

Nilpotent Singularities and Chaos: Tritrophic Food Chains

Fátima Drubi^a, Santiago Ibáñez^{a,*}, Paweł Pilarczyk^b

^a*Department of Mathematics, University of Oviedo, c/ Federico García Lorca 18, 33007 Oviedo, Spain*

^b*Faculty of Applied Physics and Mathematics, Gdańsk University of Technology, ul. Gabriela Narutowicza 11/12, 80-233 Gdańsk, Poland*

Abstract

Local bifurcation theory is used to prove the existence of chaotic dynamics in two well-known models of tritrophic food chains. To the best of our knowledge, the simplest technique to guarantee the emergence of strange attractors in a given family of vector fields consists of finding a 3-dimensional nilpotent singularity of codimension 3 and verifying some generic algebraic conditions. We provide the essential background regarding this method and describe the main steps to illustrate numerically the chaotic dynamics emerging near these nilpotent singularities. This is a general-purpose method and we hope it can be applied to a huge range of models.

Keywords: nilpotent singularities, trophic models, strange attractors.

2010 MSC: 58K45, 37D45, 37N25

1. Introduction

Mechanisms underlying the genesis of oscillations in predator-prey populations were successfully explained in the celebrated papers [1] and [2]. Since then, the study of ditrophic food chains became one of the major topics in Theoretical Ecology. Working with tritrophic food chains, Hastings and Powel [3] showed that they could exhibit chaotic behavior (see also the earlier reference [4]).

*Corresponding author
Email address: mesa@uniovi.es (Santiago Ibáñez)

7 Subsequent studies [5, 6, 7, 8, 9, 10, 11] or, more recently, [12, 13, 14, 15]), were
8 devoted to describe the dynamics of these models, particularly the mechanisms
9 that lead to the emergence of chaos.

10 In this paper we use a tool, already introduced in [16, 17, 18] and based
11 on local bifurcation theory, to prove the existence of chaotic behavior. Namely,
12 we will explain how some singularities can play a role of organizing centers for
13 chaotic dynamics. The method is applied to two very well-known models of the
14 tritrophic food chain and illustrated with numerical explorations. The steps to
15 apply this technique to other models are also described.

A general tritrophic food chain system is defined by

$$\begin{cases} x' = f_1(x) - g_1(x)y, \\ y' = f_2(y) + g_1(x)y - g_2(y)z, \\ z' = f_3(z) + g_2(y)z. \end{cases} \quad (1)$$

16 This system models the interaction between three different species, namely veg-
17 etation (x), herbivores (y) and predators (z). The functions f_i , with $i = 1, 2, 3$,
18 represent the growth rates of vegetation, herbivores and predators, respectively,
19 when the other species are absent. The interaction between different species is
20 also modeled in the system by means of those terms that depend on the functions
21 g_i with $i = 1, 2$. As mentioned in the ecological literature, the most common
22 interactions between consumers and resources are the functional responses of
23 Lotka-Volterra and Holling type II. Both types of consumer-resource interac-
24 tions can be modelled in a single system of differential equations by defining the
25 functions $g_i(u) = \alpha_i u / (1 + k_i u)$, with $\alpha_i > 0$ and $k_i \geq 0$, for $i = 1, 2$. Namely,
26 conditions $k_i = 0$ and $k_i > 0$ correspond to Lotka-Volterra and Holling type II
27 interactions, respectively.

28 We consider here two particular cases for the system in (1):

$$\text{Model A} \quad \begin{cases} x' = a(x - x_0) - \alpha_1 xy, \\ y' = -by + \alpha_1 xy - \alpha_2 yz, \\ z' = -c(z - z_0) + \alpha_2 yz, \end{cases} \quad (2)$$



29 where a, b, c, x_0 and z_0 are positive parameters, and

$$\text{Model B} \quad \begin{cases} x' = rx(1 - px) - \frac{\alpha_1 x}{1+k_1 y}y, \\ y' = -by + \frac{\alpha_1 x}{1+k_1 y}y - \alpha_2 yz, \\ z' = -c(z - z_0) + \alpha_2 yz, \end{cases} \quad (3)$$

30 where r, p, b, c, x_0 and z_0 are positive parameters.

In Model A, it is assumed the possible existence of other consumers affecting the growth of vegetation through the term x_0 and also the existence of alternative sources of food available for predators through the term z_0 . In this case, Lotka-Volterra conditions are considered for all interactions. This model was studied and discussed in [19], providing numerical evidences of chaotic dynamics when

$$a = 1, b = 1, c = 10, \alpha_1 = 0.1, \alpha_2 = 0.6, x_0 = 1.5, z_0 = 0.01.$$

Regarding the intra-specific dynamics, a natural assumption is to consider a logistic law to model the growth of herbivores. This is the case in Model B. In particular, when $p = 0$, Model B corresponds to the case studied in [20], where authors provided numerical evidences of chaotic behavior when

$$r = 1, p = 0, b = 1, c = 10, \alpha_1 = 0.2, \alpha_2 = 1, k_1 = 0.05, z_0 = 0.006.$$

31 According to [20, 19], systems (2) and (3) with $p = 0$ model, for example, a
32 classical food web of lynx, hare and vegetation. It should be noted that when
33 $z_0 = 0$ and the Lotka-Volterra interaction between predators and herbivores is
34 replaced by a Holling type II interaction, equations in (3) correspond to the
35 Hastings-Powell model (see [3]).

36 Our main aim in this paper is to show the existence of chaotic dynamics in
37 models A and B by proving that the appropriate singularities are unfolded. In-
38 deed, we demonstrate that both models unfold generically 3-dimensional nilpo-
39 tent singularities. On the other hand, literature provides results establishing
40 that close to these singularities there exist strange attractors (see [16] and also
41 [17, 18]).

42 Singular perturbation theory has also been successfully applied to explain
43 the emergence of chaotic behavior in tritrophic food chains. For instance, in [9]
44 and [6], it is used to study the existence of chaos in the Rosenzweig–MacArthur
45 (see also [21, 22, 23]). Singular perturbation analysis is also applied to a food
46 chain with four species in [24, 25, 26].

47 There are numerous models in the literature in which the arguments for the
48 existence of chaotic behavior rest on numerical evidence. However, analytical
49 proofs are considerably less common. To understand the relationship between
50 singularities and homoclinic orbits, as well as their role in the context of Chaos
51 Theory, we must go back to the first demonstrations of the existence of chaotic
52 behavior.

53 Poincaré [27] was the first to notice the dynamical complexity implied by
54 the existence of a homoclinic orbit associated with a saddle type hyperbolic
55 fixed point of a diffeomorphism. By a *homoclinic orbit* we mean the orbit of a
56 homoclinic point, that is, an intersection point between the invariant manifolds
57 of the saddle. Poincaré understood that, if such intersection is transverse, any
58 neighborhood of the primary homoclinic orbit contains an infinite number of
59 secondary ones. Later, Birkhoff [28] proved that in that situation, there also
60 exists an intricate set of periodic orbits with a wide variety of periods. This
61 complicated scenario cried out for a geometric structure that would explain the
62 dynamics as a whole. It was in 1965 that Smale [29] devised his famous horseshoe
63 and placed it in a neighborhood of a transverse homoclinic point. The Lorenz
64 attractor [30] was already known at that time and the notion of chaos was
65 being introduced in the field of dynamical systems. Later, the numerical results
66 of Hénon [31] would come as an example of what was called a strange attractor.

67 Without going into details, an attractor is called *strange* if it contains a dense
68 orbit with a positive Lyapunov exponent. This last condition is the hallmark
69 of a chaotic system and explains the divergence of orbits within the attractor
70 or, in other words, the high sensitivity of the system to initial conditions, which
71 makes it unpredictable. Despite the impressive numerical examples of Lorenz
72 and Hénon, it still took several years for the first analytical proof of the existence



73 of strange attractors to appear.

In 1991, another celebrated article [32] was published, a mathematical masterpiece in which Benedicks and Carleson managed to demonstrate the existence of strange attractors in the Hénon family

$$\begin{pmatrix} x \\ y \end{pmatrix} \rightarrow \begin{pmatrix} 1 - ax^2 + y \\ bx \end{pmatrix}, \quad (4)$$

74 where $a, b \in \mathbb{R}$. They considered (4) as a perturbation of a quadratic map
75 regarding b as a small parameter. The existence of strange attractors holds for a
76 positive measure set of parameter values. At the same time, using the techniques
77 introduced in [32], Mora and Viana [33] proved that in any generic 1-parameter
78 unfolding of a homoclinic tangency for a 2-dimensional diffeomorphism, there
79 exists a positive measure set of parameters for which the diffeomorphism ex-
80 hibits (Hénon-like) strange attractors. Once again, the starting point was to
81 understand these families as unfoldings of a 1-dimensional quadratic map. The
82 results in [33] are essential in our discussion (see also [34]).

83 The next step was to place homoclinic tangency bifurcations for 2-dimensional
84 diffeomorphisms in the context of families of 3-dimensional vector fields. Given
85 a 3-dimensional vector field with a saddle type hyperbolic equilibrium point p ,
86 any orbit γ with limit p when $t \rightarrow \pm\infty$ is said *homoclinic*. We say that the
87 homoclinic orbit is of *Shilnikov type* if p is a saddle-focus with eigenvalues λ
88 and $-\rho \pm \omega i$ satisfying $0 < \rho < \lambda$. The dynamics in a neighborhood of these
89 homoclinic orbits was first studied by Shilnikov [35]. He proved the existence
90 of infinitely many periodic orbits of saddle type in each neighborhood of the
91 homoclinic orbit. This property should remind us Birkhoff's result for trans-
92 verse homoclinic points in 2-dimensional diffeomorphisms. In fact, it can be
93 proved (see [36, 37]) that the first return map around the homoclinic orbit ex-
94 hibits an infinity of Smale horseshoes. Extended by the flow of the vector field,
95 these horseshoes generate invariant 3-dimensional sets (suspended horseshoes)
96 that accumulate in the homoclinic orbit. Each horseshoe contains an infinite
97 number of transverse homoclinic orbits, where Poincaré's intuition works again.



98 When the vector field is unfolded to produce a homoclinic bifurcation, these
99 horseshoes are destroyed. The process of creating and destroying horseshoes
100 is accompanied by unfoldings of homoclinic tangencies to hyperbolic periodic
101 points [38, 39] and, therefore, the existence of strange attractors follows from
102 [33] (see also [40, 41, 42]) .

103 Consequently, there are global configurations, the Shilnikov-type homoclinic
104 orbits, which unfold strange attractors. Since the theory predicts their existence
105 for a positive measure set of parameter values, these strange attractors are
106 observable. Unfortunately, for a given family, Shilnikov homoclinic orbits are not
107 easy to detect, even though there are several results in the literature regarding
108 the emergence of chaos that are based on the numerical location of Shilnikov
109 homoclinic orbits.

110 Fortunately, it has been proved in [16] that Shilnikov homoclinic orbits,
111 and hence Hénon-like strange attractors, arise in any generic unfolding of a 3-
112 dimensional nilpotent singularity of codimension 3 (see also [17, 43], and [18] for
113 additional technical details). The key argument is the fact that, rescaling vari-
114 ables and parameters, any of such unfoldings can be written as a perturbation
115 of a vector field that exhibits a heteroclinic cycle formed by two saddle-focus
116 equilibria with different stability indexes. Two branches of the 1-dimensional
117 invariant manifolds are coincident and the two-dimensional invariant manifolds
118 intersect transversely. This cycle is a codimension two configuration whose un-
119 folding shows, generically, Shilnikov-type homoclinic bifurcation curves. There-
120 fore, under generic assumptions to be set in Section 2, the existence of nilpotent
121 singularities implies the emergence of chaotic behavior in a given family. In this
122 paper, we show that this method (not related to singular perturbations) can be
123 applied to detect chaos in tritrophic food chains.

124 Singularities are much more manageable objects than Shilnikov homoclinic
125 orbits. It is a remarkable fact that the steps involved in finding a given sin-
126 gularity and verifying a few generic algebraic conditions become the simplest
127 technique for proving the existence of chaotic dynamics. Applications can be
128 found, for example, in [44, 45, 46, 47, 48, 49].

129 It must be mentioned, however, that the method, although results in proving
130 the existence of Shilnikov homoclinic orbits and thus strange attractors, does not
131 provide us with the (precise) location of neither the strange attractors nor the
132 Shilnikov homoclinic bifurcations in the parameter space. In order to illustrate
133 the chaotic behavior numerically, an alternative method must be used. One
134 possibility is to search for homoclinic bifurcation points by continuation of the
135 periodic orbit emerging from a Hopf bifurcation point. If the periodic orbit
136 disappears in a homoclinic bifurcation, we will see that the period of the orbit
137 tends to infinity. If the homoclinic orbit is of Shilnikov type, we will also see
138 period doubling cascades that precede the formation of the horseshoes, as argued
139 in [39, 50]. As we have already explained, the process of creating or destroying
140 horseshoes is accompanied by the appearance of strange attractors. Ultimately,
141 tracking the attracting periodic orbit in the doubling cascade allows for strange
142 attractors to be located.

143 **Remark 1.1.** *It must be remarked that three is not the lowest codimension*
144 *from which it is possible to unfold chaotic behaviors. It is known that there exist*
145 *Hopf-Zero singularities of codimension two which generically unfold Shilnikov*
146 *homoclinic orbits. However, part of the genericity conditions depend on the full*
147 *jet of the singularity and numerical techniques are required for their computa-*
148 *tion. See [51, 52] and references therein.*

149 In Section 2, we provide the essential technical background regarding 3-
150 dimensional nilpotent singularities and the generic conditions which are required
151 to guarantee the emergence of strange attractors. Existence and genericity of
152 3-dimensional nilpotent singularities in models A and B is discussed in Section
153 3. Moreover, numerical illustrations of dynamics close to nilpotent singularities
154 are given in Section 4. Finally, we discuss in Section 5 the potential applications
155 of our tool, based on local bifurcation theory, to prove the existence of chaotic
156 dynamics.



157 **2. Nilpotent singularities**

Let X be a C^∞ vector field in \mathbb{R}^3 with $X(0) = 0$ and $DX(0)$ linearly conjugated to

$$N = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}. \quad (5)$$

In appropriate C^∞ coordinates (see [53]), the equations of X can be written as

$$\begin{cases} x'_1 = x_2, \\ x'_2 = x_3, \\ x'_3 = f(x_1, x_2, x_3), \end{cases} \quad (6)$$

with $f(x_1, x_2, x_3) = O(\|(x_1, x_2, x_3)\|^2)$. It is said that X has a *nilpotent singularity of codimension 3* at 0 if the generic condition

$$d_{11} = \frac{\partial^2 f}{\partial x_1^2}(0) \neq 0 \quad (7)$$

158 is fulfilled.

159 According to [53], we can state the result below:

Lemma 2.1. *Let X_λ be a C^∞ family of 3-dimensional vector fields with $\lambda = (\lambda_1, \lambda_2, \lambda_3) \in \mathbb{R}^3$ such that X_0 has a nilpotent singularity of codimension 3 at 0. Under generic assumptions about the derivatives of the family with respect to parameters, and also after changing to new suitable coordinates \bar{x} and parameters $\bar{\lambda}$, the family X_λ can be written as*

$$\begin{cases} \bar{x}'_1 = \bar{x}_2, \\ \bar{x}'_2 = \bar{x}_3, \\ \bar{x}'_3 = \bar{\lambda}_1 + \bar{\lambda}_2 \bar{x}_2 + \bar{\lambda}_3 \bar{x}_3 + \bar{x}_1^2 + h(\bar{x}, \bar{\lambda}), \end{cases} \quad (8)$$

160 with $\bar{x} = (\bar{x}_1, \bar{x}_2, \bar{x}_3) \in \mathbb{R}^3$, $\bar{\lambda} = (\bar{\lambda}_1, \bar{\lambda}_2, \bar{\lambda}_3) \in \mathbb{R}^3$, $h(\bar{x}, \bar{\lambda}) = O(\|(\bar{x}, \bar{\lambda})\|^2)$ and
161 $h(\bar{x}, \bar{\lambda}) = O(\|(\bar{x}_2, \bar{x}_3)\|)$.

Genericity in Lemma 2.1 includes the condition in (7), regarding the singularity itself, and a transversality condition involving derivatives of the family

with respect to parameters. To be precise, assuming that only the condition in (7) is fulfilled, it was proved (see details in [53] or [46]) that, using appropriate C^∞ coordinates, the family X_λ can be written as

$$\begin{cases} \bar{x}'_1 = \bar{x}_2, \\ \bar{x}'_2 = \bar{x}_3, \\ \bar{x}'_3 = m_1(\lambda) + m_2(\lambda)\bar{x}_2 + m_3(\lambda)\bar{x}_3 + \bar{x}_1^2 + g(\bar{x}, \lambda), \end{cases} \quad (9)$$

with $g(\bar{x}, \lambda) = O(\|\bar{x}, \lambda\|^2)$ and $g(\bar{x}, \lambda) = O(\|\bar{x}_2, \bar{x}_3\|)$. The unfolding in (9) is said to be generic if $m(\lambda) = (m_1(\lambda), m_2(\lambda), m_3(\lambda))$ is a local diffeomorphism at the origin or, in other words, if the generic condition below

$$\Delta = \det(Dm(0)) \neq 0 \quad (10)$$

is satisfied. With this assumption we can introduce new parameters

$$(\bar{\lambda}_1, \bar{\lambda}_2, \bar{\lambda}_3) = (m_1(\lambda), m_2(\lambda), m_3(\lambda))$$

162 to obtain (8).

163 For the sake of completeness, we provide simple formulas to check the generic
164 assumptions. Let us write $X_\lambda(x) = (X^{(1)}(x, \lambda), X^{(2)}(x, \lambda), X^{(3)}(x, \lambda))$ and as-
165 sume that $DX_0(0) = N$. We consider the notation

$$\begin{aligned} \gamma_i^{(k)} &= \frac{\partial X^{(k)}}{\partial \lambda_i}(0, 0), & \Lambda_{ij}^{(k)} &= \frac{\partial^2 X^{(k)}}{\partial \lambda_i \partial x_j}(0, 0), \\ A_{ii}^{(k)} &= \frac{1}{2} \frac{\partial^2 X^{(k)}}{\partial x_i^2}(0, 0), & A_{ij}^{(k)} &= \frac{\partial^2 X^{(k)}}{\partial x_i \partial x_j}(0, 0) \quad (\text{when } i \neq j), \end{aligned}$$

for $i, j, k = 1, 2, 3$. It follows from [53] that

$$d_{11} = 2A_{11}^{(3)}. \quad (11)$$

The coefficient $A_{11}^{(3)}$ remains unchanged after reducing the system to the normal form. Therefore, we assume that, up to a change of coordinates, $A_{11}^{(3)} = 1$. Using the formulas provided in [46], we easily obtain

$$\Delta = \begin{vmatrix} \gamma_1^{(3)} & \gamma_2^{(3)} & \gamma_3^{(3)} \\ P_1^* + \sum_{k=1}^2 P_k \gamma_1^{(k)} & P_2^* + \sum_{k=1}^2 P_k \gamma_2^{(k)} & P_3^* + \sum_{k=1}^2 P_k \gamma_3^{(k)} \\ Q_1^* + \sum_{k=1}^2 Q_k \gamma_1^{(k)} & Q_2^* + \sum_{k=1}^2 Q_k \gamma_2^{(k)} & Q_3^* + \sum_{k=1}^2 Q_k \gamma_3^{(k)} \end{vmatrix} \quad (12)$$

166 for all $i = 1, 2, 3$, with

$$\begin{aligned}
P_i^* &= \Lambda_{i2}^{(3)} + \Lambda_{i1}^{(2)} - \frac{1}{2} \left(A_{12}^{(3)} + 2A_{11}^{(2)} \right) \Lambda_{i1}^{(3)}, \\
P_1 &= - \left(2A_{22}^{(3)} + A_{12}^{(2)} - \frac{1}{2} A_{12}^{(3)} \left(A_{12}^{(3)} + 2A_{11}^{(2)} \right) \right), \\
P_2 &= - \left(A_{23}^{(3)} + A_{13}^{(2)} - \frac{1}{2} A_{13}^{(3)} \left(A_{12}^{(3)} + 2A_{11}^{(2)} \right) \right), \\
Q_i^* &= \Lambda_{i3}^{(3)} + \Lambda_{i2}^{(2)} + \Lambda_{i1}^{(1)} - \frac{1}{2} \left(A_{13}^{(3)} + A_{12}^{(2)} + 2A_{11}^{(1)} \right) \Lambda_{i1}^{(3)}, \\
Q_1 &= - \left(A_{23}^{(3)} + 2A_{22}^{(2)} + A_{12}^{(1)} - \frac{1}{2} A_{12}^{(3)} \left(A_{13}^{(3)} + A_{12}^{(2)} + 2A_{11}^{(1)} \right) \right), \\
Q_2 &= - \left(2A_{33}^{(3)} + A_{23}^{(2)} + A_{13}^{(1)} - \frac{1}{2} A_{13}^{(3)} \left(A_{13}^{(3)} + A_{12}^{(2)} + 2A_{11}^{(1)} \right) \right).
\end{aligned}$$

Remark 2.2. *The additional condition*

$$d_{12} = \frac{\partial^2 g}{\partial x_1 \partial x_2}(0) \neq 0 \quad (13)$$

is also required to prove the existence of strange attractors (see [18]). It follows from [46] that

$$d_{12} = A_{12}^{(3)} + 2A_{11}^{(2)}. \quad (14)$$

167 Several aspects of the dynamics arising in unfoldings of the 3-dimensional
168 nilpotent singularity of codimension 3 has been studied in ([53, 17, 43, 16, 18]).
169 In [16, 18], it was proved that any unfolding satisfying the generic conditions
170 (7), (10) and (13) displays Shilnikov homoclinic orbits and hence, as argued in
171 the introduction, strange attractors.

172 **Remark 2.3.** *As the simple formulas provided in (11), (12) and (14) are effort-*
173 *less computable, in this paper we describe an easy-to-check method to prove the*
174 *existence of chaotic behavior in a given model. This will become a very helpful*
175 *technique for further applications in the detection of chaos.*

176 3. Chaos in tritrophic food chain models

177 In this section we prove that models in (2) and (3) are indeed generic un-
178 foldings of 3-dimensional nilpotent singularities and, hence, they exhibit strange

179 attractors. Note that, in both cases, some coefficients can be normalized. There-
 180 fore, in what follows, we assume that $a = 1$ and $r = 1$ in (2) and (3), respectively.

181 3.1. Nilpotent singularities in Model A

182 The study of equilibria of model in (2) provides the below result regarding
 183 the existence of a nilpotent singularity.

Proposition 3.1. *Assume that $\alpha_2 \neq \alpha_1$, $\alpha_2 \neq \alpha_1 c$ and $c \neq 1$ in (2). When $(x_0, z_0, b) = (\hat{x}_0, \hat{z}_0, \hat{b})$ with*

$$\hat{x}_0 = \frac{(\alpha_2 - \alpha_1 c)^3}{2\alpha_1^2(\alpha_2 - \alpha_1)^2(c - 1)}, \quad \hat{z}_0 = \frac{(\alpha_2 - \alpha_1 c)^3}{2\alpha_2^2(\alpha_2 - \alpha_1)^2 c(c - 1)},$$

and

$$\hat{b} = \frac{(\alpha_2 - \alpha_1 c)^2}{2\alpha_1 \alpha_2 (c - 1)},$$

system (2) has an equilibrium point at $(\hat{x}, \hat{y}, \hat{z})$ with

$$\hat{x} = \frac{(\alpha_2 - \alpha_1 c)^2}{2\alpha_1^2(\alpha_2 - \alpha_1)(c - 1)}, \quad \hat{y} = \frac{c - 1}{\alpha_2 - \alpha_1}, \quad \hat{z} = \frac{(\alpha_2 - \alpha_1 c)^2}{2\alpha_2^2(\alpha_2 - \alpha_1)(c - 1)},$$

184 where the Jacobian matrix is linearly conjugated to N as given in (5).

Proof. From the first and third equation in (2) it follows that an equilibrium $(\hat{x}, \hat{y}, \hat{z})$ must satisfy that

$$\hat{x} = \frac{x_0}{1 - \alpha_1 \hat{y}} \quad \text{and} \quad \hat{z} = \frac{cz_0}{c - \alpha_2 \hat{y}}. \quad (15)$$

Replacing x and z by \hat{x} and \hat{z} , respectively, in the second equation of system (2), we obtain that either

$$b = \alpha_1 \hat{x} - \alpha_2 \hat{z} \quad (16)$$

185 or $y = 0$. It is here assumed that (16) is fulfilled because otherwise we obtain a
 186 singularity at $(x_0, 0, z_0)$ and it can be checked that is not nilpotent.

To characterize the nilpotent singularities we need to compute the linear part of (2) at $(\hat{x}, \hat{y}, \hat{z})$. The Jacobian matrix is given by

$$\begin{pmatrix} 1 - \alpha_1 \hat{y} & -\alpha_1 \hat{x} & 0 \\ \alpha_1 \hat{y} & 0 & -\alpha_2 \hat{y} \\ 0 & \alpha_2 \hat{z} & -c + \alpha_2 \hat{y} \end{pmatrix}$$

and the characteristic polynomial is

$$c_0 + c_1\lambda + c_2\lambda^2 - \lambda^3,$$

with

$$\begin{aligned} c_0 &= \hat{y}(\alpha_1^2(-c + \alpha_2\hat{y})\hat{x} + \alpha_2^2(1 - \alpha_1\hat{y})\hat{z}), \\ c_1 &= -((1 - \alpha_1\hat{y})(-c + \alpha_2\hat{y}) + \alpha_1^2\hat{x}\hat{y} + \alpha_2^2\hat{y}\hat{z}), \\ c_2 &= 1 - c + \hat{y}(\alpha_2 - \alpha_1). \end{aligned}$$

The equilibrium at $(\hat{x}, \hat{y}, \hat{z})$ is a nilpotent singularity if $c_0 = c_1 = c_2 = 0$.

Assuming that $c_2 = 0$, we easily obtain

$$\hat{y} = \frac{c - 1}{\alpha_2 - \alpha_1}.$$

Therefore, substituting \hat{y} in (15), we get

$$\hat{x} = \frac{x_0(\alpha_2 - \alpha_1)}{\alpha_2 - \alpha_1 c} \quad \hat{z} = \frac{cz_0(\alpha_2 - \alpha_1)}{\alpha_2 - \alpha_1 c}. \quad (17)$$

Substituting \hat{x} , \hat{y} y \hat{z} in the equations $c_0 = 0$ and $c_1 = 0$, and assuming that $c \neq 1$, we obtain the system below:

$$\begin{cases} \alpha_1^2 x_0 + \alpha_2^2 c z_0 &= \frac{(\alpha_2 - \alpha_1 c)^3}{(c-1)(\alpha_2 - \alpha_1)^2} \\ \alpha_1^2 x_0 - \alpha_2^2 c z_0 &= 0, \end{cases} \quad (18)$$

which is linear in the unknown parameters x_0 and z_0 . The solutions of this systems are

$$x_0 = \frac{(\alpha_2 - \alpha_1 c)^3}{2\alpha_1^2(\alpha_2 - \alpha_1)^2(c - 1)} \quad z_0 = \frac{(\alpha_2 - \alpha_1 c)^3}{2\alpha_2^2(\alpha_2 - \alpha_1)^2(c - 1)c}.$$

Hence, substituting x_0 and z_0 in (17)

$$\hat{x} = \frac{(\alpha_2 - \alpha_1 c)^2}{2\alpha_1^2(\alpha_2 - \alpha_1)(c - 1)} \quad \hat{z} = \frac{(\alpha_2 - \alpha_1 c)^2}{2\alpha_2^2(\alpha_2 - \alpha_1)(c - 1)}$$

and then substituting \hat{x} and \hat{z} in (16) we get

$$\hat{b} = \frac{(\alpha_2 - \alpha_1 c)^2}{2\alpha_1\alpha_2(c - 1)}.$$

187 It easily follows that the rank of the Jacobian matrix is equal to 2 and hence it
188 is linearly conjugated to N . □

189 To check all the generic conditions given in Section 2, we consider x_0, z_0 and
 190 b as bifurcation parameters and fix all the others at the values provided by a
 191 bifurcation point to a nilpotent singularity. After an appropriate C^∞ change of
 192 coordinates, the equations of Model A can be written with a canonical linear
 193 part as in system (2.1). Therefore, from formulas (11) and (14), it follows that

$$d_{11} = \frac{2\alpha_2(c\alpha_1 - \alpha_2)(c-1)}{\alpha_1 - \alpha_2} \quad (19)$$

and

$$d_{12} = \frac{\alpha_1(c-3) + \alpha_2(3c-1)}{(c\alpha_1 - \alpha_2)(c-1)}. \quad (20)$$

Moreover, using (12), we get

$$\Delta = \frac{c\alpha_1^2\alpha_2^2(c\alpha_1 - \alpha_2)(c-1)^3}{(\alpha_1 - \alpha_2)^3}. \quad (21)$$

It easily follows that the values \hat{x}_0, \hat{z}_0 and \hat{b} and also \hat{x}, \hat{y} and \hat{z} (as given in Proposition 3.1) are all positive if and only if $c > 1$ and $\alpha_2 > \alpha_1 c$. Such conditions also imply that $d_{11} \neq 0$ and $\Delta \neq 0$. Moreover, $d_{12} \neq 0$ under the additional condition

$$\alpha_1(c-3) + \alpha_2(3c-1) \neq 0. \quad (22)$$

194 Thus, as the conditions given in (7), (10) and (13) fulfill, Model A unfolds
 195 generically 3-dimensional nilpotent singularities and exhibits strange attractors.

196 **Remark 3.2.** *Formulas given in (19), (20) and (21) are not unique but depend*
 197 *on the C^∞ change of coordinates. Nevertheless, after any change of variables,*
 198 *it can be easily check that $d_{11} \neq 0$ and $\Delta \neq 0$ when $c > 1$ and $\alpha_2 > \alpha_1 c$, as well*
 199 *as $d_{12} \neq 0$ under the additional condition (22).*

200 3.2. Nilpotent singularities in Model B

201 The study of equilibria of model in (3) provides the below result regarding
 202 the existence of a nilpotent singularity.

203 **Proposition 3.3.** *Let*

$$\begin{aligned}\Phi_1 &= p + k_1(2ps - 1), \\ \Phi_2 &= 2(ps - 1)^2(1 + k_1s)^2\alpha_2 - s^2\Phi_1^3.\end{aligned}$$

204 *When $(z_0, b, c, \alpha_1) = (\hat{z}_0, \hat{b}, \hat{c}, \hat{\alpha}_1)$ with*

$$\begin{aligned}\hat{z}_0 &= \frac{-s^5\Phi_1^7}{4(1 + k_1s)^3(ps - 1)^2\alpha_2^2\Phi_2}, \\ \hat{b} &= \frac{-s^2\Phi_1^2(2(ps - 1)(1 + k_1s)^2\alpha_2 + s\Phi_1^2)}{4(1 + k_1s)^3(ps - 1)^2\alpha_2}, \\ \hat{c} &= \frac{\Phi_2}{s(1 + k_1s)\Phi_1^2}, \\ \hat{\alpha}_1 &= \frac{-s\Phi_1^2}{2(ps - 1)},\end{aligned}$$

205 *system (3) has an equilibrium point at $(\hat{x}, \hat{y}, \hat{z})$ with*

$$\hat{x} = s, \quad \hat{y} = \frac{2(1 + k_1s)(ps - 1)^2}{s(p + k_1(2ps - 1))^2}, \quad \hat{z} = \frac{s^3(p + k_1(2ps - 1))^4}{4(1 + k_1s)^3(ps - 1)^2\alpha_2^2}.$$

206 *Whenever $\hat{x}, \hat{y}, \hat{z} > 0$, the Jacobian matrix at the equilibrium point is conjugated*
207 *to N as given in (5).*

208 *Proof.* From the first and third equation in (3), it follows that an equilibrium
209 $(\hat{x}, \hat{y}, \hat{z})$ satisfies that

$$\hat{y} = -\frac{(1 + k_1\hat{x})(p\hat{x} - 1)}{\alpha_1} \quad \text{and} \quad \hat{z} = \frac{cz_0}{c - \alpha_2\hat{y}}.$$

Replacing z by \hat{z} in the second equation of system (3), we also obtain that
either

$$\hat{y} = \frac{c((b + z_0\alpha_2)(1 + k_1\hat{x}) - \alpha_1\hat{x})}{(b(1 + k_1\hat{x}) - \alpha_1\hat{x})\alpha_2} \quad (23)$$

210 or $\hat{y} = 0$. It is here assumed that (23) is fulfilled because it can be checked that
211 otherwise the singularities are not nilpotent. Therefore, it is also assumed that
212 $\hat{x} \neq \frac{1}{k_1}$ and $\hat{x} \neq \frac{1}{p}$.

Hence, we get that

$$-\frac{(1 + k_1\hat{x})(p\hat{x} - 1)}{\alpha_1} = \frac{c((b + z_0\alpha_2)(1 + k_1\hat{x}) - \alpha_1\hat{x})}{(b(1 + k_1\hat{x}) - \alpha_1\hat{x})\alpha_2}.$$

213 Solving the above equation to find c , we obtain

$$\hat{c} \equiv \hat{c}(\hat{x}, p, k_1, \alpha_1, \alpha_2, z_0) = -\frac{(1 + k_1 \hat{x})(p \hat{x} - 1)(b(1 + k_1 \hat{x}) - \alpha_1 \hat{x})\alpha_2}{\alpha_1((b + z_0 \alpha_2)(1 + k_1 \hat{x}) - \alpha_1 \hat{x})}.$$

The characteristic polynomial of the Jacobian matrix at $(\hat{x}, \hat{y}, \hat{z})$ is

$$c_0 + c_1 \lambda + c_2 \lambda^2 - \lambda^3,$$

214 where c_0 , c_1 and c_2 are functions of $(\hat{x}, p, b, z_0, \alpha_1, \alpha_2, k_1)$.

The equilibrium at $(\hat{x}, \hat{y}, \hat{z})$ is a nilpotent singularity if $c_0 = c_1 = c_2 = 0$. Assuming that $c_2 = 0$, we easily obtain $\hat{b} \equiv \hat{b}(\hat{x}, p, k_1, \alpha_1, \alpha_2, z_0)$. Substituting b by \hat{b} in $c_0 = 0$, we obtain

$$\hat{z}_0 \equiv \hat{z}_0(\hat{x}, p, k_1, \alpha_1, \alpha_2) = \frac{\alpha_1^3 \hat{x}^2 (p + k_1(-1 + 2p\hat{x}))}{\alpha_2^2 (1 + k_1 \hat{x})^3 g(\hat{x}, p, k_1, \alpha_1, \alpha_2)}.$$

with $g(\hat{x}, p, k_1, \alpha_1, \alpha_2) = k_1^2 \hat{x}^2 (p \hat{x} - 1) \alpha_2 + p \hat{x} (\alpha_1 + \alpha_2) - \alpha_2 + k_1 \hat{x} [(2p \hat{x} - 1) \alpha_1 + 2(p \hat{x} - 1) \alpha_2]$. Substituting b by \hat{b} and z_0 by \hat{z}_0 in $c_1 = 0$, we get

$$\hat{\alpha}_1 \equiv \hat{\alpha}_1(\hat{x}, p, k_1) = \frac{-\hat{x}(p + k_1(2p\hat{x} - 1))^2}{2(p\hat{x} - 1)}.$$

215 Substituting α_1 by $\hat{\alpha}_1$ in \hat{z}_0 , the formula of \hat{z}_0 can be written as a function
216 of $(\hat{x}, p, k_1, \alpha_2)$. Similarly, substituting α_1 by $\hat{\alpha}_1$ and z_0 by \hat{z}_0 in \hat{b} , we obtain a
217 formula for \hat{b} that depends only on $(\hat{x}, p, k_1, \alpha_2)$. In addition, we can also write
218 \hat{c} as a function of $(\hat{x}, p, k_1, \alpha_2)$. Finally, we replace \hat{x} by an extra parameter s
219 to get all the formulas provided in the statement.

220 It easily follows that, when $\hat{x}, \hat{y}, \hat{z} > 0$, the rank of the Jacobian matrix is
221 equal to 2 and hence it is linearly conjugated to N . \square

222 To prove that Model B is a generic unfolding of the 3-dimensional nilpo-
223 tent singularity characterized in Proposition 3.3, the generic conditions given in
224 Section 2 have to be checked as well. In this case, we consider z_0 , b and c as
225 bifurcation parameters and fix the others at the values provided by a bifurca-
226 tion point to a nilpotent singularity. Therefore, from formulas (11) and (14), it
227 follows that

$$d_{11} = \frac{2\alpha_2(ps - 1)(k_1^3 s^2 \Psi_1 + k_1^2 s^2 \Psi_2 + 2k_1 s \Psi_3 - 2\alpha_2(ps - 1))}{(1 + k_1 s)^2 (p + k_1(2ps - 1))}, \quad (24)$$

$$d_{12} = \frac{2\alpha_2(\Psi_4 + p^2 \Psi_5 + k_1^2 s \Psi_6 + 2k_1 s \Psi_7)}{s(1 + k_1 s)(p + k_1(2ps - 1))^2 d_{11}}. \quad (25)$$

228 Using (12), it follows

$$\Delta = \frac{s \alpha_2^2 (ps - 1)^2 \Psi_8 (\Psi_9 + k_1^2 s^2 \Psi_{10} + k_1 s \Psi_{11})}{(1 + k_1 s)^3 (p + k_1 (2ps - 1))^2}. \quad (26)$$

229 In the above expressions,

$$\begin{aligned} \Psi_1 &= 1 - 5ps + 6p^2 s^2, \\ \Psi_2 &= 7p^2 s + 2\alpha_2 - p(3 + 2s\alpha_2), \\ \Psi_3 &= p^2 s + 2\alpha_2 - 2ps\alpha_2, \\ \Psi_4 &= p^3 s^2 + 2k_1^3 p s^3 (2ps - 1) - 6\alpha_2 + 12ps\alpha_2, \\ \Psi_5 &= s - 6s^2 \alpha_2, \\ \Psi_6 &= 1 - 6s\alpha_2 - 6p^2 s^2 (s\alpha_2 - 2) + ps(12s\alpha_2 - 7), \\ \Psi_7 &= p^3 s^2 - 6\alpha_2 + 3p^2 s(1 - 2s\alpha_2) + p(12s\alpha_2 - 1), \\ \Psi_8 &= -p + k_1 - 6psk_1 + 4p^2 s^2 k_1, \\ \Psi_9 &= p^3 s^2 + s^2 (2ps - 1)^3 k_1^3 - 2\alpha_2 + 4ps\alpha_2 - 2p^2 s^2 \alpha_2 \\ \Psi_{10} &= 12p^3 s^2 - 2\alpha_2 - 2p^2 s(6 + s\alpha_2) + p(3 + 4s\alpha_2), \\ \Psi_{11} &= 6p^3 s^2 - 4\alpha_2 + 8ps\alpha_2 - p^2 s(3 + 4s\alpha_2). \end{aligned}$$

230 In this case, it is not easy to state simple conditions to guarantee that (24), (25)
 231 and (26) do not vanish and also that coordinates and parameters are all of them
 232 positive at the bifurcation point. In the next section, we find positive parameter
 233 values s , p , α_2 and k_1 for which \hat{z}_0 , \hat{b} , \hat{c} and \hat{a}_1 and also \hat{x} , \hat{y} and \hat{z} (as given in
 234 Proposition 3.3) are all positive. Moreover, we check that generic conditions (7),
 235 (10) and (13) are fulfilled. Therefore, it follows that Model B unfolds generically
 236 3-dimensional nilpotent singularities and, hence, exhibits strange attractors.

237 **Remark 3.4.** *Computations are straightforward through formulas (11), (12)*
 238 *and (14). Nevertheless, most of them are lengthy and we have used the Symbolic*
 239 *Math Toolbox in Matlab[®] to carry out many of them.*

240 4. Numerical simulations

241 In this section, we study numerically the bifurcation diagram of both mod-
242 els A in (2) and B in (3). For the purpose of simulations, the equations are
243 solved numerically in Matlab[®], using the MatCont package [54] for numerical
244 bifurcation analysis. We also show the emergence of chaotic dynamics near the
245 nilpotent singularity generically unfolded in these models. In section 2, the
246 well-known techniques to ensure that a given family of differential equations
247 exhibits chaotic dynamics were reduced to a small number of algebraic calcu-
248 lations. Thus, the necessary conditions become easy to check for any family.
249 Nevertheless, although the theoretical results guarantee that generic unfoldings
250 of 3-dimensional nilpotent singularities include strange attractors, this technique
251 is not a tool in itself to find numerically strange attractors and extra work has
252 to be done to locate a region in the parameter space where chaotic behavior
253 emerges. As we believe that formulae in section 2 will be useful to study the
254 emergence of chaotic dynamics in many other models, we describe here the main
255 steps to show numerically the chaotic dynamics near the nilpotent singularity
256 in our models.

257 4.1. Model A

We work with parameters values close to those considered in [19] and, there-
fore, in what follows in this section we set

$$c = 3, \quad \alpha_1 = \frac{3}{25}, \quad \text{and} \quad \alpha_2 = \frac{4}{5}.$$

Using formulae provided in Proposition 3.1, we get

$$\hat{x}_0 = \frac{33275}{10404}, \quad \hat{z}_0 = \frac{1331}{55488}, \quad \hat{b} = \frac{121}{240},$$

and hence the equilibrium point is at

$$\hat{x} = \frac{3025}{612}, \quad \hat{y} = \frac{50}{17}, \quad \hat{z} = \frac{121}{1088}.$$

Substituting these parameter values in formulae (19), (20) and (21), we easily
obtain

$$d_{11} = \frac{176}{85}, \quad d_{12} = \frac{-80}{11}, \quad \text{and} \quad \Delta = \frac{38016}{122825}.$$



258 Therefore, Model A is a generic 3-parametric unfolding of a 3-dimensional
 259 nilpotent singularity. The parameters of the unfolding are x_0 , z_0 and b and a
 260 nilpotent singularity appears at $(\hat{x}, \hat{y}, \hat{z})$ when $x_0 = \hat{x}_0$, $z_0 = \hat{z}_0$ and $b = \hat{b}$.

To study the bifurcation diagram near the nilpotent singularity, we consider
 (μ_1, μ_2, μ_3) as new parameters and work with the family below

$$\begin{cases} x' = x - \hat{x}_0 - \mu_1 - \alpha_1 xy, \\ y' = -(\hat{b} + \mu_2)y + \alpha_1 xy - \alpha_2 yz, \\ z' = -c(z - \hat{z}_0 - \mu_3) + \alpha_2 yz. \end{cases} \quad (27)$$

261 The theoretical results in section 3 guarantee that family (27) includes
 262 strange attractors. To illustrate this result we set $\mu_3 = 0.01$ and study the
 263 bifurcation diagram of (27) in the (μ_1, μ_2) -parameter plane. A Hopf bifurcation
 264 curve and a saddle-node bifurcation curve are detected near the 3-dimensional
 265 nilpotent singularity (see Figure 1(a)). Moreover, by continuation in the param-
 266 eter μ_2 (see Figure 1(b)) of the periodic orbit emerging from the Hopf bifurcation
 267 detected when $\mu_1 = 0.6182493995438856$, a period doubling bifurcation is de-
 268 tected (see the blue curve in Figure 1(c)). An additional period doubling is
 269 shown in Figure 1(c). In Figure 1(d) we provide a bifurcation diagram of period
 270 doubling cascades.

271 The existence of period doubling cascades is itself an evidence of chaos,
 272 but because we have put the emphasis in the existence of Shilnikov homoclinic
 273 orbits, we show an example in Figure 2. We plot, as approximations of the
 274 homoclinic connection, the orbit which is computed at the end point of the
 275 numerical continuation of the 1-periodic orbit (see the blue curve in Figure
 276 1(c)). Note that there exists an infinite sequence of saddle-node bifurcations
 277 and the period of the orbit tends to infinity. As period increases, parameter μ_2
 278 tends to a certain limit which can be approached by the value of μ_2 at the end
 279 point of the continuation, namely, 0.0784693743654685.

280 It is known that, moving parameters to break the homoclinic orbit, one
 281 should be able to detect the existence of strange attractors. In this case, we
 282 perturb the vector field by changing slightly the value of the μ_2 (see Figure 3).

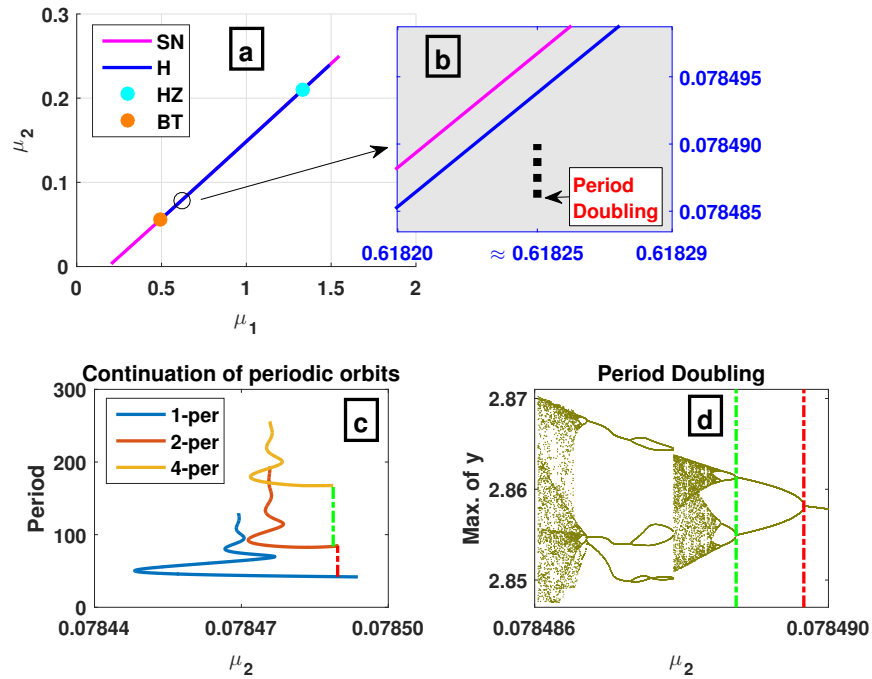


Figure 1: Model A: Numerical bifurcation analysis of the 3-parametric family (27) near the 3-dimensional nilpotent singularity. (a) A bifurcation diagram is shown in the (μ_1, μ_2) -parameter plane, with fixed parameter $\mu_3 = 0.01$. A saddle-node bifurcation curve (SN) and a Hopf bifurcation curve (H) as well as a Hopf-Zero bifurcation point (HZ) and a Bogdanov-Takens bifurcation point (BT) are found. (b) A region in the (μ_1, μ_2) -parameter plane is enlarged to show the segment where the cascades of period doubling bifurcations are detected. Along such segment $\mu_1 = 0.6182493995438856$ is fixed. (c) Two period doubling bifurcations are shown. (d) Cascades of period doubling bifurcations. The red and green dashed lines are in correspondence with those in (c).

283 The graphs of the solutions are included to show that the oscillations have a
 284 regular phase rhythm while the abundance peaks in each cycle are unpredictable.
 285 This features of uniform phase and chaotic amplitudes are exhibited by many
 286 biological systems ([20, 19]).

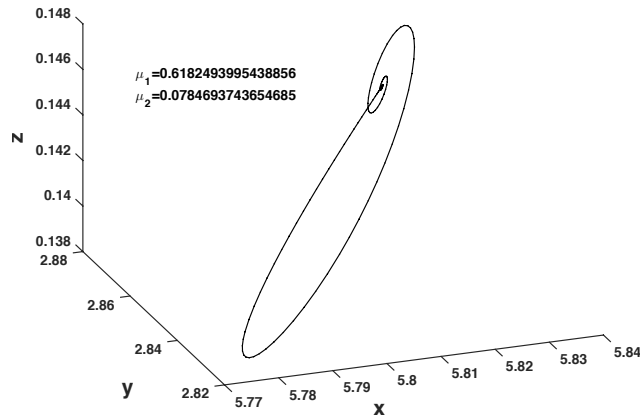


Figure 2: Model A: Shilnikov homoclinic orbit. The parameters μ_1 and μ_3 are set as in Figure 1(c). The value of μ_2 is 0.0784693743654685, which corresponds to the value at which the period of the 1-periodic orbit tends to infinity. For that value, the 1-periodic orbit is close enough to a homoclinic orbit.

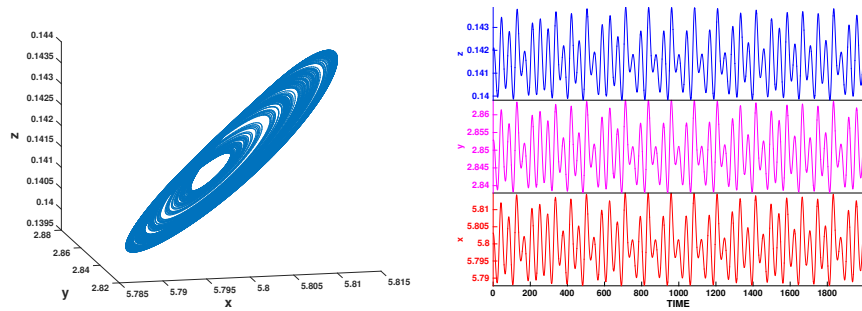


Figure 3: Model A: A strange attractor (left) and the solutions along the strange attractor (right). When the Shilnikov homoclinic orbit is broken, strange attractors can arise. The parameters μ_1 and μ_3 are set as in Figure 1(c) and $\mu_2 = 0.078487896$. The initial point in the plotted orbit is $(x_i, y_i, z_i) = (5.803149567, 2.852761453, 0.142024188)$. This strange attractor was detected exploring the cascade of period doubling bifurcations. The Maximal Lyapunov Exponent is close to 0.01.

287 4.2. Model B

We work with parameters values close to those considered in [20] and, therefore, in what follows in this section we set

$$p = 0, \quad \alpha_2 = \frac{38}{45}, \quad \text{and} \quad k_1 = \frac{7}{20}.$$

Using formulae provided in Proposition 3.3 with $s = 11$, we get

$$\hat{z}_0 = 0.070896246, \quad \hat{b} = 1.4762613, \quad \hat{c} = 6.8725611, \quad \hat{\alpha}_1 = 0.673750,$$

and hence the equilibrium point is at

$$\hat{x} = 11, \quad \hat{y} = 7.1985158, \quad \hat{z} = 0.061379431.$$

Substituting these parameter values in formulae (24), (25) and (26), we easily obtain

$$d_{11} = 9.2137978, \quad d_{12} = -3.3049085, \quad \text{and} \quad \Delta = -8.8232932.$$

288 Therefore, Model B is a generic 3-parametric unfolding of a 3-dimensional
 289 nilpotent singularity. The parameters of the unfolding are z_0 , b and c and a
 290 nilpotent singularity appears at $(\hat{x}, \hat{y}, \hat{z})$ when $z_0 = \hat{z}_0$, $b = \hat{b}$ and $c = \hat{c}$.

To study the bifurcation diagram near the nilpotent singularity, we consider (μ_1, μ_2, μ_3) as new parameters and work with the family below

$$\begin{cases} x' = x(1 - px) - \frac{\hat{\alpha}_1 x}{1+k_1 y} y, \\ y' = -(\hat{b} + \mu_2)y + \frac{\hat{\alpha}_1 x}{1+k_1 y} y - \alpha_2 yz, \\ z' = -(\hat{c} + \mu_3)(z - \hat{z}_0 - \mu_1) + \alpha_2 yz. \end{cases} \quad (28)$$

291 The theoretical results in section 3 guarantee that family (28) exhibits strange
 292 attractors. To illustrate numerically the chaotic behavior in this family, we set
 293 $\mu_3 = 0.005$ and study the bifurcation diagram of (28) in the (μ_1, μ_2) -parameter
 294 plane. Working with MatCont we obtain the results given in Figure 4. The
 295 explanation of the different panels is identical to the case of Model A and we
 296 do not repeat it here. Only mention that now the cascades of period doublings

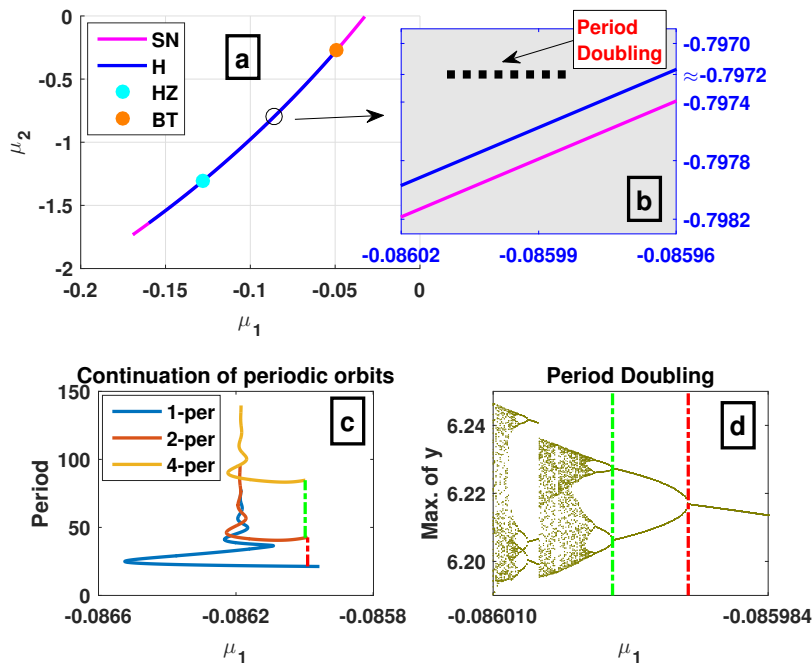


Figure 4: Model B: Numerical bifurcation analysis of the 3-parametric family (28) near the 3-dimensional nilpotent singularity. (a) A bifurcation diagram is shown in the (μ_1, μ_2) -parameter plane, with fixed parameter $\mu_3 = 0.005$. A saddle-node bifurcation curve (SN) and a Hopf bifurcation curve (H) as well as a Hopf-Zero bifurcation point (HZ) and a Bogdanov-Takens bifurcation point (BT) are found. (b) A region in the (μ_1, μ_2) -parameter plane is enlarged to show the segment where the cascades of period doubling bifurcations are detected. Along such segment $\mu_2 = -0.797211509659839$ is fixed. (c) Two period doubling bifurcations are shown. (d) Cascades of period doubling bifurcations. The red and green dashed lines are in correspondence with those in (c).

297 are detected fixing $\mu_2 = -0.797211509659839$ and considering μ_1 as the contin-
 298 uation parameter.

299 We show an example of Shilnikov homoclinic orbit in Figure 5. Namely, we
 300 plot the orbit which is computed at the end point of the numerical continuation
 301 of the 1-periodic orbit (see blue curve in Figure 4(c)). As period tends to infinity,
 302 parameter μ_2 tends to a certain limit which can be approached by the value of
 303 μ_1 at the end point of the continuation, namely, -0.0861858348181701 .

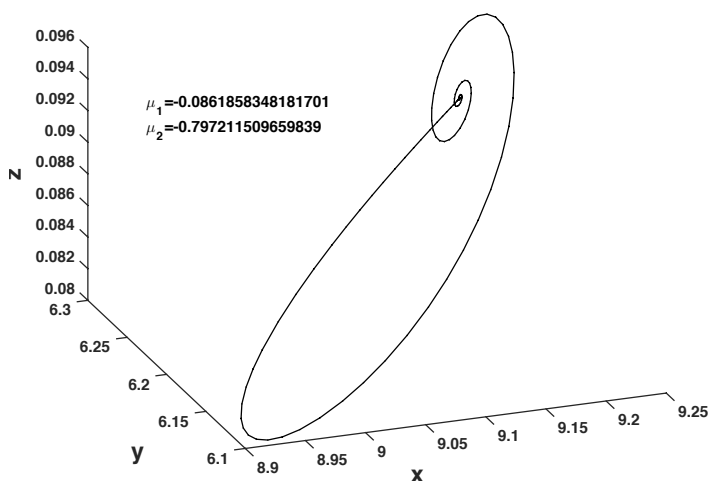


Figure 5: Model B: Shilnikov homoclinic orbit. The parameters μ_2 and μ_3 are set as in Figure 4(c). The value of μ_1 is -0.0861858348181701 , which corresponds to the value at which the period of the 1-periodic orbit tends to infinity. For that value, the 1-periodic orbit is close enough to a homoclinic orbit.

304 Finally, we perturb the vector field by changing slightly the value of the μ_1
 305 to get an example of strange attractor (see Figure 6). As in case of Model A, the
 306 graphs of the solutions are included to show the uniform phase and the chaotic
 307 amplitudes, features exhibited by many biological systems ([20, 19]).

308 5. Conclusions

309 In this paper, we provide an easy-to-check method, based on local bifurcation
 310 theory, to prove the existence of chaotic dynamics in a given model. The generic
 311 conditions which are required to guarantee the emergence of strange attractors
 312 in a generic unfolding of the 3-dimensional nilpotent singularity are reduced to
 313 simple formulas in section 2 (see (11), (12) and (14)). Therefore, this technique
 314 becomes very helpful for further applications in the detection of chaos. In par-
 315 ticular, we apply this method to prove that two different tritrophic chain models

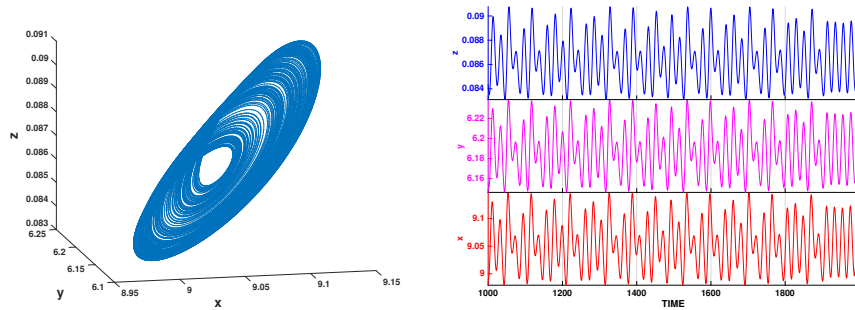


Figure 6: Model B: A strange attractor (left) and the solutions along the strange attractor (right). The parameters μ_2 and μ_3 are set as in Figure 4(c) and $\mu_1 = -0.086005637$. The initial point is $(x_i, y_i, z_i) = (9.1412254, 6.2329186, 0.089506456)$ and the chaotic orbit are detected exploring the cascade of period doubling bifurcations. The Maximal Lyapunov Exponent is close to 0.02.

316 are indeed generic unfoldings of 3-dimensional nilpotent singularities and hence
 317 they exhibit strange attractors (see section 3).

318 For completeness, in section 4, we numerically illustrate the existence of
 319 strange attractors in the two tritrophic chain models considered and explain
 320 the steps taken. Shortly, for any given model we first consider a point in the
 321 parameter space that satisfies the generic conditions. This means that the model
 322 is a generic 3-parametric unfolding of a 3-dimensional singularity. Second, we
 323 study the bifurcation diagram near the nilpotent singularity to detect a Hopf
 324 bifurcation curve. Third, using numerical techniques for continuation of periodic
 325 orbits, we are able to find a cascade of period doubling bifurcations and hence
 326 strange attractors. Moreover, continuation also allows to allocate parameter
 327 values for which the systems exhibits Shilnikov homoclinic orbits.

328 Acknowledgements

329 The authors Fátima Drubi and Santiago Ibáñez gratefully acknowledge fund-
 330 ing provided by the Spanish MICINN (grant MTM2017-87697-P).

331 **References**

- 332 [1] A. J. Lotka, *The elements of physical biology.*, XXX + 460 p. Baltimore,
333 Williams & Wilkins Co.; London, Baillière, Tindall & Cox (1925). (1925).
- 334 [2] V. Volterra, *Variazioni e fluttuazioni del numero d'individui in specie an-*
335 *imali conviventi.*, Mem. Accad. naz. Lincei, Cl. Sci. fis. mat. nat. (6) 2
336 (1927) 31–113.
- 337 [3] A. Hastings, T. Powell, *Chaos in a 3-species food-chain*, Ecology 72 (3)
338 (1991) 896–903. doi:10.2307/1940591.
- 339 [4] P. Hogeweg, B. Hesper, *Interactive instruction on population interactions*,
340 Comput. Biol. Med. 8 (4) (1978) 319–327. doi:10.1016/0010-4825(78)
341 90032-X.
- 342 [5] M. P. Boer, B. W. Kooi, S. A. L. M. Kooijman, *Homoclinic and heteroclinic*
343 *orbits to a cycle in a tri-trophic food chain*, J. Math. Biol. 39 (1) (1999)
344 19–38. doi:10.1007/s002850050161.
- 345 [6] O. De Feo, S. Rinaldi, *Singular homoclinic bifurcations in tritrophic food*
346 *chains*, Math. Biosci. 148 (1) (1998) 7–20. doi:10.1016/S0025-5564(97)
347 10001-3.
- 348 [7] A. Klebanoff, A. Hastings, *Chaos in 3-species food-chain*, J. Math. Biol.
349 32 (5) (1994) 427–451. doi:10.1007/BF00160167.
- 350 [8] Y. A. Kuznetsov, O. De Feo, S. Rinaldi, *Belyakov homoclinic bifurcations*
351 *in a tritrophic food chain model*, SIAM J. Appl. Math. 62 (2) (2001) 462–
352 487. doi:10.1137/S0036139900378542.
- 353 [9] Y. A. Kuznetsov, S. Rinaldi, *Remarks on food chain dynamics*, Math.
354 Biosci. 134 (1) (1996) 1–33. doi:10.1016/0025-5564(95)00104-2.
- 355 [10] K. McCann, A. Hastings, *Re-evaluating the omnivory-stability relationship*
356 *in food webs*, Proceedings: Biological Sciences 264 (1385) (1997) 1249–
357 1254. doi:10.1098/rspb.1997.0172.



- 358 [11] K. McCann, P. Yozdis, Bifurcation structure of a three-species food-chain
359 model, *Theor. Popul. Biol* 48 (2) (1995) 93–125. doi:10.1006/tpbi.1995.
360 1023.
- 361 [12] R. K. Upadhyay, R. K. Naji, Dynamics of a three species food chain model
362 with crowley-martin type functional response, *Chaos, Solitons & Fractals*
363 42 (3) (2009) 1337–1346. doi:10.1016/j.chaos.2009.03.020.
- 364 [13] B. Sahoo, S. Poria, The chaos and control of a food chain model supplying
365 additional food to top-predator, *Chaos, Solitons & Fractals* 58 (2014) 52–
366 64. doi:10.1016/j.chaos.2013.11.008.
- 367 [14] M. Saifuddin, S. Samanta, S. Biswas, J. Chattopadhyay, An eco-
368 epidemiological model with different competition coefficients and strong-
369 Allee in the prey, *Internat. J. Bifur. Chaos Appl. Sci. Engrg.* 27 (8) (2017)
370 1730027, 23. doi:10.1142/S0218127417300270.
- 371 [15] P. Panday, N. Pal, S. Samanta, J. Chattopadhyay, Stability and bi-
372 furcation analysis of a three-species food chain model with fear, *Inter-
373 nat. J. Bifur. Chaos Appl. Sci. Engrg.* 28 (1) (2018) 1850009, 20. doi:
374 10.1142/S0218127418500098.
- 375 [16] S. Ibáñez, J. A. Rodríguez, Shil'nikov configurations in any generic unfold-
376 ing of the nilpotent singularity of codimension three on \mathbb{R}^3 , *J. Differential
377 Equations* 208 (1) (2005) 147–175. doi:10.1016/j.jde.2003.08.006.
- 378 [17] F. Dumortier, S. Ibáñez, H. Kokubu, New aspects in the unfolding of the
379 nilpotent singularity of codimension three, *Dyn. Syst.* 16 (1) (2001) 63–95.
380 doi:10.1080/02681110010017417.
- 381 [18] P. G. Barrientos, S. Ibáñez, J. A. Rodríguez, Heteroclinic cycles arising in
382 generic unfoldings of nilpotent singularities, *J. Dynam. Differential Equa-
383 tions* 23 (4) (2011) 999–1028. doi:10.1007/s10884-011-9230-5.

- 384 [19] L. Stone, D. He, Chaotic oscillations and cycles in multi-trophic ecological
385 systems, *J. Theoret. Biol.* 248 (2) (2007) 382–390. doi:10.1016/j.jtbi.
386 2007.05.023.
- 387 [20] B. Blasius, A. Huppert, L. Stone, Complex dynamics and phase synchrono-
388 zation in spatially extended ecological systems, *Nature* 399 (6734) (1999)
389 354–359. doi:10.1038/20676.
- 390 [21] B. Deng, G. Hines, Food chain chaos due to Shilnikov’s orbit, *Chaos* 12 (3)
391 (2002) 533–538. doi:10.1063/1.1482255.
- 392 [22] B. Deng, G. Hines, Food chain chaos due to transcritical point, *Chaos* 13 (2)
393 (2003) 578–585. doi:10.1063/1.1576531.
- 394 [23] B. Deng, Food chain chaos with canard explosion, *Chaos* 14 (4) (2004)
395 1083–1092. doi:10.1063/1.1814191.
- 396 [24] B. Bockelman, B. Deng, E. Green, G. Hines, L. Lippitt, J. Sherman,
397 Chaotic coexistence in a top-predator mediated competitive exclusive web,
398 *J. Dynam. Differential Equations* 16 (4) (2004) 1061–1092. doi:10.1007/
399 s10884-004-7833-9.
- 400 [25] B. Bockelman, B. Deng, E. Green, G. Hines, L. Lippitt, J. Sherman,
401 Erratum to: “Chaotic coexistence in a top-predator mediated competi-
402 tive exclusive web” [*J. Dynam. Differential Equations* 16 (2004), no. 4,
403 1061–1092], *J. Dynam. Differential Equations* 17 (1) (2005) 217. doi:
404 10.1007/s10884-005-4560-9.
- 405 [26] B. B., B. D., Food web chaos without subchain oscillators, *Internat. J.*
406 *Bifur. Chaos Appl. Sci. Engrg.* 15 (11) (2005) 3481–3492. doi:10.1142/
407 S0218127405014179.
- 408 [27] H. Poincaré, Sur une forme nouvelle des équations du problème des trois
409 corps, *Acta Math.* 21 (1) (1897) 83–97. doi:10.1007/BF02417977.



- 410 [28] G. D. Birkhoff, Nouvelles recherches sur les systèmes dynamiques, Memo-
411 riae Pont. Acad. Sci. Novi Lyncaei 1 (1935) 85–216.
- 412 [29] S. Smale, Differentiable dynamical systems, Bull. Amer. Math. Soc. 73
413 (1967) 747–817. doi:10.1090/S0002-9904-1967-11798-1.
- 414 [30] E. N. Lorenz, Deterministic nonperiodic flow, J. Atmospheric Sci. 20 (2)
415 (1963) 130–141. doi:10.1175/1520-0469(1963)020<0130:DNF>2.0.CO;
416 2.
- 417 [31] M. Hénon, A two-dimensional mapping with a strange attractor, Comm.
418 Math. Phys. 50 (1) (1976) 69–77.
419 URL <http://projecteuclid.org/euclid.cmp/1103900150>
- 420 [32] M. Benedicks, L. Carleson, The dynamics of the Hénon map, Ann. of Math.
421 133 (1) (1991) 73–169. doi:10.2307/2944326.
- 422 [33] L. Mora, M. Viana, Abundance of strange attractors, Acta Math. 171 (1)
423 (1993) 1–71. doi:10.1007/BF02392766.
- 424 [34] C. Bonatti, L. J. Díaz, M. Viana, Dynamics beyond uniform hyperbolic-
425 ity, Vol. 102 of Encyclopaedia of Mathematical Sciences, Springer-Verlag,
426 Berlin, 2005.
- 427 [35] L. P. Šil'nikov, A case of the existence of a denumerable set of periodic
428 motions, Dokl. Akad. Nauk SSSR 160 (1965) 558–561.
- 429 [36] L. P. Shil'nikov, A contribution to the problem of the structure of an ex-
430 tended neighborhood of a rough equilibrium state of saddle-focus type,
431 Math. USSR, Sb. 10 (1970) 91–102.
- 432 [37] C. Tresser, About some theorems by L. P. Sil'nikov, Ann. Inst. H. Poincaré
433 Phys. Théor. 40 (4) (1984) 441–461.
- 434 [38] L. J. Díaz, V. Horita, I. Rios, M. Sambarino, Destroying horseshoes via
435 heterodimensional cycles: generating bifurcations inside homoclinic classes,



- 436 Ergodic Theory Dynam. Systems 29 (2) (2009) 433–474. doi:10.1017/
437 S0143385708080346.
- 438 [39] J. Palis, F. Takens, Hyperbolicity and sensitive chaotic dynamics at homo-
439 clinic bifurcations, Vol. 35 of Cambridge Studies in Advanced Mathematics,
440 Cambridge University Press, Cambridge, 1993.
- 441 [40] A. J. Homburg, Periodic attractors, strange attractors and hyperbolic dy-
442 namics near homoclinic orbits to saddle-focus equilibria, Nonlinearity 15 (4)
443 (2002) 1029–1050. doi:10.1088/0951-7715/15/4/304.
- 444 [41] A. Pumariño, J. A. Rodríguez, Coexistence and persistence of strange at-
445 tractors, Vol. 1658 of Lect. Notes Math., Springer-Verlag, Berlin, 1997.
446 doi:10.1007/BFb0093337.
- 447 [42] A. Pumariño, J. A. Rodríguez, Coexistence and persistence of infinitely
448 many strange attractors, Ergodic Theory Dynam. Systems 21 (5) (2001)
449 1511–1523. doi:10.1017/S0143385701001730.
- 450 [43] F. Dumortier, S. Ibáñez, H. Kokubu, Cocoon bifurcation in three-
451 dimensional reversible vector fields, Nonlinearity 19 (2) (2006) 305–328.
452 doi:10.1088/0951-7715/19/2/004.
- 453 [44] A. Algaba, M. Merino, E. Freire, E. Gamero, A. J. Rodríguez-Luis, Some
454 results on Chua’s equation near a triple-zero linear degeneracy, Internat.
455 J. Bifur. Chaos Appl. Sci. Engrg. 13 (3) (2003) 583–608. doi:10.1142/
456 S0218127403006741.
- 457 [45] S. A. Campbell, Y. Yuan, Zero singularities of codimension two and three
458 in delay differential equations, Nonlinearity 21 (11) (2008) 2671–2691. doi:
459 10.1088/0951-7715/21/11/010.
- 460 [46] F. Drubi, S. Ibáñez, J. A. Rodríguez, Coupling leads to chaos, J. Differential
461 Equations 239 (2) (2007) 371–385. doi:10.1016/j.jde.2007.05.024.

- 462 [47] E. Freire, E. Gamero, A. J. Rodríguez-Luis, A. Algaba, A note on the triple-
463 zero linear degeneracy: normal forms, dynamical and bifurcation behaviors
464 of an unfolding, *Internat. J. Bifur. Chaos Appl. Sci. Engrg.* 12 (12) (2002)
465 2799–2820. doi:10.1142/S0218127402006175.
- 466 [48] F. Drubi, S. Ibáñez, J. A. Rodríguez, Singularities and chaos in coupled
467 systems, *Bull. Belg. Math. Soc. Simon Stevin* 15 (5, Dynamics in pertur-
468 bations) (2008) 797–808. doi:10.36045/bbms/1228486408.
- 469 [49] J. Sieber, B. Krauskopf, Bifurcation analysis of an inverted pendulum with
470 delayed feedback control near a triple-zero eigenvalue singularity, *Nonlin-
471 earity* 17 (1) (2004) 85–103. doi:10.1088/0951-7715/17/1/006.
- 472 [50] J. A. Yorke, K. T. Alligood, Period doubling cascades of attractors: a
473 prerequisite for horseshoes, *Comm. Math. Phys.* 101 (3) (1985) 305–321.
474 URL <http://projecteuclid.org/euclid.cmp/1104114178>
- 475 [51] I. Baldomá, S. Ibáñez, T. M. Seara, Hopf-Zero singularities truly unfold
476 chaos, *Commun. Nonlinear Sci. Numer. Simul.* 84 (2020) 105162. doi:
477 10.1016/j.cnsns.2019.105162.
- 478 [52] F. Dumortier, S. Ibáñez, H. Kokubu, C. Simó, About the unfolding of a
479 Hopf-zero singularity, *Discrete Contin. Dyn. Syst.* 33 (10) (2013) 4435–
480 4471. doi:10.3934/dcds.2013.33.4435.
- 481 [53] F. Dumortier, S. Ibáñez, Nilpotent singularities in generic 4-parameter fam-
482 ilies of 3-dimensional vector fields, *J. Differential Equations* 127 (2) (1996)
483 590–647. doi:10.1006/jdeq.1996.0085.
- 484 [54] A. Dhooge, W. Govaerts, Y. A. Kuznetsov, H. G. E. Meijer, B. Sautois,
485 New features of the software MatCont for bifurcation analysis of dynamical
486 systems, *Math. Comput. Model. Dyn. Syst.* 14 (2) (2008) 147–175. doi:
487 10.1080/13873950701742754.