = CAK/R$, $\theta = kR/C$ and $h = M/(\gamma R) = M/(CAK)$. For simulations we will consider $\gamma = 3$, unless stated otherwise. The RM model has two trivial steady states $(0, 0)$ and $(1, 0)$, and one nontrivial steady state $Y^* = (Y_1^*, Y_2^*)$, where

$$Y_1^* = -h(\gamma h\theta - 1)^{-1}, \quad Y_2^* = -(\gamma h\theta + h - 1)(\gamma h\theta - 1)^{-2}\gamma^{-1}. \quad (16)$$

It has been proven that the nontrivial steady state is globally stable [31], and in case that this steady state is not stable, that the periodic solution is unique, and thus a globally stable limit cycle exists [32]. No global bifurcations are known for the two-dimensional RM model.

For the RM model $N_v = 2$ and $N_p = 3$, which means there are six sensitivities to be determined. Because there are symbolic expressions available for the nontrivial steady state equation (16) we can obtain symbolic expressions for all local sensitivities evaluated at this steady state by direct differentiation of equation (16) with respect to the individual parameters. These local sensitivities are given as

$$s_{h,1}^* = \frac{1}{(\gamma h\theta - 1)^2}, \quad s_{h,2}^* = \frac{\gamma^2 h\theta^2 + \gamma\theta(h - 1) + 1}{\gamma(\gamma h\theta - 1)^3}, \quad (17a)$$

$$s_{\gamma,1}^* = \frac{h^2\theta}{(\gamma h\theta - 1)^2}, \quad s_{\gamma,2}^* = \frac{2\gamma^2 h^2\theta^2 + 3(h - 1)\gamma h\theta - h + 1}{\gamma^2(\gamma h\theta - 1)^3}, \quad (17b)$$

$$s_{\theta,1}^* = \frac{h^2\gamma}{(\gamma h\theta - 1)^2}, \quad s_{\theta,2}^* = \frac{h(\gamma h\theta + 2h - 1)}{(\gamma h\theta - 1)^3}, \quad (17c)$$

which can also be used to verify numerical results.

3.2 Generalized model

A general predator-prey model version was introduced to understand the impact of different functional forms of predator-prey interaction [5, 11]. Consider the general predator-prey model

$$\frac{dX_1}{dt} = R(X_1) - F(X_1)X_2, \quad \frac{dX_2}{dt} = EF(X_1)X_2 - MX_2, \quad (18)$$

where $R(X_1)$ is now a prey growth rate function, $F(X_1)$ is a now undetermined functional response, E is the yield or conversion efficiency, and M again the predator removal rate. Note that the RM model is a sub-class of this more generalized model version. Equation (18) can be normalized using the method by Gross et al. ([5, 11]), which can also be used to normalize general food chain or more complex ecosystem models (see e.g., [33]).

We assume that there exists a positive steady state X_1^* and X_2^* . We then define normalized variables

$$x_1 = \frac{X_1}{X_1^*}, \quad x_2 = \frac{X_2}{X_2^*}, \quad (19)$$

Fig. 1. E_0 : $Y_1^* = Y_2^* = 0$, E_1 : $Y_1^* > 0, Y_2^* = 0$, E_2 : $Y_1^* > 0, Y_2^* > 0$, L_2 : $Y_1(t) > 0, Y_2(t) > 0$, E : stable equilibrium, L : stable limit cycle. The following bifurcation curves are plotted ($\gamma = 3$): TC indicates transcritical, and H indicates supercritical Hopf.

and normalized functions

$$r(x_1) = \frac{R(x_1 X_1^*)}{R(X_1^*)}, \quad g(x_1) = \frac{F(x_1 X_1^*)}{F(X_1^*)}, \quad e = E. \quad (20a)$$

The normalized general model now can be written as

$$\frac{dx_1}{dt} = \alpha_{x_1}(r(x_1) - g(x_1)x_2), \quad \frac{dx_2}{dt} = \alpha_{x_2}(eg(x_1)x_2 - x_2), \quad (21)$$

where

$$\alpha_{x_1} = \frac{F(X_1^*)}{X_1^*}, \quad \alpha_{x_2} = EF(X_1^*) = M. \quad (22)$$

By definition we have $x_1^* = x_2^* = 1$ as steady state.

4 Model analysis results

4.1 Specific RM model

With the use of MAPLE [27] symbolic expressions can be found of the elements of the Jacobian matrix of the RM model. Evaluated in the nontrivial steady state equation (16) the Jacobian is given as

$$\mathbf{J}|_{Y^*} = \begin{pmatrix} h(\gamma^2 h\theta^2 + \gamma h\theta - \gamma\theta + 1)(\gamma h\theta - 1)^{-1} - \gamma h & -\gamma h \\ -\gamma h\theta - h + 1 & 0 \end{pmatrix}. \quad (23)$$

Then, using criteria equation (3) and equation (4) curves of the transcritical and Hopf bifurcations in two-parameter diagrams can be determined algebraically (see Fig. 1). They are given as

$$\text{Det}(\mathbf{J}) = 0 \Rightarrow h_{TC} = \frac{1}{1 + \gamma\theta}, \quad (24a)$$

$$\text{Tr}(\mathbf{J}) = 0 \Rightarrow h_H = \frac{\gamma\theta - 1}{\gamma\theta(1 + \gamma\theta)}, \quad (24b)$$

Fig. 2. Steady state values: Left: prey Y_1^* (light grey on paper or red in electronic version). Right: predator Y_2^* (dark grey on paper or blue in electronic version). In the horizontal plane the bifurcation curves from Figure 1 are plotted. The same colouring for prey and predator is used in the consecutive figures.

Fig. 3. Sensitivity coefficients distribution. Left: with respect to θ prey: s_{θ, Y_1}^* and predator: s_{θ, Y_2}^* . Right: with respect to h , prey: s_{h, Y_1}^* and predator s_{h, Y_2}^* .

Fig. 4. Sensitivity coefficients for $Y_2^* \geq 0$, i.e., a restriction is added that biomass of Y_2 should be non-negative. Left: with respect to θ prey: s_{θ, Y_1}^* and predator: s_{θ, Y_2}^* . Right: with respect to h , prey: s_{h, Y_1}^* and predator s_{h, Y_2}^* . In the horizontal plane the transcritical bifurcation curve is plotted. At this TC curve the sensitivities become unbounded.

where the subscript TC indicates transcritical bifurcation, and H supercritical Hopf bifurcation. The results can be verified numerically by using AUTO [24].

The nontrivial steady state values are plotted in a three-dimensional space in Figure 2, in which the expressions given in (16) and (17) are used. Also depicted again are the transcritical and Hopf bifurcation curves. The sensitivities equation (5) evaluated at the nontrivial steady state are depicted in Figure 3. In Figure 4 the restriction is added that predator biomass has to be positive. In Figure 5 the additional restriction is that the nontrivial steady state is stable. This shows that the stability properties of the steady states have to be used to obtain relevant sensitivity indices.

Time-dependent local sensitivities have been obtained through numerical integration with a Runge-Kutta 4th order implementation of the model with equation (9) and equation (10), where parameter h has been varied step-wise.

Fig. 5. Sensitivity coefficients where $Y_2^* \geq 0$ and stable, i.e., restrictions are added that biomass of Y_2 should be non-negative and the steady state should be stable. Left: with respect to θ prey: s_{θ, Y_1}^* and predator: s_{θ, Y_2}^* . Right: with respect to h , prey: s_{h, Y_1}^* and predator s_{h, Y_2}^* . In the horizontal plane the transcritical and the Hopf bifurcation curves are plotted. At the TC curve the sensitivities become unbounded.

Fig. 6. Sensitivity coefficients. Left panel: for the stable equilibrium $s_{\theta, Y_2}(t)$ (upper, green in electronic version), $s_{Y_2^0, Y_2}$ (middle, red), and $s_{h, Y_2}(t)$ (lower, blue), with $h = 0.25$ and $\theta = 0.5$. Right panel: for the unstable equilibrium, with $h = 0.1$. All sensitivities become unbounded.

The results for individual sensitivity coefficients $s_{\theta, Y_2}(t)$, $s_{h, Y_2}(t)$ (with $\gamma = 3$) are presented in Figure 6. With $\theta = 0.5$, $h = 0.25$ the steady state is stable and also the sensitivity coefficients converge to their equilibrium values, see Figure 6, left panel. With $\theta = 0.5$, $h = 0.1$ the steady state is unstable and a stable limit cycle exists. The sensitivities in this case become unbounded, as can be seen in Figure 6, right panel. Observe, that the period of the limit cycle generally changes with varying model parameters. One can consider a sensitivity to be a finite difference approximation of the partial derivative, e.g., by comparing a difference $\Delta h = 0.01$. The difference between the two resulting limit cycles for h and $h + \Delta h$ becomes infinite for increasing time, see Figure 7 left panel. The actual dynamics depend on whether the two frequencies, which are related to the two resulting periods belonging to the two different values of h , are rational [34]. In the right panel of Figure 7 these results are shown for the initial condition of the predator population $Y_2(0) = Y_2^0$ and $Y_2(0) = Y_2^0 + 0.01$ where the two frequencies belonging to the two different values of $Y_2(0)$ are the same.

The sensitivity with respect to the initial condition of the predator population is shown in Figure 8. This sensitivity remains bounded albeit in a cyclic fashion, see Figure 8. This can be understood by taking the finite difference approximation results. As only the initial condition is perturbed the period of the cycle is exactly equal. This is similar to following two points that are both on the same cycle. Another

Fig. 7. Solution $Y_1(t), Y_2(t)$, $\theta = 0.5$, left: $h = 0.1$ (light grey on paper or red in electronic version) and $h = 0.1 + 0.01$ (dark grey on paper or blue in electronic version). Right: for $Y_2(0) = Y_2^0$ and $Y_2(0) = Y_2^0 + 0.01$ (same colouring). In the left case the difference increases consistently, in the right case the difference remains unchanged.

Fig. 8. Sensitivity coefficients $s_{Y_2^0, Y_2}$, $\theta = 0.5$, $h = 0.1$. The sensitivity grows initially but remains bounded.

interpretation is that the frequency is the same, but the phase differs, see also Figure 7 right panel.

As an alternative definition of local sensitivity for periodic solutions one can consider the amplitude a_j and cycle period τ_0 as output variables. The amplitude is then defined as the difference between the maximum and minimum peaks in the state variables

$$s_{p_i, Y_j}^a = \frac{\partial a_j}{\partial p_i} \quad i = 1, 2, \dots, N_p, \quad j = 1, 2, \dots, N_v. \quad (25)$$

Due to the boundedness of the solution this measure remains finite, see Figure 9. The results presented in this figure indicate that the sensitivity of the amplitude of the limit cycle s_{θ, Y_1}^a becomes unbounded when the Hopf bifurcation is approached from the unstable steady state branch, which is in accordance with the Hopf bifurcation point analysis; compare to [17, p. 86] for the square root function of the amplitude of the stable limit cycle from the Hopf bifurcation point.

Fig. 9. Steady state and amplitude sensitivity coefficients $h = 0.1$, and variable θ . Below Hopf bifurcation H steady state s_{θ,Y_1}^* (light grey on paper or red in electronic version), s_{θ,Y_2}^* (dark grey on paper or blue in electronic version) and above H amplitude s_{θ,Y_1}^A , s_{θ,Y_2}^A (same colouring).

Finally, if one want to use local sensitivities for practical purposes like model calibration, the results obtained for the dimensionless model have to be translated back to those for the original model. In our study case, the results for equation (15) have to be converted to sensitivities for equation (14). For example, we can calculate the sensitivity of X_1 with respect to parameter K

$$s_{K,Y_1}^* = \frac{\partial Y_1^*}{\partial K} = s_{\gamma,Y_1}^* \frac{\partial \gamma}{\partial K} + s_{\theta,Y_1}^* \frac{\partial \theta}{\partial K} + s_{h,Y_1}^* \frac{\partial h}{\partial K}, \quad (26a)$$

$$s_{K,X_1}^* = \frac{\partial X_1^*(K)}{\partial K} = \frac{\partial KY_1^*(K)}{\partial K} = Y_1^*(K) + K s_{K,Y_1}^* = 0, \quad (26b)$$

i.e., the chain and the product rule are applied, and $X_1 = KY_1$ is used. In this particular case $Y_1^*(K) = M(AK(C - Mk))^{-1} = -K s_{K,Y_1}^*$ after substitution of $\gamma = CAK/R$, $\theta = kR/C$ and $h = M/(\gamma R) = M/(CAK)$, which gives zero. Another example is the sensitivity of X_2 with respect to parameter K

$$s_{K,Y_2}^* = \frac{\partial Y_2^*}{\partial K} = s_{\gamma,Y_2}^* \frac{\partial \gamma}{\partial K} + s_{\theta,Y_2}^* \frac{\partial \theta}{\partial K} + s_{h,Y_2}^* \frac{\partial h}{\partial K}, \quad (27a)$$

$$s_{K,X_2}^* = \frac{\partial X_2^*(K)}{\partial K} = \frac{\partial CKY_2^*(K)}{\partial K} = CY_2^*(K) + CK s_{K,Y_2}^* = \frac{MCR}{K^2 A^2 (C - Mk)^2}, \quad (27b)$$

where $X_2 = CKY_2$ is used. Obviously, Y_1^* and Y_2^* should be considered as functions of the parameter to which differentiation occurs. The sensitivities of the dimensional model calculated from those for the non-dimensional model can be checked by comparing them against the sensitivities obtained from the original RM model equation (14).

4.2 Results for the generalized model

It is well-known that the stability of a system depends on the eigenvalues of the Jacobian matrix $\mathbf{J}$ evaluated at the steady state. The Jacobian matrix $\mathbf{J}^*$ of the

generalized predator-prey model equation (18) is

$$\mathbf{J}^* = \begin{pmatrix} \sigma - \phi & -1 \\ q\phi & 0 \end{pmatrix}, \quad (28)$$

where

$$q = \frac{\alpha_{x_2}}{\alpha_{x_1}}, \quad (29)$$

which can be interpreted as the predator turnover rate; α_{x_1} and α_{x_2} were defined earlier in equation (22). We have now the following expressions

$$\sigma = \frac{d}{dx_1} r(x_1)|_{x=x^*}, \quad \phi = \frac{d}{dx_1} g(x_1)|_{x=x^*}. \quad (30)$$

Here σ is the sensitivity of production to prey density. Alternatively, σ can be interpreted as a measure of the availability of nutrient for the prey, where $\sigma = 1$ means the nutrient availability is high while for $\sigma = 0$ nutrients are scarce [5]. The quantity ϕ can be interpreted as the sensitivity of the functional response function to prey density. For $\phi = 1$ the predation rate increases linearly with prey abundance, while for $\phi = 0$ the predation rate is independent of prey abundance (i.e., not sensitive to x).

The fold bifurcation in the generalized predator-prey model is fixed by

$$\text{Det}(\mathbf{J}^*) = q\phi = 0. \quad (31)$$

Since $F(x)$ is monotonously increasing (i.e., there is a hyperbolic relationship) the nontrivial steady state does not have a tangent bifurcation; a transcritical bifurcation is not studied in the generalized predator-prey model because then the predator is extinct and division by its steady state value gives issues. Transcritical bifurcations can be detected when an adapted normalization is used [8, 11].

The Hopf bifurcation is fixed by the condition

$$\text{Tr}(\mathbf{J}^*) = \sigma - \phi = \frac{d(r(x_1) - g(x_1))}{dx_1} = 0. \quad (32)$$

In other words, these bifurcation criteria are directly expressed using state-dependent parameters that have a simple ecological interpretation. Because there are no explicit parameter-dependent expressions in equation (18), no local sensitivities can be evaluated.

5 Discussion

In this paper we combine bifurcation and sensitivity analysis to analyse three representations of a predator-prey model (one dimensional, and two non-dimensional representations) and compare the information that is exposed about the model using different methodologies. In all cases bifurcations can be found numerically using AUTO, while sensitivities can be calculated using the direct differential method. The dimensionalized representation allows for direct comparison to observational data, but the disadvantage is that the results for different parameters are not directly comparable because of differences in dimensions or units. When the model is made dimensionless using several parameters the results become comparable, at the cost of having

to convert non-dimensional parameters to dimensional parameters before comparison to observational data is possible. The model can also be made dimensionless using the approach by Gross et al. [5, 11], named the generalized model representation. The advantage of this approach is that bifurcations are directly expressed in composite parameters that have a clear ecological interpretation, e.g., as *per capita* rates. The disadvantage is that sensitivities cannot be evaluated numerically. Each approach, using bifurcation and sensitivity analysis, and representing the model as dimensional or non-dimensional, has its advantages and drawbacks and sheds a different light on model behaviour.

Bifurcation and sensitivity analysis are not commonly applied together, although there are possibilities to do this. For instance, the numerical calculation of local sensitivities has been combined with the Routh-Hurwitz criteria known from control engineering to analyse a model that combines cell signalling and cell population dynamics [35]. In fact, there are even standardized toolboxes available in which methodologies for bifurcation and sensitivity analysis are included, for example, the Systems Biology Toolbox for MATLAB [36]. By combining bifurcation and sensitivity analysis more information is revealed that may help in explaining observations that are otherwise not comprehensible. For instance, models in the neighbourhood of bifurcations have been reported to display a drastically increased uncertainty [4]. More importantly, it should become good practice to combine bifurcation and sensitivity analysis to reduce the probability of getting the wrong impression of how a model behaves. For instance, it has been shown that global sensitivity analysis can lead to ‘false’ statistics, because a sampling is made from parameter space without considering regions of qualitatively different behaviour [25]. Such statistics then give incorrect information about the model behaviour. Combining bifurcation and sensitivity analysis allows researchers to ‘cut their chains’ and obtain a better overview of how the model behaves.

There is also a clear connection between bifurcation and sensitivity analysis. Bifurcation point types are typically determined by criteria based on normal form analysis, which make use of partial derivatives of the function with respect to parameters $\partial f / \partial p$. These partial derivatives connect bifurcations (based on the Jacobian) with local sensitivities, as becomes clear from the direct differential method for simulation of local sensitivities equation (9). In fact, continuation techniques make use of $\partial f / \partial p$ [37, Sect. 8.2.2]. For steady states, for instance in the RM system equation (14), we follow a branch where

$$\mathbf{f}(\mathbf{Y}^*, p_i) = \mathbf{0}, \quad (33)$$

where one starts at a steady state, and p_i is the bifurcation parameter. To calculate the slope at a point on the branch the following relationship is used

$$\mathbf{J} \mathbf{f}(\mathbf{Y}^*, p_i) dY + \mathbf{D}_{p_i} \mathbf{f}(\mathbf{Y}^*, p_i) dp_i = \mathbf{0}, \quad (34)$$

where $\mathbf{D}_{p_i} \mathbf{f}$ is the ‘parameter Jacobian’, and p_i is a scalar. In the ecological literature sensitivities are also used in a bifurcation analysis context, see for instance [38, Sect. 2.2] where a three-trophic food chain has been analysed, or [33]. There, $\mathbf{J}^*$ represents the ‘community matrix’ and $\partial f_j^* / \partial p_i$ represents elements of the $N_v \times N_p$ community sensitivity matrix with respect to the N_p parameters.

Bifurcation and sensitivity analysis can be combined in different ways. One possibility is to perform bifurcation analysis before starting with sensitivity analysis to uncover the ‘skeleton’ of the model behaviour. However, it may be impractical or even impossible to perform bifurcation analysis, in particular when no symbolic solutions are available. An alternative is to perform sensitivity analysis based on numerical approaches and look for clues of bifurcations. For instance, distributions of model output may be multi-modal because a bifurcation is separating two or more modes

in the model [4]. This seems to be particularly useful when searching for hysteresis, for example to distinguish between alternative stable vegetation states [39]. In a methodology referred to as *one-factor-at-a-time* (OFAT) [25] one parameter is varied step-wise while keeping all other parameters at their nominal values, while after each step the model is integrated again. This methodology is in fact an extended version of what is known as *one-at-a-time* (OAT) sensitivity analysis [19,20], in which the effect of one parameter is estimated by making a single step and calculating $\Delta Y_j / \Delta p_i$. By plotting the simulation end points of the OFAT as function of the varied parameter for instance transcritical bifurcations may be revealed [25], as certain model outputs go to zero on one side of the bifurcation while converging to a positive steady state value at the other side. Another approach is to vary all parameters except one, and then proceed step-wise for this one parameter, which is referred to as *all-but-one-simultaneously* (ABOS) [25]. The means of the simulation end points for each step-wise value of the one parameter are plotted as function of this parameter. Transcritical bifurcations but also limit cycles and possibly heteroclinic orbits (i.e., global bifurcations) may become visible through clusters that appear around means or far away from means, where the latter may indicate an unstable state.

When applying the direct differential method equation (9) the original dynamical system is augmented with that for the sensitivities, having two systems that are uncoupled, and therefore the time solution of the original system can be regarded as a forcing function. When the steady state for the original system is stable this works well since also the sensitivities converge to the local sensitivities. Models with $N_v \geq 2$ can have limit cycles, and then local parameter sensitivities become unbounded. On the other hand local sensitivities for initial values remain bounded. For models with $N_v > 2$ there may also be dynamics on a torus, periodic or quasi-periodic dynamics, or chaotic attractors (depending on the Lyapunov exponents). As a result the dynamics of the sensitivities (where the extended system is possibly not conservative or its dynamics becomes unbounded) can be of the same type, but also resemble a so-called strange non-chaotic attractor [34] when the system is quasi-periodically (Lyapunov exponent zero). For higher-order systems where more than two frequencies can be involved, the situation becomes even more complex. In summary, with non-steady states of the original system, local sensitivities may not be well-defined and alternative measures for sensitivities have to be used. In this paper we redefined local sensitivities for limit cycles as amplitudes. This could also work for quasi-periodic or even chaotic dynamics.

Parameters commonly differ in their units, which can hinder a straightforward relative quantification of their effects on model output. In a dimensionless representation the sensitivities are rescaled such that comparison between them becomes ‘fair’. A common way to rescale sensitivities is by representing them as *elasticities*, given as

$$\epsilon_{i,j} = \frac{p_i}{Y_j(t)} \frac{\partial Y_j(t)}{\partial p_i}, \quad (35)$$

of which the interpretation is straightforward. E.g., an elasticity of ‘3’ indicates a 1% change in the value of parameter p_i leads to a 3% change in model output, in comparison to the nominal set of parameter values. Elasticities are not well-defined in cases where Y_j approaches zero. Furthermore, often there is no direct expression of Y_j available, in which case the elasticity is approximated numerically. Another way to perform normalisation of local sensitivities is by using variances [20]

$$\left(\frac{V_{p_i}}{V_{Y_j(t)}} \frac{\partial Y_j(t)}{\partial p_i} \right)^2, \quad (36)$$

where V_{p_i} is the variance in the parameter p_i , and $V_{Y_j}(t)$ is given as

$$(V_{Y_j}(t))^2 \approx \sum_i V_{p_i}^2 \left(\frac{\partial Y_j(t)}{\partial p_i} \right)^2. \quad (37)$$

This may be a decent approximation for (near) linear systems, but not necessarily for (strongly) nonlinear systems. A different alternative is to formulate a generalized model by making state variables dimensionless, e.g., by division by their steady state variables, as is done in the approach used in [5,11]. The resulting elements in the Jacobian matrix contain functions with an ecological interpretation. This gives a direct link to bifurcation analysis when these functions are varied. These functions however are not explicitly expressed in parameters, which makes it difficult to obtain sensitivities. Elasticities similar to those used in economics or metabolic control theory have been used to analyse generalized models [33].

Much work is still to be done in combining bifurcation and sensitivity analysis. Future extensions of work on bringing together bifurcation and sensitivity analysis should involve quantification of the sensitivity to the initial conditions in regard to in particular *separatrices*, manifolds in state space that separate different domains of attraction. This is relevant for instance for identifying regions with hysteresis dynamics and fitting models with hysteresis to data. It may also be helpful in dealing with global bifurcations, which can have considerable consequences in an ecological context [28]. Additional numerical techniques and quantitative measures are required for calculating sensitivities for limit cycles, and to deal with more complex dynamics. Techniques to approximate local sensitivities altogether are needed to deal with stochasticity, be it from the model itself (as with stochastic ODEs) or simply from model fitting residuals, because finite differences may not be sufficiently accurate for all applications.

Model analysis can benefit from combining bifurcation and sensitivity analysis methodologies. Bifurcation analysis may help in obtaining proper estimates of model uncertainties and in model identification, because it allows the user to identify the model behaviour structure. Sensitivity analysis is helpful in quantifying effects of model parameters on model output, given the underlying statistical assumptions are valid. The dimensional model results allow for the comparison of sensitivities to observational data, while a non-dimensional representation of the model may allow for a comparison of the numerical results or for a direct ecological interpretation. Bifurcation and sensitivity analysis methodologies may thus complement each other, which aids model development and application, and we argue the two methodologies should be used together when analyzing ecological models.

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