Ecological consequences of global bifurcations in some food chain models

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A B S T R A C T

Food chain models of ordinary differential equations (ODE’s) are often used in ecology to gain insight in the dynamics of populations of species, and the interactions of these species with each other and their environment. One powerful analysis technique is bifurcation analysis, focusing on the changes in long-term (asymptotic) behaviour under parameter variation. For the detection of local bifurcations there exists standardised software, but until quite recently most software did not include any capabilities for the detection and continuation of global bifurcations. We focus here on the occurrence of global bifurcations in four food chain models, and discuss the implications of their occurrence. In two stoichiometric models (one piecewise continuous, one smooth) there exists a homoclinic bifurcation, that results in the disappearance of a limit cycle attractor. Instead, a stable positive equilibrium becomes the global attractor. The models are also capable of bistability. In two three-dimensional models a Shil’nikov homoclinic bifurcation functions as the organising centre of chaos, while tangencies of homoclinic cycle-to-cycle connections ‘cut’ the chaotic attractors, which is associated with boundary crises. In one model this leads to extinction of the top predator, while in the other model hysteresis occurs. The types of ecological events occurring because of a global bifurcation will be categorized. Global bifurcations are always catastrophic, leading to the disappearance or merging of attractors. However, there is no 1-on-1 coupling between global bifurcation type and the possible ecological consequences. This only emphasizes the importance of including global bifurcations in the analysis of food chain models.

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1. Introduction

Ecological modeling is the field that studies the time dynamics of populations of species, and how these populations interact with each other and with their abiotic environment. A large portion of the ecological modeling consists of studies of food chain models, where sets of ordinary differential equations (ODE’s) are used to describe population sizes in time. It is a useful tool to investigate diverse subjects, like extinction thresholds, the effects of sub-lethal toxicants or global warming on ecosystem functioning and structure, to name a few examples.

To test the ecological validity of these models, extensive analysis is required. A powerful way of analysing ODE models is by using bifurcation theory [1–5], where the asymptotic behaviour of the system (equilibria, periodic cycles, chaos) is evaluated under parameter variation for qualitative changes. A qualitative change in the asymptotic behaviour is then referred to as a bifurcation point.

There is already an extensive history in the use of bifurcation theory for the analysis of food chain models. For examples of an ecological application see [6–8], and recently [9]. Four types of bifurcation points are often encountered in food chain models: the transcritical bifurcation (an equilibrium that did not exist in the positive plane shifts to the positive plane, which in an ecological context gives an existence or extinction boundary), the tangent bifurcation (two equilibria, with usually different stability properties, coincide and disappear, ecologically often associated with the disappearance of a system separatrix), the Hopf bifurcation (a stable equilibrium that changes stability, while a limit cycle is born, which marks the transition to periodic behaviour), and the flip bifurcation (a limit cycle undergoes periodic doubling, and usually a series of these bifurcations marks the onset of chaotic behaviour). The occurrence of bifurcation points has potentially radical effects, because small changes in a parameter lead to significant changes in the asymptotic behaviour, and potentially also changes that cannot be easily reverted by restoring the parameter to its old value, as for instance in the case of hysteresis [10].

Although the application of bifurcation theory has long been limited to theoretical results, there have been promising results. The past decade it has been shown that experimental settings, representing small food chains in chemostats, show the transitions in asymptotic behaviour under parameter variation as predicted by bifurcation theory. For instance, in [11] the transition from a stable...
equilibrium to a stable limit cycle (i.e. a Hopf bifurcation) under increase of the dilution rate was reported for a food chain chemostat system, consisting of planktonic rotifers feeding on green algae, with nitrogen as the limiting resource. Later in [12] it was shown that chaos can occur in a system consisting of two competing bacterial prey species and a bacterivorous ciliate, again under variation of the dilution rate. These results motivate the use of bifurcation theory to analyse food chain models, and show that bifurcation theory does not only provide theoretical results without further ecological implications.

Despite these promising results, not all potentially significant and drastic changes can be explained by the occurrence of any of the above-mentioned local bifurcations. There are at least a few examples, that, although they are still theoretical, predict the occurrence of global bifurcations, where we define a global bifurcation as either a structurally unstable connecting orbit, that disappears when one parameter is varied, or the tangency of a structurally stable connecting orbit. These examples also indicate there can be serious consequences resulting from these global bifurcations. One example is given by the bifurcation analyses of some two-dimensional food chain models with Allee-effect [6,13], that revealed that extinction events named overexploitation, where the whole system collapses, were coupled to global bifurcations [14]. A similar type of collapse is observed in food chain chemostat models after the introduction of sub-lethal toxicants [15]. And in the three-dimensional prey–predator–top predator Rosenzweig–MacArthur model it has been shown that the parameter region of chaotic behaviour is bounded by a global bifurcation [16–18].

The observation, that in all of these cases global bifurcations are linked to extinction events or switching to another positive attractor, suggests that it is of significant interest to take a closer look at global bifurcation analysis. However, until recently it proved to be notoriously difficult to detect and continue global bifurcations, where either a saddle equilibrium or saddle limit cycle is connected to itself (homoclinic), or where two saddle equilibria and/or saddle limit cycles are connected via their manifolds (heteroclinic). Local information, that suffices to track local bifurcations, reveals nothing about the existence of globally connecting orbits other than whether or not one of more saddles exist. In the cases in which global bifurcations were successfully detected and continued in parameter space, clues were used. For instance, limit cycles can grow to asymptotically large period under parameter variation, and this can be an indication that a homoclinic point-to-point connection exists (this was the also the case with the initial detection of the heteroclinic cycle in [14]). The existence of a bifurcation point of higher codimension (like Bogdanov–Takens or Gavrilov–Guckenheimer) can indicate there must be a point-to-point connection existing (this was the also the case with the initial detection of the heteroclinic cycle in [14]). The existence of a bifurcation point of higher codimension (like Bogdanov–Takens or Gavrilov–Guckenheimer) can indicate there must be a point-to-point connection [5]. But in general, more sophisticated techniques are required for a more systematic search for global bifurcations.

Recently there has been a significant jump in the development of successfully tested techniques to both find and continue global bifurcations. Now it is possible to find homoclinic connections in 2D models (homcont [19–21], as part of AUTO [22]), 2D heteroclinic connections [14], and point-to-cycle and cycle-to-cycle connections in 3D systems [23–25,18,26,22]. It is therefore possible to take the next step, by analysing food chain models in search for global bifurcations, and investigate the possible ecological implications of occurring global bifurcations.

Without a claim on generality, we discuss in this paper three previously published and one adapted food chain models, and apply our previously developed techniques to detect and continue occurring global bifurcations. Furthermore, we aim to obtain a clear ecological interpretation of the occurrence of these global bifurcations. The four models were selected, since the occurring global bifurcations have clearly distinct ramifications as compared to the extinction events discussed above. In Section 2, we discuss the two-dimensional stoichiometric food chain model by Loladze et al. [27], and a smooth analog of the model. In these models a homoclinic point-to-point connection exists that is associated with the destruction of a system’s attractor. As there is a different equilibrium that becomes the system’s attractor, there is no extinction of species. In Section 3, we revisit the analyses of the 3D food chain models by Rosenzweig and MacArthur [28,16,17,29] and by Letellier and Aziz-Alaoui [30]. In these models there are homoclinic point-to-point connections that form the ‘skeleton’ in the generation of chaos (Shilnikov bifurcation), while there are homoclinic cycle-to-cycle connections that are associated with the disappearance of the chaotic behaviour. Finally, in the discussion in Section 4, we combine the findings with results of previous studies on global bifurcations in ecological food chain models. Two overviews are given, one on the types of global bifurcations found thus far, and one on the observed ecological consequences of their occurrence.

2. 2D Stoichiometric models

In this section, we revisit the stoichiometric model by Loladze et al. [27]. As the model is non-smooth, we also develop a smooth analog of the model in Section 2.2.

2.1. Model by Loladze et al.

The first two-dimensional model we discuss is given as

\[
\frac{dX_1}{dt} = b \left(1 - \frac{X_1}{K_1}\right)X_1 - cf(X_1)X_2, \quad (1a)
\]

\[
\frac{dX_2}{dt} = e \min\left(1, \frac{P - X_2}{\theta}\right)X_1X_2 - dX_2, \quad (1b)
\]

and was first described by Eqs. (6a) and (6b) in [27], where \(f(X_1)\) is the Holling type II functional response [31]

\[
f(X_1) = \frac{X_1}{a + X_1}.
\]

The parameter values are given in Table 1. The individuals of both the producer and grazer populations are composed of two nutrients, carbon (an energy source) and phosphorus. \(X_1\) and \(X_2\) denote the carbon content of the two populations. The phosphorus in the system is divided over the grazer and producer populations. The ratio in phosphorus and carbon (P:C) can vary in the producer population, but by introduction of the parameter \(q\) it is assumed that there is a minimum in this ratio.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Value</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>(p)</td>
<td>0.025</td>
<td>Total phosphorus</td>
</tr>
<tr>
<td>(e)</td>
<td>0.8</td>
<td>Maximal production efficiency</td>
</tr>
<tr>
<td>(b)</td>
<td>1.2</td>
<td>Maximal growth rate of producer</td>
</tr>
<tr>
<td>(d)</td>
<td>0.25</td>
<td>Assimilation preference for (P)</td>
</tr>
<tr>
<td>(q)</td>
<td>0.03</td>
<td>Grazer constant</td>
</tr>
<tr>
<td>(q)</td>
<td>0.0038</td>
<td>Producer minimal</td>
</tr>
<tr>
<td>(c)</td>
<td>0.81</td>
<td>Maximum ingestion rate of grazer</td>
</tr>
<tr>
<td>(a)</td>
<td>0.25</td>
<td>Half-saturation of functional response</td>
</tr>
<tr>
<td>(K)</td>
<td>–</td>
<td>Producer carrying capacity</td>
</tr>
<tr>
<td>(C)</td>
<td>–</td>
<td>Total carbon</td>
</tr>
<tr>
<td>(B_P)</td>
<td>0.002</td>
<td>Assimilation preference for (C)</td>
</tr>
<tr>
<td>(B_P)</td>
<td>2.0</td>
<td>Assimilation preference for (P)</td>
</tr>
<tr>
<td>(K_{P})</td>
<td>1.0</td>
<td>Saturation constant</td>
</tr>
<tr>
<td>(j)</td>
<td>–</td>
<td>Maximum predator ingestion rate</td>
</tr>
</tbody>
</table>
The populations can be limited either by carbon or by phosphorus, as is given by the Liebig minimum function. The use of this switch-function results in a piecewise continuous model, which satisfies the Lipschitz condition with respect to both variables \( X_1 \) and \( X_2 \). The initial value problem is therefore mathematically well-defined, and there is generally continuous dependence on initial conditions and parameters in the system. The derivative of the system, the Jacobian matrix, is however, undetermined at the switching point.

In [27] the two types of displayed qualitative behaviour were discussed. In Fig. 1(a) (a replica of Fig. 4 in [27]) it is shown that for the situation where \( 0.17 < K < 0.979435 \) the producer population is limited by energy (carbon). There are only two equilibria, the trivial unstable equilibrium \( E_0 = (0,0) \) and the stable internal equilibrium \( E_1 \). The system displays the classical ‘paradox of enrichment’ (POE) [32,33]. It occurs, when under an increase of the carrying capacity a stable limit cycle \( L_1 \) is born at a Hopf bifurcation that becomes the dominant system attractor, while the equilibrium \( E_1 \) becomes unstable. A further increase in carrying capacity results in an increase in amplitude of the limit cycle, until the minima of the limit cycle become such that extinction through stochastic effects is plausible. However, in this model the minima of the limit cycle do not become very low, because for \( 0.979435 < K < 1.9 \) the producer population is limited by phosphorus, and a different type of behaviour occurs. The limit cycle (and hence POE) is not present, but instead there are four equilibria: the unstable equilibria \( E_0 \) and \( E_1 \), the stable equilibrium (and global attractor) \( E_2 \), and a saddle equilibrium \( E_3 \).

The switch at \( K \approx 0.979 \) in Fig. 1(a) was described in [27] as an ‘infinite period bifurcation’, and coincides with a tangent bifurcation where the two equilibria \( E_2 \) and \( E_3 \) collide. At this bifurcation the limit cycle \( L_1 \) disappears and the principle system’s attractor becomes \( E_2 \), which explains why the POE no longer occurs. This infinite period bifurcation is in fact a homoclinic bifurcation, that coincides with a tangent bifurcation. Exactly at the tangent bifurcation there is one equilibrium, \( E_2 = E_3 \), that is a saddle-node point. The limit cycle touches this equilibrium and forms a saddle-node homoclinic connection, as can be seen in Fig. 1(b). This connection can be obtained either by tracking the limit cycle \( L_1 \) up to a period that approximates infinity, or by using homotopy as described in the Appendix in [14].

An interesting point is now whether the limit cycle \( L_1 \) disappears through the tangent bifurcation or through the connecting orbit. By varying a second parameter \( d \) we find that it is possible that the point-to-point connection exists as a saddle connection from \( E_2 \) to itself, while there is also the stable equilibrium \( E_3 \). This situation is depicted in Fig. 2 where \( d = 0.32 \) and \( K \approx 0.879726 \). In Fig. 2(a), the one-parameter bifurcation diagram of the system is shown, and it can be seen that besides the two types of behaviour described above (POE and stable equilibrium \( E_2 \)) there is also a third type of behaviour in the region \( 0.849 < K < 0.879726 \), namely bistability. In this region there are two attractors, the limit cycle \( L_1 \) and the equilibrium \( E_2 \), separated by the stable manifold to the saddle equilibrium \( E_3 \), as can be seen in Fig. 2(b).

Fig. 3(a) shows the two-parameter bifurcation diagram of the model, where the bifurcation parameters are \( K \) and \( d \). Observe that,
Besides regular bifurcation curves and bifurcation points of higher codimension, there are the discontinuous Jacobian also discontinuity curves, where one of the minimum functions for the producer and grazer species switch. The curve $A_i$ is determined by $P = Kq + OX_2$, while $A_j$ by $P = O(X_1 + X_2)$. These curves can be continued using sets of boundary conditions, as shown in Appendix A. Furthermore, there are ‘pseudo-bifurcation’ points $Z_i$, where $i = 1, 2, \ldots$, in which bifurcation curves join with either $A_i$ or $A_j$. The point-to-point connection can be found and continued in two-parameter space by using the homotopy techniques discussed in [14,25,18].

There are two transcritical bifurcations $TC_1$ and $TC_2$ that connect to each other in point $Z_1$. The tangent bifurcation $T_{bc}$ where $E_2 = E_3$ connects to the curve $A_i$ in point $Z_2$, which in a sense replaces a Cusp bifurcation. The Hopf bifurcation curve $H^-$ terminates at the curve $A_j$ in $Z_2$. The global bifurcation curve $C_G$ indicates the saddle homoclinic connection and terminates at one end at the curve $A_y$ in point $Z_4$, where the point-to-point connection has shrunk to a point, and at the other end at the point of higher codimension $N$, where it is transformed into a saddle-node connection. The saddle-node homoclinic orbit is indicated by $C_{GN}$ and terminates at $A_x$ in point $Z_5$.

We can now distinguish the following parameter regions with different dynamical behaviour. A limit cycle attractor occurs in the region right of the $H^+$, left of the global bifurcation curves $G_S$ and $G_{SN}$, below $A_x$. In the rest of the region below $TC_1$ and $TC_2$ there are equilibrium attractors. Bistability occurs in the approximately triangular-shaped parameter region bounded between $Z_2$, $Z_4$ and $N$. Hence this region partly overlaps with the region where limit cycles exist, and there is one limit cycle attractor and one point attractor. In the rest of the bistability region there are two point attractors.

### 2.2. Smooth stoichiometric model

Because of problems generated by the non-smoothness of the model, a smooth version of the above-discussed stoichiometric model was developed, where all variables and parameters are kept equal to their counterparts in the original stoichiometric formulation, and all parameter values remain the same. In this model, the $su$-formulation [34,35] is used to describe the assimilation in the producer species where both the phosphorus and the carbon are essential nutrients, i.e. the growth depends on both nutrients. The producer species consists of two components, structure and an internal phosphorus reserve pool.

It is assumed that the structure has a fixed stoichiometry, so the phosphorus density of the structure $P/C$ is fixed. The total phosphorus density in the producer is denoted by $\eta$. We furthermore assume a closed system, which means that the mass conservation principle applies (it is not applied in the original model by Loladze et al. [27]). The growth depends on the carbon influx from the environment and equals $C - X_1 - X_2$, where $C$ is the total carbon in the system, and the internal phosphorus $P - 0X_2 - qX_1$. Since all phosphorus is in the biota, the pool $\eta - q$ and the total phosphorus density in the producer $\eta$ are time-dependent. The whole formulation is given as

\[
\begin{align*}
\frac{dX_1}{dt} &= b - \frac{j}{g(X_1, X_2)}X_1 - cf(X_1)X_2, \quad (2a) \\
\frac{dX_2}{dt} &= e - \frac{1.2}{1 + \frac{q}{n}}[cf(X_1)X_2 - dX_2], \quad (2b)
\end{align*}
\]

where the functional response is Holling type II again as given by Eq. (2a).

The producer intake flux is written as

\[
j = 1 + \frac{K_{NC}}{CB_p + PB_p} - \frac{K_{PC}}{CB_p + PB_p}
\]

and

\[
g(X_1, X_2) = 1 + \frac{X_1}{(C - X_1)CB_p} + \frac{X_2}{(P - 0X_2 - qX_1)BP_p} - \frac{K_{PC}}{(C - X_1)BP_p + (P - 0X_2 - qX_1)BP_p}
\]

where the extra parameters are also given in Table 1. In Eq. (2b) it is assumed that after ingestion the carbon and phosphorus are independently available again for growth. The factor $1.2$ is a scaling factor in order to better match the original model by Loladze et al. [27].

The dynamics of this smooth version of the stoichiometric model are summarised in Fig. 3 (b). Apart from qualitative there are also qualitative differences between the two models. In the smooth model version neither the points $Z_i$ nor the discontinuity curves $A_i$ and $A_j$ exist. The two transcritical bifurcation curves $TC_{1}$ and $TC_{2}$ are here the same curve $TC_e$. There are now two tangent bifurcation curves $TC_{1} - 1$ and $TC_{2} - 2$ that collide in a cusp bifurcation $C_p$. The Hopf bifurcation $H^-$ terminates in a Bogdanov–Takens point $BT$ that is on one of the tangent bifurcation curves. The $BT$ is also the origin for the global bifurcation curve $C_G$, depicted in solid line type. In the point $N$ the curve $C_G$ merges with the lower tangent bifurcation curve, and continues as a saddle-node connection $C_{SN}$.

There are the following regions of dynamical behaviour. In the region right of $H^+$ and below $TC_e$ there is a point attractor. This turns into a limit cycle attractor in the region right of $H^+$ and left of the global bifurcation curves $G_S$ and $G_{SN}$. There is a point attractor right of the global bifurcation curves, below $TC_e$. There is also a point attractor in the small region between $H^ - , TC_{1} - 1$ and $TC_e$. Bistability occurs in the four-cornered region bounded by $G_S$, $TC_{2} - 2$, $TC_{1} - 1$ and $TC_e$. Left of $H^+$ there are two point attractors, right of $H^-$ there is a point attractor and stable limit cycle.
2.3. Comparison of the two model versions

The original stoichiometric model in [27] displays not only bifurcation curves and bifurcation points of higher codimension, but also discontinuity curves, and bifurcation-like points. At these points bifurcation curves coincide with switches of the Liebig minimum associated with the model formulation of the trophic interaction. These points seem to be the analogue of real codim-2 points that occur in the smooth version of the stoichiometric model. The tangent curve in the original model terminates in a pseudo-bifurcation point, while in the smooth model there is also a second tangent curve that terminates together with the first tangent curve in a Cusp bifurcation. Also, in the original model the Hopf and saddle homoclinic bifurcation curves terminate separately in pseudo-bifurcation points, while in the smooth model it terminates at the same point of higher codimension on a tangent curve, as corresponding with theory on the Bogdanov–Takens point [5].

2.4. Global bifurcations in the stoichiometric models

In the stoichiometric models, we have found two possible scenarios. In the first scenario there is only one system attractor, the limit cycle. With increased K the saddle-node connection occurs at the exact point where a tangent bifurcation takes place. In this case, a global bifurcation coincides with a local bifurcation. Upon the immediate destruction of the system attractor a new attractor is created. There is no extinction of species, and there is no disappearance or creation of bistability properties. However, the time dynamics of the system changes from periodic to steady state.

In the second scenario, the occurrence of a (saddle) homoclinic orbit, not connected to any local bifurcation, plays an important role. In this scenario, there is a parameter region where there are two attractors, namely a stable limit cycle and a stable equilibrium, separated by the stable manifold to the saddle equilibrium E3. With the occurrence of the connecting orbit to this saddle equilibrium, both the limit cycle and the separatix are destroyed. As such, with this global bifurcation, a system attractor and the bistability properties of the model disappear.

This second scenario resembles the phenomenon of ‘overexploitation’ in Allee-models [14]. However, in contrast to the previously studied Allee-models, where after the destruction of the limit cycle attractor a zero-equilibrium becomes the new global attractor, the equilibrium that remains after the global bifurcation in the stoichiometric model is positive, and no extinction occurs. Nevertheless, the occurrence of the global bifurcation results in a significant effect, as the steady state value of the grazer density is lower than that of the minimum of the destroyed limit cycle attractor (see Fig. 1, right panel). Therefore, although no overexploitation occurs, a small, stochastic shift in K can result in a sudden drop in biomass densities. Also, the new lower grazer density cannot be reverted back to its old state without a larger step back in K, since the system is in its new attractor. As such we have some kind of ‘catastrophic shift’ [10], but now occurring because of a global bifurcation instead of a local bifurcation (tangent).

3. 3D Food chain models with chaos

In this section, we review the analysis of the three-dimensional Rosenzweig–MacArthur food chain model (abbreviated RM), before revisiting the analysis of a second three-dimensional food chain model that is described in [30].

3.1. Rosenzweig–MacArthur food chain model

The RM food chain model is given as

\[
\begin{align*}
\frac{dx_1}{dt} &= f_1(x_1) - f_2(x_2)x_1, \\
\frac{dx_2}{dt} &= f_2(x_2)x_1 - f_3(x_3)x_2, \\
\frac{dx_3}{dt} &= f_3(x_3)x_2 - f_4(x_4)x_3,
\end{align*}
\]

which is dimensionless. The functional responses are given as

\[
\begin{align*}
f_1(x_1) &= \frac{a_1x_1}{a_1 - b_1d_1}, \\
f_2(x_2) &= \frac{a_2x_2}{a_2 - b_2d_2}, \\
f_3(x_3) &= \frac{a_3x_3}{a_3 - b_3d_3}.
\end{align*}
\]

The variables and parameters are given in Table 2. The carrying capacity K has disappeared in the rescaling process, therefore it can no longer be used as bifurcation parameter. The two death rate parameters d are the most obvious selection to perform a two-dimensional bifurcation analysis of the model, since the other remaining parameters are associated to physiological properties and can therefore be assumed to remain fixed.

The equilibria of system (6) are

\[
\begin{align*}
E_0 &= (0, 0, 0), \\
E_1 &= (1, 0, 0), \\
E_2 &= \left( \frac{d_1}{a_1 - b_1d_1}, \frac{a_1 - d_1(b_2 + 1)}{(a_1 - b_1d_1)^2}, 0 \right), \\
E_3 &= (x_1^*, x_2^*, x_3^*),
\end{align*}
\]

where

\[
\begin{align*}
x_1^* &= \frac{b_1 - 1 + \sqrt{(b_1 + 1)^2 - 4a_1b_1d_1}}{2b_1}, \\
x_2^* &= \frac{d_2}{a_2 - b_2d_2}, \\
x_3^* &= \frac{f_1(x_1^*) - d_3}{a_3 - b_3d_3},
\end{align*}
\]

for 0.16 ≤ d1 ≤ 0.32, 0.0075 ≤ d2 ≤ 0.015 (see also [36]).

The stability of the equilibria, and the local bifurcation analysis of the RM model, are described in detail in [37]. We will give a

Table 2

<table>
<thead>
<tr>
<th>(x_1^*)</th>
<th>(a_1)</th>
<th>(b_1)</th>
<th>(d_1)</th>
<th>(d_2)</th>
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<td>(x_2^*)</td>
<td>(a_2)</td>
<td>(b_2)</td>
<td>(d_2)</td>
<td>(d_3)</td>
</tr>
<tr>
<td>(x_3^*)</td>
<td>(a_3)</td>
<td>(b_3)</td>
<td>(d_3)</td>
<td>(d_4)</td>
</tr>
<tr>
<td>(f_1(x_1^*) - \frac{a_1}{b_1d_1})</td>
<td>(\frac{a_2}{b_2d_2})</td>
<td>(\frac{a_3}{b_3d_3})</td>
<td>(\frac{a_4}{b_4d_4})</td>
<td></td>
</tr>
</tbody>
</table>
short overview here of the system, that is rich in bifurcations, both for equilibria and limit cycles.

**Fig. 4(a)** shows a one-parameter local bifurcation diagram, with $d_1 = 0.25$ and $d_2$ as free parameter. The value of $x_3$ is displayed as a function of $d_2$. In the case that it is a limit cycle, the minimal and maximal values of $x_3$ are also displayed. The system has a stable equilibrium $E_3$ where all three species exist only between the two Hopf bifurcations $H^-$ and $H^+$. Increasing the value of $d_2$, beyond the subcritical $H^+$ the stable equilibrium becomes a saddle point, while an unstable limit cycle is born. The unstable limit cycle can be continued up to a cycle tangent bifurcation $T_e$, where also a stable limit cycle emerges. This stable limit cycle disappears from the positive plane at a transcritical bifurcation $T_c$. The saddle point collides with an unstable equilibrium, born from a transcritical bifurcation $T_c$, in the tangent bifurcation $T_e$.

On the other side, when decreasing the value of $d_2$, at the supercritical $H^-$, the stable equilibrium $E_3$ is replaced by a stable limit cycle as the system’s attractor. The equilibrium becomes a saddle point. When decreasing the value of $d_2$ further the stable limit cycle goes through a series of flip bifurcations, until a chaotic attractor appears, as is depicted in **Fig. 4(b)**.

In **Fig. 5(a)**, a two-parameter diagram is shown, where $d_2 = 0.1$, and $d_1$ and the cycle period $T_0$ are varied. The cycle period goes to infinity at $d_1 = 0.3166$, after an infinite number of tangent and flip bifurcations. This figure indicates there is a Shil’nikov global bifurcation, of which the connection has one spiralling end. The ‘skeleton’ of the route to chaos is this Shil’nikov bifurcation, a point-to-point connection to itself of the equilibrium $E_3$ that has become a saddle point after the Hopf bifurcation $H^-$.

The point-to-point connection can be detected, and continued, using HOMCONT [19,20], or the techniques discussed by Doedel et al. [25] in adapted form. There are actually two connections very close to each other in parameter space, that are depicted in **Fig. 5(b)**. One connecting orbit connects from the saddle equilibrium to itself after one rotation (dashed–dotted). The other orbit makes two full rotations before connecting (dotted).

In **Fig. 4(b)** it can be seen that the chaos suddenly disappears. This happens at the parameter values of $d_2$ where the minimal value of $x_3$ of the chaotic attractor collides with the minimal value of the unstable limit cycle. At these parameter values the chaotic attractor is destroyed by a cycle-to-cycle homoclinic bifurcation [16,17] in a boundary crisis [38,39] (see also the LA model in the next section, and Appendix B).

In **Fig. 5(a)**, a two-parameter diagram is shown with $d_1$ and $d_2$ as bifurcation parameters. Two extra local bifurcations are visible now. The first is the transcritical bifurcation $T_c$, where the stable positive equilibrium appears. The second is the planar Hopf bifurcation $H_p$. For values of $d_1$ lower than where $H_p$ occurs, a two-dimensional stable limit cycle exists, that is the system attractor when the top predator does not exist. Most local bifurcations ($T_e$, both $T_c$, $H_p$, $T_c$, and $H^-$) originate from the same organising centre, a point $M$ of higher codimension. This bifurcation point has been analysed in detail in [37]. The two Hopf bifurcations $H^-$ and $H^+$ collide in a second codim-2 point, a Bautin point $B$, which is also the end point for the curve $T_c$.

In **Fig. 5(b)**, a detail of the two-parameter bifurcation diagram is shown. The first and second order flip bifurcations $F^{1,2}$ of the stable limit cycle are displayed, and indicate where approximately the region of chaos is located. They are associated to the Shil’nikov bifurcation curve, labeled as $G_c$. Also originating from the Shil’nikov are cycle tangent bifurcations $T_c$, of which one is depicted. The full unfolding around a Shil’nikov bifurcation has been discussed in

![Fig. 4](image1.png)

![Fig. 5](image2.png)
3.2. Letellier and Aziz-Alaoui food chain model

The food chain model described in [30] (abbreviated as LA) is given as

\[
\begin{align*}
\frac{dX_1}{dt} &= (a_1 - b_1 X_1)X_1 - \alpha_2 X_1 X_2, \quad (10a) \\
\frac{dX_2}{dt} &= -a_2 X_2 + \alpha_2 X_1 X_2 - \alpha_3 X_2 X_3 - d_2, \quad (10b) \\
\frac{dX_3}{dt} &= (c_0 - \alpha_3 X_2 + d_3)X_3, \quad (10c)
\end{align*}
\]

for which the parameters are given in Table 3. We focus on the same parameter ranges as in the original paper, where the system has six equilibria: the trivial \( E_0 = (0,0,0) \), \( E_1 = (1,0,0) \), \( E_2 \) has \( X_1 = 0 \), \( E_3 = (X_1, X_2, 0) \), and \( E_4 \) and \( E_5 \) are internal equilibria. The last two equilibria play no role in the system dynamics since they are imaginary, and hence \( E_3 \) must be the principle positive equilibrium [30].

The model displays bistability for a significant parameter range. Depending on the exact parameter value there are two positive stable limit cycles (of different period), a stable limit cycle and a chaotic attractor or even two chaotic attractors, as was also found by the original authors. In their paper it is shown that, for the parameter values given in Table 3 with \( a_1 \) as bifurcation parameter, there are two regions of chaos that partly occur simultaneously. This is demonstrated in Fig. 7(b), comparable to Fig. 9 in [30]. One chaotic attractor is born through a series of period-doubling bifurcations, after a Hopf bifurcation of the internal stable equilibrium at \( a_1 \approx 1.2966 \). The other chaotic attractor is born through a series of period-doubling bifurcations of a stable, period-one limit cycle, that in turn is born in a tangent bifurcation \( T_c \) at \( a_1 \approx 1.7805 \).

Two important questions can now be raised that are not yet answered. First, what is unclear from their Fig. 9 is why the first region of chaos is interrupted. A dotted curve has been drawn that suggests to terminate together with the chaotic attractor. However, with the use of AUTO it is found that there is a saddle limit cycle also born in the tangent bifurcation, that goes away from it in a straight fashion, rather than that it curves backward again. This saddle limit cycle functions as separatrix of the two basins of attraction. This specific detail cannot be found when results are obtained by numerical integration. Furthermore, an alternative one-parameter diagram in \( a_1 \) for \( c_0 = 0.032 \) given in Fig. 7(a) shows that the right boundary of the first region of chaos coincides with the tangent bifurcation, that gives rise to the stable limit cycle that eventually generates the second region of chaos. On the other hand, in a second alternative one-parameter diagram in \( a_1 \) for \( c_0 = 0.041 \) the two chaotic attractors appear simultaneously Fig. 7(c). Also, Fig. 7(a) shows that there are even more than two chaotic regions. This raises the question on how all the different chaotic attractors are coupled.

With regard to the first point, the sudden interruption of chaos resembles that which occurs in the RM model, for which we know that a global bifurcation is responsible for the termination of chaos. With regard to the second point it was correctly reported by Letellier and Aziz-Alaoui that a Shil’nikov bifurcation occurs in the model. Like in the RM model, we can expect a Shil’nikov bifurcation to function as the organising centre of the dynamics, where an infinite series of tangent and flip bifurcations eventually generates

| Table 3 |
| List of parameters used in the model in [30]. |
| (a) | (b) | (c) | (d) |
| \( a_1 = 1.0 \) | \( a_2 = 1.0 \) | \( b_1 = 0.06 \) | \( d_2 = 10.0 \) |
| \( d_1 = 10.0 \) | \( d_2 = 10.0 \) | \( d_3 = 10.0 \) | \( c_0 = 0.038 \) |
chaos. Apparently several global bifurcations play an important role in the dynamics of this model.

In Fig. 8 next-minimum maps of the model are displayed for some parameter values of $a_1$. Each map has been generated by integration of the system, meanwhile scoring the extrema (the minimal and maximal values are given as Eq. (10)). To avoid the effects of the transient behaviour the first part of the simulation run is skipped. From that point onwards every minimum is plotted as a function of the previous minimum. With a sufficiently long integration run the dots merge together to reveal the basins of attraction. In Fig. 8(a) at $a_1 = 1.89138$, a globally connecting orbit can be spotted as the $Y_{n+1}$-value of the right boundary of the curve $Y_n \approx 7.438$ equals that of the left boundary $Y_n \approx 5.059$. As a result, the orbit starting at the top of the parabola-like shaped curve ends up after two iterations at the minimum value of the attractor $Y_n = Y_{n+1} = 5.059$, while all other orbits do not end up in this point. This point is hence a saddle fixed point on the map. In Fig. 8(b) ($a_1 = 1.95882$) and Fig. 8(c) ($a_1 = 1.95883$) it is revealed in the same fashion that there is another globally connecting orbit that is of period two. After this homoclinic orbit the basin of attraction of the chaotic attractor has increased drastically and includes the 'old' basin of attraction of the other chaotic attractor that disappeared in the first global bifurcation. This indicates that there is a difference between the two homoclinic connecting orbits, and thus that the two boundaries of the involved chaotic attractor differ.

Using the techniques discussed in [25,18], we can calculate the bifurcation curves of the Shil’nikov and the tangencies of the cycle-to-cycle connections in the two parameters $a_1$, $c_0$. The cycle-to-cycle connections are structurally stable and can be continued using one free parameter up to tangencies. These tangencies are structurally unstable and can than be continued into two free parameters, where the connection time remains fixed. The results are shown in Fig. 9 for $a_1, c_0$, where the thin, solid lines are intersection curves to correspond with Fig. 7(a)–(c).

In Fig. 9(a), we see the route to chaos for the upper chaotic attractor in Fig. 7(b). The positive equilibrium can be tracked through a Hopf bifurcation, after which the stable limit cycle undergoes an infinite number of period doublings, of which two are shown. Fig. 9(b) shows the route to chaos for the lower chaotic attractor, starting at a cycle tangent bifurcation. Notice that the bifurcation curves make a sharp turn. Fig. 9(c) reveals the Shil’nikov bifurcation, indicated by $G_c$, that functions as the centre of unfolding. Each flip bifurcations branch off of a cycle tangent bifurcations at one end, and terminates at the other end at a different cycle tangent bifurcation of ‘lower order’. In this figure, only two cycle tangent and a few flip bifurcation curves are shown, that can be traced back in Fig. 7(a)–(c), but observe that there are infinitely many.

The curves $G_c$ indicate the tangencies of homoclinic cycle-to-cycle connections that exist in this model, shown in Fig. 9(d). In
contrast with the RM model, where there is only one such homoclinic orbit, there are two in this model, as already revealed by the next-minimum maps. To obtain these tangency curves we first need approximate connections, and then use the homotopy method to obtain connecting orbits that can be continued into two parameters. Approximate connections can be obtained by starting from a base point \( x \) on a saddle limit cycle and making a small step \( \varepsilon \) on the unstable manifold of the cycle. In the RM model only starting in one direction, either a small step ‘above’ (say \( \varepsilon = +0.001 \)) or a small step ‘below’ the cycle (say \( \varepsilon = -0.001 \)), leads to an approximate connection. In the LA model starting in either direction gives an approximate connecting orbit, and after homotopy also two different connecting orbits are obtained. The tangency curves of these two orbits are named \( G_+^{bc} \) and \( G_-^{bc} \) for distinction, where the superscript corresponds to the sign of \( \varepsilon \).

Both curves \( G_+^{bc} \) and \( G_-^{bc} \) intersect, as can be seen in Fig. 9(e) and in more detail in Fig. 9(f). Also indicated in this figure is how the chaotic attractor disappears at the global bifurcation. Reviewing Fig. 7(a)-(c), we see that the chaotic attractor at the left-hand side collides with the saddle limit cycle that is not connected to the chaotic attractor directly (although everything is indirectly coupled through the Shil’nikov unfolding). This event occurs at \( G_-^{bc} \) and is referred to as a boundary crisis (bc) [38,39]. At the right-hand side, the (same) saddle limit cycle collides with the chaotic attractor that is directly coupled with it through the cycle tangential bifurcation. This event occurs at \( G_+^{ic} \) and is an interior crisis (ic), because the basin of the chaotic attractor does not disappear, but suddenly changes shape [38,39]. After the intersection of the two global bifurcation curves they exchange their crisis type: the boundary crisis still occurs at a smaller value of \( a_1 \) than the interior crisis but is now coupled to \( G_-^{ic} \), and the interior crisis to \( G_+^{ic} \), or vice versa, but the boundary crisis always occurs at a smaller value of \( a_1 \) than the interior crises.

In Appendix B, we will analyse the bifurcation structure of a one-dimensional cubic map that is an extension of the classical quadratic map, to show that global homoclinic bifurcations are associated with boundary and interior crises.

3.3. Comparison of RM and LA models

We compare the two three-dimensional food chain models of similar structure, the 3D RM model and the LA model, that differ in the growth term of the top predator.

In both models the Shil’nikov homoclinic point-to-point connection is the organizing centre of chaos in the system. Around
the Shil'nik'ov there is an unfolding of tangent and flip bifurcations, that generates chaotic behaviour in these models. The Shil'nik'ov bifurcation, although a global bifurcation, is however, not the origin for the cycle-to-cycle connections in these models. It is likely that the Shil'nik'ov bifurcation is a general property of these type of food chain models.

In the 3D RM model there exists one chaotic attractor in a region of parameter space. Depending on the initial condition the system evolves to this positive attractor or to a planar limit cycle, where the top predator is extinct. The chaotic attractor disappears through the tangency of a homoclinic cycle-to-cycle connection. This tangency is coupled to the existence of a saddle limit cycle, born at a subcritical Hopf bifurcation. After this boundary crisis there remains only the saddle limit cycle and no coexistence of the three species is possible [17]. The boundary crisis occurs at the tangency of the cycle-to-cycle connection, and the continuation curve of the tangency forms an 'eye' in two-parameter space.

The model by Letellier and Aziz-Alaoui [30] shows bistability for a significant parameter range, in which it depends on the initial condition in what attractor the system settles. Depending on the exact parameter value there can be two chaotic attractors, of which the basins of attraction are separated by the stable manifold of a saddle limit cycle. Also there is not one but there are two homoclinic cycle-to-cycle connections, that both connect to the same saddle limit cycle but start on different sides of the unstable manifold. The ‘first’ chaotic attractor disappears through either the tangency of a limit cycle or a boundary crisis, leaving the other positive attractor as the sole attractor of the system. The disappearance of bistability in the system in a boundary crisis can thus be coupled to a global bifurcation. In this way the global bifurcation fulfills a similar role as the tangent bifurcation in a ‘catastrophic shift’ [10]. Biologically a small increase in a parameter value can result in a sudden drop in average biomass densities. However, as is typical for hysteresis, a small decrease in the parameter value thereafter does not restore the old biomass densities, but instead the system settles in a cycle of low frequency and smaller amplitude.

After a boundary crisis, under further parameter increase the ‘second’ chaotic attractor can expand its basin of attraction in an interior crisis, that is coupled to the tangency of the second homoclinic cycle-to-cycle connection. In this latter event the sole chaotic attractor of the system connects with the separatrix and merges with the ‘ghost’ of the basin of attraction of the other chaotic attractor that was destroyed in the boundary crisis. This second global bifurcation does not restore the bistability in the system, but the biological implication of this event is that under a small parameter increase the biomasses start to fluctuate with much larger amplitude.

Depending on the parameter value of the system the boundary crisis is coupled to $G_1$ and the interior crisis to $G_2$, or vice versa. That is, the boundary crisis always occurs at a smaller value of $\alpha_1$ than the internal crises [40]. Because there are two global bifurcation events under increase of one parameter that are not connected, there is no ‘eye’ as in the three-dimensional RM model.

4. General discussion

Four food chain models have been analysed in this paper with a specific focus on global bifurcations. Although it is not certain that we have detected or identified all existing global bifurcations in these models, we can put the findings in a broader context when comparing them to the previous analyses of other models. In this discussion, we view the findings in two ways. In the first part, the more mathematical view, we list which types of global bifurcations have been encountered so far in ecological food chain models, and review some technical aspects. In the second part, a more ecological view is adopted, and we list the global bifurcations by effect. Conclusions can be drawn from comparing both lists, such as which global bifurcation type has which kind of ecological consequence.

4.1. Mathematical aspects

From what we have encountered we can give the following list of connections in food chain models:

- Homoclinic point-to-point, for example in stoichiometric models by Loladze et al. [27] and Koopman et al. [43], in a chemostat model with added sub-lethal toxicants [15], and the Shil'nikov bifurcation in the three-dimensional food chain models [30].
- Heteroclinic point-to-point, for example in two-dimensional food chain models with Allee-effect [14], and in three-dimensional models with forest–pest interactions [42].
- Heteroclinic point-to-cycle, for example in the three-dimensional Rosenzweig–MacArthur food chain model [25].
- Homoclinic cycle-to-cycle, for example in the same RM model [18] and the model by Letellier and Aziz-Alaoui [30].

To our knowledge, heteroclinic cycle-to-cycle connections have not yet been found in theoretical ecological models thus far (for an example outside biology see [23]).

Almost all of these connections have been obtained or confirmed by using the homotopy techniques as discussed in [25,18]. This shows that solving boundary value problems implemented in AUTO is a powerful addition to the repertoire of bifurcation analysis techniques, and that the use of continuation software for model analysis is preferred over simulation techniques. A simulator is a useful tool to study transient dynamics and non-periodic limit sets. It is also useful to obtain initial guesses for equilibria and limit cycles, and connecting orbits, but a poor tool to obtain a good bifurcation diagram. Especially near the bifurcation points the integration time required to get an approximation of the stable asymptotic state increases, and detection of the exact bifurcation point is almost impossible. Furthermore, saddle points and saddle cycles cannot be found by doing simulations, since any orbit that approaches a saddle in the stable direction will be diverted again when nearing the saddle. Because saddles are the start and end points of global connections, knowledge of their location is of vital importance. A demonstrating example of this point is the dynamics of the model by Letellier and Aziz-Alaoui [30], where it is crucial to know the location of the saddle cycle that is involved in both the boundary and interior crises. The use of continuation software like AUTO can result in the detection of the saddle cycle by continuing the stable limit cycle through a tangent bifurcation. The saddle cycle data can then be used in the application of the homotopy techniques to find global bifurcations as developed by Doedel et al. [25,18].

4.2. Ecological aspects

From the obtained results in this paper and in other papers, we observe that the occurrence of the same mathematical type of global bifurcation can have different ecological consequences in different models. The reverse also occurs, that the same type of ecological consequences occur through different mathematical types of global bifurcations. We therefore summarize below the ecological events that have been found to occur because of global bifurcations:
• Attractor replacement [27] (Fig. 1(a)).
• Loss of bistability because of loss of attractor, possibly followed by a simplification of dynamics and coupled to hysteresis [27,30] (Figs. 2(a) and 7(b)).
• Development of chaotic behaviour through a cascade of period doublings, close to a Shil’nikov bifurcation [29,30] (Fig. 6(b)).
• Single species extinction because of loss of attractor [17,41] (Fig. 4(b)).
• Multispecies extinction, often because of loss of bistability [42,43,14,15].

We discuss these events in more detail below.

4.2.1. Attractor replacement

Although abrupt, the attractor replacement is the least ‘dramatic’ of the ecological events occurring because of a global bifurcation. In stoichiometric models under certain conditions ($d = 0.25$) there is an ‘infinite period’ bifurcation, identified as a homoclinic saddle-node bifurcation, that destroys the limit cycle. However, the tangent bifurcation involved in the homoclinic bifurcation generates a new attractor, a stable steady state, under increasing carrying capacity ($K$). In [27] it was argued that this event solves the ‘paradox of enrichment’ [32,33]. The paradox describes that the limit cycle grows in amplitude under an increase of the enrichment parameter, until extinction because of demographic stochastic processes from an ecological point of view.

4.2.2. Loss of bistability and possible hysteresis

Many of the examples of global bifurcations in food chain models studied in this paper result in events that resemble the ‘catastrophic shift’ normally associated with a tangent bifurcation [10], where after a small parameter change there is a loss of bistability. This is automatically coupled to hysteresis, meaning that a larger decrease of the parameter is required to restore the system to its old state. Because the bistability region is re-entered after a small decrease, the system remains in the ‘new’ state that only disappears after the bistability is left again at the other side. This also results in a sudden change in average biomass. For example, in the stoichiometric model [27] after the occurrence of the saddle homoclinic connection the remaining stable equilibrium has a lower biomass than the minimum value of the stable limit cycle that has disappeared.

Another effect, next to loss of bistability and a sudden change in average biomass densities, is not found in a catastrophic shift caused by a tangent. That is that there is a ‘simplification’ of the dynamics. For example, in the stoichiometric models [27] after a saddle homoclinic bifurcation the dynamics simplify from periodic to steady state. In the LA model [30] the chaotic attractor disappears after a global bifurcation, leaving a limit cycle of low frequency as sole attractor. An interesting note here is that the simplification in combination with bistability can be perceived as ‘stabilising’. For example, in the stoichiometric model [27] after a saddle homoclinic bifurcation the steady state remains and only disappears after a significant decrease in the parameter $K$, where the system reverts to the periodic behaviour again. In a similar fashion, in the model by Letellier and Aziz-Alaoui [30] the chaotic behaviour is only restored after a significant decrease in $q_1$. As such, the system could become more stable after a ‘parameter-shift trick’, a small increase followed by a small decrease in the parameter.

4.2.3. Chaos close to Shil’nikov

The occurrence of chaotic behaviour in ecological models is also due to a global bifurcation, a homoclinic saddle point-to-point connection named Shil’nikov bifurcation. This bifurcation is the organizing centre for chaos in the three-dimensional models [29]. In the RM model there is one chaotic attractor born through a series of flip bifurcations that sprout from the Shil’nikov. In the LA model [30] there can be two chaotic attractors at the same parameter set, that seem to be unrelated: one chaotic attractor traces back to a stable equilibrium like in the RM model, and the other to a stable limit cycle born in a cycle tangent bifurcation. However, the tangent bifurcation again stems from the Shil’nikov, just like the flip bifurcations.

4.2.4. Single species extinction because of loss of attractor

It was already shown in [41] that in three-dimensional deterministic models the top predator can go extinct as the result of a boundary crisis [38,39]. In the three-dimensional RM model there is bistability in some regions of parameter space, where orbits can converge either to a chaotic attractor, or a planar attractor where the top predator goes extinct. The basins of attraction have a very complicated structure, and it is not obvious to which attractor an initial condition will converge. The tangency of the point-to-cycle connection is the boundary of the region in parameter space where these complicated basins of attraction exist, and after this global bifurcation has occurred the basin of attraction for the chaotic attractor is ‘closed’ and non-complicated [17]. Biologically these complicated basins of attraction could lead to very dramatic changes in biomass densities under stochastic fluctuations in species densities. The tangency of the homoclinic cycle-to-cycle connection in the RM model results in the destruction of the chaotic attractor. With the chaotic attractor gone, the planar attractor becomes the global attractor. The top predator goes extinct only after a transient that appears to be on the chaotic attractor [41].

4.2.5. Multiple species extinction

The most dramatic observed effect resulting from a global bifurcation is complete disappearance of the system after a parameter change, often after a loss of bistability. In predator–prey models with Allee-effect the bistability is lost after a global bifurcation that destroys the stable positive limit cycle, leaving only a stable zero-equilibrium. This event was named ‘overharvesting’ because it occurs under a decrease of the predator mortality parameter [14]. In [15] it was shown that chemostat models display bistability after the addition of sub-lethal toxicants. The system goes extinct after a global bifurcation that destroys a stable limit cycle. In three-dimensional models of forest–pest interactions, a global bifurcation result in disappearance of the limit cycle attractor. Thereafter, any small pest invasion leads to a pest outbreak, followed by extinction of both pest and trees [42]. A stochastic model of producers and consumers also displays full system extinction after a global bifurcation that destroys the limit cycle attractor [43]. The responsible global bifurcation in these cases is either a homoclinic point-to-point connection [43,15] or a heteroclinic point-to-point connection [42,14].

5. Conclusions

The results seen and discussed here suggest that global bifurcation analysis is vital for a good understanding of the dynamics of food chain models. Global bifurcations are catastrophic and always lead to the merging or disappearance of attractors. A list of global bifurcation types is compared to a list of ecological consequences of occurring global bifurcations. The comparison reveals that there seems to be no 1-on-1 relationship between global bifurcation type
and the ecological ramifications. Also, it remains to be seen what other possible global bifurcations there might exist, especially in food chain models of more than three variables, and what the ramifications of their occurrence are. The global bifurcations studied so far can have potentially significant effects that cannot be understood without knowledge of their occurrence. We argue that global bifurcation analysis will be an important tool in our understanding of complex ecosystems.

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Appendix A. Discontinuity curves

The set of boundary conditions used to calculate the discontinuity curve $A_r$ in Fig. 3, upper panel, is given by the equations

$$\begin{cases}
\phi(\zeta, x) = 0, \\
P - \partial X_2 - qK = 0,
\end{cases} \quad (11)$$

where $\phi(\zeta, x)$ is a vector, of which the elements are the right-hand side of Eq. (1), $x$ is the parameter set, and $\zeta$ is the equilibrium of Eq. (1). In a two-dimensional system, like the stoichiometric model, these are three equations with four free parameters. We select as parameters the two equilibrium values $\zeta = X_1; X_2$, and the two bifurcation parameters $K$ and $d$.

The second boundary condition is the minimum function for the producer species. For the discontinuity curve $A_p$ a similar set can be given

$$\begin{cases}
\phi(\zeta, x) = 0, \\
P - \partial X_2 + X_1 = 0,
\end{cases} \quad (12)$$

where the second condition is the minimum function for the grazer species.

Appendix B. Cubic map

Different types of crises are described by the study of the following one-dimensional system:

$$x_{n+1} = f_{a,b}(x_n),$$

$$f_{a,b}(x) = -2(\alpha + \beta)x^3 + \frac{3}{2}(\alpha + \beta)x + \frac{1}{2}(\beta - x), \quad (13)$$

where $f_{a,b} : \mathbb{R} \rightarrow \mathbb{R}$, $n \in \mathbb{N}$ and parameters $\alpha, \beta \in \mathbb{R}$. Moreover, two critical points $c_1 = -0.5$ and $c_2 = 0.5$ exist where the derivative is zero.

$$f_{a,b}'(c_1) = 0, \quad f_{a,b}'(c_2) = 0.$$  

The following features of the map can easily be derived:

$$f_{a,b}'(1) = -\alpha \quad \text{and} \quad f_{a,b}'(-1) = \beta.$$  

For $0 < \alpha < 1$ and $0 < \beta < 1$ system, Eq. (13) is invariant in the interval $[-\max(\alpha, \beta), \max(\alpha, \beta)]$. Degenerated homoclinic orbits are fixed by the requirement that the second iterate of the critical point lands at a fixed point $p$

$$f_{a,b}(p) = p. \quad f_{a,b}'(c_1) = p. \quad (14)$$

B.1. Bifurcation diagrams

Fig. 10 gives the two-parameter bifurcation diagram of the cubic map equation (13). In addition to the local tangent bifurcation $T$ there are two global homoclinic bifurcations for orbits of the critical points $c_1$ and $c_2$, denoted by $G_c^-$ and $G_c^+$, respectively. At $T$,
called a subduction, the non-chaotic attractor, which is a fixed point situated within the chaotic attractor, replaces the chaotic attractor. In codim-2 point $T G_c$, the tangent bifurcation curve $T$ and the homoclinic bifurcations curve $G_c^+$ intersect. Let $p$ denote a fixed point, then for the three variables $x$, $\beta$ and $p$ the two requirements Eq. (14) yield the two homoclinic bifurcation curves $G_c^+$ and $G_c^-$. The two-parameter bifurcation diagram (Fig. 10) for $i = 1$ and $i = 2$, respectively. Codim-2 point $G$ is the intersection of the two curves $G_c^+$ and $G_c^-$ with $x = \beta = \frac{1}{2} \sqrt{3} \approx 0.866$.

In Fig. 11 the one-parameter bifurcation diagrams are depicted for three values of the parameter $\beta$. In Fig. 11(a) where $\beta = 1$ a large period-one window is shown. At the tangent bifurcation $T$, the chaotic attractor is destroyed abruptly when the bifurcation parameter $x$ is varied. Furthermore, there is an interior crisis at $G_c$ where the chaotic band suddenly widens.

Two attractors coexist for lower values of $\beta$ in the region between the tangent bifurcation $T$ and the homoclinic bifurcations. In Fig. 11(b) where $\beta = 0.9$, the bifurcation point $G_c^+$ is the boundary crisis which originated in point $T G_c$. The other bifurcation point $G_c^-$ is a continuation of the point present with $\beta = 1.0$. This bifurcation marks an interior crisis. In Fig. 11(c) where $\beta = 0.85$ at the tangent bifurcation $T$ a stable and an unstable fixed point originate, however, for the two homoclinic orbits the sequence of events alters with respect to the system for $\beta = 0.9$.

In Fig. 12(a)–(f) for the points indicated in Fig. 10 the orbits of both critical points $c_1$ and $c_2$ are shown together with the graph of the map (13). Observe that $G_c^-$ is the degenerated homoclinic orbit that visits critical point $c_1$ and $G_c^+$ visits critical point $c_2$. The orbit for parameter $x$ and $\beta$ values belonging to the point 1 in Fig. 10, which is close to the tangent bifurcation, is drawn in Fig. 12(d). At point $T G_c$, the tangent bifurcation occurs simultaneously with a boundary crisis $G_c^-$ and the orbit of the critical point $c_2$ lands exactly on the non-hyperbolic fixed point at the tangent bifurcation.

In order to explain what happens in codim-2 point $G$ at the intersection of the two curves $G_c^+$ and $G_c^-$, which is called an attractor merging crisis, we consider the graph shown in Fig. 12(a). The origin $x = 0$ is an unstable fixed point $p = 0$. The orbits of both critical points $c_1$ and $c_2$ land at this fixed point after two iterates. Hence, these are degenerated orbits, homoclinic with respect to the unstable fixed point $p = 0$. This situation shows that for a region in the parameter space close to point $G$, the cubic map possesses two coexisting chaotic attractors, one for positive and one for negative $x$-values, which we call the top-branch and the bottom-branch attractors, respectively. The unstable fixed point $p$ in the origin separates the basins of attraction of the two attractors. Each branch of the graph is similar to the logistic map when the cubic map is restricted to positive and negative $x$-values. For parameter values $x = \beta = \frac{1}{2} \sqrt{3}$ there is with each branch a bifurcation of the homoclinic orbit similar to the logistic map. At this attractor merger crisis, the unstable fixed point collides with the chaotic attractor on the boundary of its basin. With the cubic map this occurs on the intersection point of both branches. The point $G$ is simultaneously a boundary and an interior crisis. In order to show this we make a tour around point $G$.

In point 2, the orbits of points $c_1$ and $c_2$ are shown in Fig. 12(b). This plot clarifies why there is one attractor as $\beta = 0.9$ and $x = 0.8$. The unstable fixed point $p$, now close to the origin $x = 0$, does not separate the basins of attraction of the two attractors. As a result, orbits starting at the top-branch eventually converge to the bottom-branch attractor, as indicated by the fact that the orbit of the critical point $c_2$ intersects the diagonal below the fixed point $p = 0$. The range of the attractor is shown as a thick line on the diagonal of the plot.

In point 3, see Fig. 12(c), orbits starting from both branches also visit the other branch. For, now the second iterate of point $c_1$ also intersects the diagonal on the other side of the fixed point $p$. This means that both attractors are merged. This happens when $x$ passes the homoclinic orbit $G_c^-$ in Fig. 11(b) which represents an interior crisis.

In point 4 where $x = 0.8$ the unstable fixed point $p$ is a separatrix and consequently the two chaotic attractors coexist (see Figs. 12(e) and 11(c)). For increasing $x$-values the unstable fixed point coincides with the bottom-branch chaotic attractor leading to a boundary crisis. The associated degenerated homoclinic orbit $G_c^-$ is now of critical point $c_1$ instead of $c_2$ with $\beta = 0.9$. Hence, with this degenerated homoclinic orbit $G_c^-$ a boundary crisis occurs while for $\beta = 0.9$ it was an interior crisis. For $\beta = 0.85$ and $x = 0.9$ (Fig. 12(f)) in point 5 only the top-branch attractor exists, since the fixed point $p$ is not a separatrix anymore. Increasing $x$ further the degenerated homoclinic orbit $G_c^-$ of the top-branch is passed where an interior crisis occurs and the chaotic attractor widens suddenly.

![Fig. 12. Cubic map equation (13). From top to bottom, left to right, (a) $x = \beta = \frac{1}{2} \sqrt{3} \approx 0.866$ at the intersection of $G_c^+$ and $G_c^-$ in Fig. 10(a)–(c); (b) $x = 0.40$ and $\beta = 0.90$ ($\ast_1$); (c) $x = 0.90$ and $\beta = 0.90$ ($\ast_2$); (d) $x = 0.90$ and $\beta = 0.90$ ($\ast_3$); (e) $x = 0.60$ and $\beta = 0.85$ ($\ast_4$); (f) $x = 0.9$ and $\beta = 0.85$ ($\ast_5$). Between the panels the bifurcations crossed in Fig. 10 are indicated.](image-url)
References


[22] E.J. Doedel, B. Oldeman, AUTO07P: Continuation and Bifurcation Software for Ordinary Differential Equations, Concordia University, Montreal, Canada, 2007.


