

Homoclinic organization in the Hindmarsh-Rose model: a three parameter study

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Bursting phenomena are found in a wide variety of fast-slow systems. In this article we consider the Hindmarsh-Rose neuron model, where, as it is known in the literature, there are homoclinic bifurcations involved in the bursting dynamics. However, the global homoclinic structure is far from being fully understood. Working in a three-parameter space, the results of our numerical analysis show a complex atlas of bifurcations, which extends from the singular limit to regions where a fast-slow perspective no longer applies. Based on this information we propose a global theoretical description. Surfaces of codimension-one homoclinic bifurcations are exponentially close to each other in the fast-slow regime. Remarkably, explained by the specific properties of these surfaces, we show how the Hindmarsh-Rose model exhibits isolas of homoclinic bifurcations when appropriate two-dimensional slices are considered in the three-parameter space. On the other hand, these homoclinic bifurcation surfaces contain curves corresponding to parameter values where additional degeneracies are exhibited. These codimension-two bifurcation curves organize the bifurcations associated with the spike-adding process and they behave like the “spines-of-a-book”, gathering “pages” of bifurcations of periodic orbits. Depending on how the parameter space is explored, homoclinic phenomena may be absent or far away, but their organizing role in the bursting dynamics is beyond doubt, since the involved bifurcations are generated in them. This is shown in the global analysis and in the proposed theoretical scheme.

Keywords: fast-slow dynamics, neuron models, homoclinic bifurcations, spike-adding, fold/hom bursting

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As a fundamental element in the study of nervous system dynamics, the analysis of behaviours and changes in isolated neurons is a first step in the theoretical/experimental research in mathematical/computational neuroscience. In addition, it is common to find synchronization in neuronal networks showing dynamical states which include different bursting regimes. From the physiological point of view, bursting is characterized by trains of spikes alternating with quiescent periods. Studying the different changes in the bursts fired by an isolated neuron will help provide detailed mathematical mechanisms to explain them. This work aims to understand the hidden mechanisms behind the processes that lead neurons to add (or subtract) spikes in a signal: the homoclinic bifurcations (in the case of fold/homoclinic bursters). Their relationship with the processes of creation of new spikes has been discussed earlier in the literature, but the global picture is not yet fully understood. We work with the Hindmarsh-Rose neuron model, one of the most popular neuronal dynamics models. To perform the analysis, we use continuation techniques and brute-force methods to locate and describe the changes. When exploring a three-dimensional space of parameters, we discover a complex structure of bifurcations that allows us to propose a new global structure, which we call, due to its geometry, homoclinic “mille-feuille” + “spines-of-the-book”. This skeleton of homoclinic bifurcations allows an explanation of the different phenomena observed in the literature, such as the influence of homoclinic bifurcations, even when not observed, the disappearance of bursting dynamics with a large number of spikes when the small parameter in the models grows (in fast-slow dynamics) and the spike-adding process.

1 I. INTRODUCTION

2 Fast-slow dynamics is a quite common phenomenon in theoretical and practical models in many
3 disciplines where different time scales are present. Computational/mathematical neuroscience is
4 one of the fields where these models are more abundant. In neuroscience, to understand how an
5 incredibly sophisticated system such as the brain *per se* functions dynamically, it is imperative to
6 study the dynamics of its constitutive elements – neurons. Since Hodgkin and Huxley developed
7 the first model of action potentials in the membrane¹, the design of mathematical models for
8 neurons has arisen as a trending topic in science for a few decades, and a lot of models and
9 variations describing different kinds of neuron cells in numerous animals have been proposed in

10 the literature. What all these systems have in common is the existence of fast-slow dynamics²,
 11 that is also quite usual in a lot of other practical applications, like in chemical reactions³ and laser
 12 dynamics⁴. In all these models, one of the key magnitudes is the time that a neuron, or other
 13 dynamical system, is active, and this is related to the number of oscillations (spikes) in the fast
 14 subregime.

15 In order to help in the analysis of neuron models simulated realistically within the Hodgkin-
 16 Huxley framework¹, a common approach is to use some simplified models. In particular, the
 17 3D Hindmarsh-Rose (HR) model⁵ reproduces fairly well the basic oscillatory activities routinely
 18 observed in isolated biological cells and in neural networks. It fulfills the two basic conditions
 19 of being computationally simple but, at the same time, able to reproduce the main behaviour (the
 20 rich firing patterns) exhibited by the real biological neuron. The HR model is described by three
 21 nonlinear ODEs:

$$\begin{cases} \dot{x} = y - ax^3 + bx^2 - z + I, \\ \dot{y} = c - dx^2 - y, \\ \dot{z} = \varepsilon[s(x - x_0) - z], \end{cases} \quad (1)$$

22 where x is the membrane potential, y the fast and z the slow gating variables for ionic current. In
 23 our study we will consider a typical choice of parameters: $a = 1$, $c = 1$, $d = 5$, $s = 4$, $x_0 = -1.6$.
 24 Parameters b and I determine the bursting or spiking behaviour and their values are considered in
 25 specific ranges where such phenomena are present. Parameter ε governs the fast-slow behaviour
 26 and we will study dynamics for ε small, but including scenarios far from the singular limit $\varepsilon = 0$.
 27 In the sequel we consider (1) as a family of vector fields depending on parameters (b, I, ε) , and
 28 say fast subsystem to refer to the z -family obtained after taking $\varepsilon = 0$.

29 Roughly speaking, we can say that a fast-slow system exhibits bursting when orbits exhibit
 30 periods of fast spiking followed by periods of quiescence. When the jump between these two
 31 different regimes can be explained by a fold bifurcation of equilibria and a homoclinic bifurcation
 32 of periodic orbits (both bifurcations occurring in the fast subsystem) we say that the bursting is of
 33 fold/hom type⁶. In Section II (see Fig. 3), we will describe how fold/hom bursters arise in the HR
 34 model.

35 One of the big challenges regarding bursting phenomena is to understand the mechanisms ex-
 36 plaining the variation in the number of spikes (Fig. 4 in Section II B provides an illustrative
 37 example in the HR model). These spike-adding processes have been studied for several mathe-
 38 matical neuron models (see for example Refs. 7–9), but also in other contexts as laser dynamics,

39 chemical reactions or discrete maps, with the alternative name of period-adding^{10–14}. This process
40 is quite important in that it progressively modifies the spectrum of periodic orbits of the system
41 and the structure of chaotic attractors^{15–18}. As argued by Terman¹⁸, these transitions may be ei-
42 ther continuous, with the period of the bursting solution increasing along the process, or they may
43 involve chaotic behaviours (see also Ref. 19). Recently, these transitions have been studied in
44 detail²⁰ providing a theoretical scheme for ε fixed. The relevance of fold bifurcations of periodic
45 orbits in this process was pointed out earlier in Ref. 21. Dealing with fold/hom bursting, the spike-
46 adding process has also been related to the existence of canard orbits^{22–25} and with the existence
47 of certain codimension-two homoclinic bifurcations^{15,26,27}. Working with a fixed value $\varepsilon = 0.01$,
48 the role of homoclinic bifurcations of codimension-one and two in the spike-adding mechanisms
49 was discussed in Ref. 26 and some preliminary results were advanced. Namely, bifurcations of
50 periodic orbits around flip and Belyakov bifurcations (see Section II A for background) were iden-
51 tified as crucial ingredients to understand some spike-adding transitions which are present in the
52 HR model. Again working with that fixed value of ε , codimension-two homoclinic bifurcations
53 were again considered in Ref. 27, but providing a much more thorough study. Different homo-
54 clinic curves were discussed and their sharp fold points were already detected in that reference
55 and linked to the spike-adding processes. Codimension-two homoclinic bifurcations in Refs. 26
56 and 27 are also organizing centers of chaotic regions in the bifurcation diagram. All these chaotic
57 phenomena were discussed in Ref. 15.

58 What is missing in the literature is a global study of how homoclinic bifurcations are organized,
59 and to that goal we need, at least, to describe them in a three parameter space. Note that it is intrin-
60 sic to the notion of bifurcation the possibility of observing its effects without the bifurcation point
61 being present. In the HR model, one can explore the parameter space without detecting homoclinic
62 bifurcations (see Fig. 4), although their consequences (fold and period doubling bifurcations) are
63 exhibited. The organizing points (the codimension-two homoclinic bifurcations) may be placed
64 far away in the space or parameters, and even, they may be outside a particular set of parameters
65 that we are visualizing, but they continue being the organizing centers. Taking all of this into
66 account, the goal of this article is to provide a model of the homoclinic organization that explains
67 all these facts.

68 As already mentioned, previous work in the literature was focused in studying, for some ε
69 fixed, the curves of homoclinic bifurcation at equilibria displayed by the system^{15,26,27}. A bifurca-
70 tion diagram in a three-parameter space, including variation of ε , was first considered in Ref. 46.

71 Changes in the spike-adding structures and the underlying bifurcations were observed. Moreover,
 72 foldings in the curves of inclination flip bifurcation were already detected. In Ref. 20 a theoret-
 73 ical scheme giving a complete scenario of bifurcations involved in the spike-adding processes in
 74 fold/hom bursters was introduced. This theoretical scheme provides a complete description of the
 75 connections of the different codimension-two points and the organization of the homoclinic curves
 76 for ε fixed. Also in this paper, the validity of the scheme is checked for a pancreatic β -cell neuron
 77 model.

78 In this article, we are interested in understanding the global structure of the homoclinic surfaces
 79 in the three parameter space. To that goal, a detailed numerical study with continuation techniques
 80 is required (we use the well-known software AUTO^{28,29}) as well as the spike counting (SC in the
 81 sequel) technique, as introduced in Refs. 15, 26, and 30.

82 Supported by numerical evidences, we conjecture that the intersection of each homoclinic sur-
 83 face with horizontal planes (with ε fixed) produces isolas in the plane of parameters (compare
 84 with results in Ref. 31 for the FitzHugh-Nagumo system), that is, simple closed curves in the cor-
 85 responding slice. We show how, for each ε fixed, the model exhibits a finite number (number that
 86 grows when the small parameter decreases) of isolas corresponding to primary homoclinic bifur-
 87 cations. Isololas are not only exponentially close each other, but they exhibit a pair of extremely
 88 sharp folds, so that the width of each isola is also exponentially small. These folds allow two sides
 89 of the isola to be distinguished (and also two faces of the surface of homoclinic bifurcations). On
 90 one of the faces the corresponding homoclinic orbits on the fold/hom regime exhibits n spikes and,
 91 on the other, $n + 1$. It is because of this fact that, from now on, we use the notation $hom^{(n,n+1)}$
 92 to refer to the different homoclinic bifurcation surfaces (or isolas if working with two-parameter
 93 plots).

94 **Remark 1** Notation $hom^{(n,n+1)}$ was already introduced in Ref. 20. In Refs. 26 and 27 authors
 95 use a different option to label homoclinic bifurcation curves. Namely, they do not emphasize that
 96 a given homoclinic bifurcation curve can correspond to homoclinic orbits with a different number
 97 of spikes. For instance, in Ref. 27 authors use the notation $hom^{(n)}$ where we use $hom^{(n,n+1)}$.
 98 Nevertheless, one should note that when required (see Figs. 4, 5 and 7 in Ref. 27) they also
 99 use two different notations for a unique curve of homoclinic bifurcation, changing the label from
 100 $hom^{(n)}$ to $hom^{(n+1)}$ after a sharp fold of the curve is crossed, pointing out that the number of
 101 spikes changes from n to $n + 1$.

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102 Homoclinic surfaces are the main focus of this article. We show how they are disposed in
103 the parameter space, taking into account that, as numerics show, they are exponentially close to
104 each other when $\varepsilon \rightarrow 0$. Because of their tubular shape and the proximity of the surfaces, we can
105 compare the whole structure with a “mille-feuille” pastry. There, we observe pencils of curves
106 of fold and period-doubling (PD) bifurcations of periodic orbits generated on codimension-two
107 bifurcation points. Moving ε , each of the curves in the pencil gives rise to a surface. Hence,
108 we can compare the codimension-two bifurcation curves with the “spines-of-a-book” with pages
109 correspondent to surfaces of bifurcations of periodic orbits. Besides, the ε -level reached by each
110 surface $hom^{(n,n+1)}$ decreases as n increases. This allows us to explain the simplification mecha-
111 nisms (bursting with a lower number of spikes) that can be observed as ε increases.

112 The article is organized as follows. In Section II we provide general information about the
113 HR model: fast-slow decomposition, spike-adding process linked to fold/hom bursters exhibited
114 by the model and a discussion about existence of equilibria in the full system. A short survey
115 about homoclinic bifurcations and an overview about the literature regarding the HR model are
116 also provided in Section II. In Section III we pay attention to some particular slices (with ε fixed)
117 inside the three-parameter space. Here we show how the base shape of the homoclinic curves
118 evolves as ε varies, but much more significant, how the codimension-two homoclinic bifurcation
119 points move on the homoclinic curves and, in fact, how they disappear when ε grows. Section IV
120 presents a three-parameter study explaining some of the phenomena which are observed when ε
121 is fixed and shows isolas of codimension-one homoclinic bifurcations. Section V introduces the
122 global theoretical scheme creating the structure that we call “homoclinic mille-feuille”, bearing in
123 mind the codimension-one bifurcation surfaces. In them, we find “spines-of-a-book”, bearing in
124 mind the codimension-two bifurcation curves, holding pencils of bifurcations of periodic orbits.
125 Both structures give rise to the theoretical model proposed in this article. Finally, we present some
126 conclusions in Section VI.

127 II. BACKGROUND

128 In this section we recall some basic aspects about homoclinic bifurcations and fast-slow dy-
129 namics, including a description of fold-hom bursters, one of the mechanisms exhibited by the HR
130 model for the creation of bursting orbits. In addition, to facilitate further discussions, the equilib-
131 rium points displayed by the full system (1) are explained. In our revision on bifurcations, only

132 those that play a relevant role in the global organization of dynamics in the HR model are included.

133 A. Homoclinic bifurcations

134 First, we review some theoretical features regarding homoclinic bifurcations. For additional
135 details and references see Ref. 37 or the books Refs. 38 and 39. Essential, but technical references
136 are Refs. 40–43.

137 Consider a smooth family of vector fields X_μ on \mathbb{R}^3 with $\mu \in \mathbb{R}^k$ and suppose that there exist
138 $\mu_0 \in \mathbb{R}^k$ and $p_0 \in \mathbb{R}^3$ such that p_0 is a saddle type hyperbolic equilibrium of X_{μ_0} . Without loss
139 of generality we assume that $\mu_0 = 0$ and $p_0 = 0$. Let $W^s(0)$ (resp. $W^u(0)$) be the stable (resp.
140 unstable) invariant manifolds of X_0 at 0. Up to time reversal we can assume that $\dim(W^s(0)) = 1$.

141 To state certain conditions, we will need to use the notions of strong unstable manifold and cen-
142 ter stable manifold. Assume that $DX_0(0)$ has real eigenvalues λ_s , λ_u and λ_{uu} with $\lambda_s < 0 < \lambda_u <$
143 λ_{uu} . The strong unstable manifold $W^{uu}(0)$ is a one-dimensional invariant manifold whose tangent
144 space at 0 is given by the eigenspace corresponding to the eigenvalue λ_{uu} (the so called strong un-
145 stable direction). On the other hand, the center stable manifold $W^{cs}(0)$ is a two-dimensional invari-
146 ant manifold whose tangent space at 0 is given by the eigenspace corresponding to the eigenvalues
147 λ_u and λ_s .

148 Let $\Gamma_0 \subset W^s(0) \cap W^u(0)$ be a homoclinic orbit. In the sequel we assume that the family X_μ
149 unfolds Γ_0 generically. To understand this condition, consider a cross section Σ at a point in Γ_0
150 and define the distance $\Delta(\mu)$ between the point $W^s(p_\mu) \cap \Sigma$ and the curve $W^u(p_\mu) \cap \Sigma$, where p_μ
151 denotes the saddle type hyperbolic equilibrium of X_μ which exists close to 0 for μ small enough.
152 We say that Γ_0 is generically unfolded with respect to μ if $D_\mu \Delta(0) \neq 0$. Under this generic
153 assumption, there always exists a hypersurface H in the parameter space such that $0 \in H$ and X_μ
154 has a homoclinic orbit asymptotic to p_μ for all $\mu \in H$.

155 There exist four classes of codimension-one homoclinic orbits.

156 **Case 1:** Eigenvalues of $DX_0(0)$ are λ_s , λ_u and λ_{uu} , with $\lambda_s < 0 < \lambda_u < \lambda_{uu}$ and $\lambda_s + \lambda_u > 0$.

157 **Case 2:** Eigenvalues of $DX_0(0)$ are λ_s , λ_u and λ_{uu} , with $\lambda_s < 0 < \lambda_u < \lambda_{uu}$ and $\lambda_s + \lambda_u < 0$.

158 Moreover,

159 **(H1):** $\Gamma_0 \not\subset W^{uu}(0)$.

160 **(H2):** $W^{cs}(0)$ intersects $W^u(0)$ transversally along Γ_0 .

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161 **Case 3:** Eigenvalues of $DX_0(0)$ are $\lambda_s < 0$ and $\rho_u \pm \omega_u i$, with $\rho_u > 0$, $\omega_u \neq 0$ and $\lambda_s + \rho_u > 0$.

162 **Case 4:** Eigenvalues of $DX_0(0)$ are $\lambda_s < 0$ and $\rho_u \pm \omega_u i$, with $\rho_u > 0$, $\omega_u \neq 0$ and $\lambda_s + \rho_u < 0$.

163 Conditions $\lambda_s + \lambda_u \neq 0$ and $\lambda_s + \rho_u \neq 0$ are non-resonance hypothesis. Condition **(H1)** implies
164 that Γ_0 is tangent to the weak unstable direction, that is, the direction given by the eigenspace
165 associated with the weak unstable eigenvalue λ_u . Condition **(H2)** is a “non-inclination” property.

166 In **Case 1** and **Case 3**, a single unstable (repelling) periodic orbit is born from the homoclinic
167 connection for parameter values on one side of the hypersurface H . In **Case 2**, a saddle periodic
168 orbit emerges from the homoclinic orbit. Its stable manifold is orientable or not, depending on the
169 orientability of $W^u(0)$. In **Case 4**, there exist infinitely many saddle type periodic orbits in any
170 neighbourhood of the homoclinic orbit. In fact, as argued in Ref. 44, there exist infinitely many
171 horseshoes in any neighbourhood of the homoclinic orbit Γ_0 . When the connection is destroyed,
172 finitely many of the horseshoes persist and hence it follows the existence of an infinite number
173 of periodic solutions. The appearance or disappearance of horseshoes is accompanied by unfold-
174 ings of homoclinic tangencies of saddle-type periodic orbits and hence, strange repellers should
175 emerge⁴⁵. Reader can find more extended explanations about all these bifurcation results in Refs.
176 37 and 38.

177 Regarding codimension-two homoclinic bifurcations, we only pay attention to the inclination
178 flip, orbit flip and Belyakov bifurcations because they are the only cases that we will discuss in the
179 context of the Hindmarsh-Rose model. So, we distinguish the cases below.

180 **Inclination Flip (IF):** Assume all conditions in **Case 2** except **(H2)**, that is, we assume that the
181 intersection between $W^{cs}(0)$ and $W^u(0)$ is non-transversal along Γ_0 .

182 **Orbit Flip (OF):** Assume all conditions in **Case 2** except **(H1)**, that is, we assume that $\Gamma_0 \subset$
183 $W^{uu}(0)$.

184 **Belyakov Point:** Assume that the equilibrium point is a saddle-node with eigenvalues λ_s and λ_u
185 with $\lambda_s < 0 < \lambda_u$. The eigenvalue λ_u has geometric multiplicity one and algebraic multi-
186 plicity two.

187 To characterize the different types of inclination and orbit flip bifurcations we need to introduce
188 the following ratios between eigenvalues

$$\alpha = -\frac{\lambda_{uu}}{\lambda_s}, \quad \beta = -\frac{\lambda_u}{\lambda_s} \quad (2)$$

189 Note that $\alpha > \beta$.

190 Bifurcation diagrams corresponding to IF and OF bifurcation points are quite similar and they
191 can be described simultaneously. First, we observe that the hypersurface H of homoclinic bifur-
192 cation splits in two regions separated by a manifold of codimension-two homoclinic bifurcations.
193 The orientation of the unstable invariant manifold at the equilibrium point reverses when such
194 manifold is crossed.

195 For either IF or OF bifurcations there are three cases (see Fig. 1):

	Inclination Flip	Orbit Flip
196 Case A	$\beta > 1$	$\beta > 1$
Case B	$\alpha > 1$ and $\frac{1}{2} < \beta < 1$	$\beta < 1$ and $\alpha > 1$
Case C	$\alpha < 1$ or $\beta < \frac{1}{2}$	$\alpha < 1$

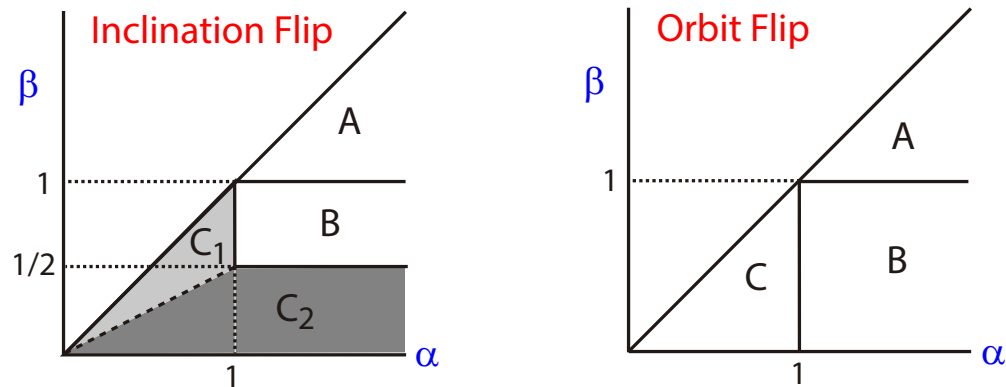


FIG. 1. Types of inclination and orbit flips. Values of the ratios α and β are given in (2).

197 We are only interested in **Case C** because the other two cases are not detected in our exploration
198 of the HR model. Homoclinic flip bifurcations in **Case C** require additional generic assumptions.
199 Namely, for inclination flips we assume:

200 **(I1)** $\beta \neq \frac{1}{2}\alpha$.

201 **(I2)** If $\beta > \frac{1}{2}\alpha$ (region C_1 in the left panel of Fig. 1), the homoclinic orbit does not lie in the
202 unique smooth leading unstable manifold.

203 **(I3)** If $\beta < \frac{1}{2}\alpha$ (region C_2 in the left panel of Fig. 1), there is a quadratic tangency between
204 $W^{cs}(0)$ and $W^u(0)$ along the homoclinic orbit.

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205 **Remark 2** Regions labelled SN1 (red) and SN2 (white) in the bottom panels shown for each ε
 206 in Figs. 5 and 6 correspond to saddle-node equilibria where conditions $\beta > \frac{1}{2}\alpha$ and $\beta < \frac{1}{2}\alpha$,
 207 respectively, are satisfied.

208 On the other hand, for orbit flips in **Case C** we assume:

209 **(O1)** $W^{cs}(0)$ intersects $W^u(0)$ transversally along Γ_0 .

210 Hypothesis **(I2)** (resp. **(I3)**) makes sense in the region C_1 (resp. C_2) depicted in Fig. 1. We do not
 211 extend in details about these two cases because they make no difference in the unfoldings. The
 212 essential distinction has to do with the way in which the unstable manifold approach the origin
 213 when it is followed along the homoclinic orbit by the forward flow (see Figure 2 in Ref. 40).

214 There are two possible bifurcation diagrams in case C. In both cases, horseshoes exist in a
 215 region of the parameter space. We remark that chaotic regions have been observed in the HR
 216 model⁴⁶ connected with the infinite fans of period doubling and fold bifurcations of periodic orbits
 217 generated at these codimension-two points. Depending on how they are formed, cases C (in) and
 218 C (out) are distinguished (see Fig. 2). In both, infinitely many one-sided curves of N -homoclinic
 219 orbits emerge for each $N \geq 2$ from the flip point on the branch of primary homoclinic orbits
 220 (labelled hom in Fig. 2). These are homoclinic orbits which follow N times the primary one before
 221 closing up. Also in both cases, the bifurcation diagram exhibits an infinite fan of bifurcation
 222 curves corresponding to period doublings and folds of periodic orbits. The horseshoe dynamics
 223 appear in between that cascade and the infinite fans of N -homoclinic orbits. In case C (in), shift
 224 dynamics and the homoclinic cascade are separated by the curve hom, whereas, in case C (out), the
 225 homoclinic cascade, the shift dynamics and the fan of bifurcations of periodic orbits are located
 226 on the same side of the curve hom (see Fig. 2). A complete description of the bifurcation diagrams
 227 can be found in Refs. 37, 40, and 41.

228 Regarding Belyakov bifurcations we remark that the hypersurface H of homoclinic bifurcation
 229 splits in two regions separated by a manifold of codimension-two homoclinic bifurcations. Saddles
 230 change from saddle-node type to saddle-focus type when such manifold is crossed. Additional
 231 generic conditions include global assumptions on the behaviour of the invariant manifolds (see
 232 Refs. 37 and 43 for a complete description and particularly Figure 14 in the second reference).

233 If $\lambda_s + \rho_u < 0$, a unique unstable limit cycle bifurcates from the homoclinic orbit (see Ref. 43).
 234 Otherwise, a two-parameter bifurcation diagram is quite similar to those in Fig. 2. Infinitely many
 235 one-sided curves of N -homoclinic orbits emerge for each $N \geq 2$ from the Belyakov point and they

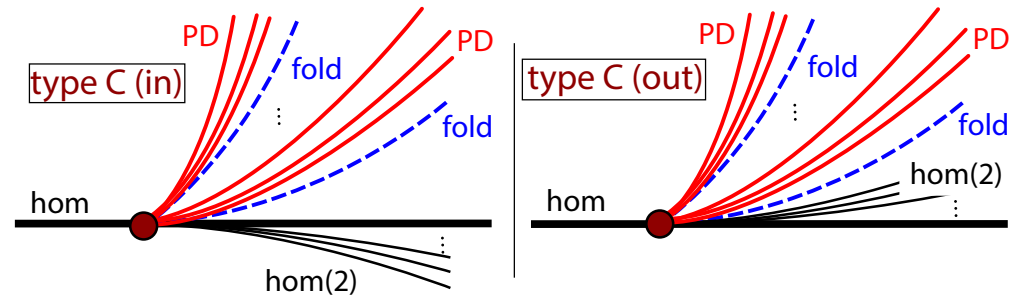


FIG. 2. Theoretical two-parameter unfolding of the codimension-two OF and IF homoclinic bifurcations of type **C (in)** and **C (out)** describing the fans of period doubling and fold bifurcations of periodic orbits. Bifurcation diagrams for Belyakov bifurcations are similar, but folds and period doublings accumulate from both sides of the primary homoclinic bifurcation (see details in Ref. 43). A fan of 2-homoclinic orbits (labelled $\text{hom}(2)$) is also depicted.

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236 are tangent at the flip point to the branch of primary homoclinic orbits corresponding to saddle-
 237 focus. The bifurcation diagram also exhibits infinite fans of bifurcation curves corresponding to
 238 period doublings and folds of periodic orbits, but, on the contrary to what is shown in Fig. 2, they
 239 accumulate on the branch of saddle-focus homoclinic orbits from both sides (see Figure 14 in Ref.
 240 43).

241 Codimension-three homoclinic bifurcations have been studied in Ref. 40. Namely, transitions
 242 from **Case A** to **Case B** and also from **Case B** to **Case C** were discussed and conjectural bifurca-
 243 tion diagrams were provided. See also Ref. 42 regarding the case of the coalescence of resonances
 244 between eigenvalues with an orbit flip degeneracy. In both references, particular attention is de-
 245 voted to the existence of homoclinic doubling cascades. Our study of the homoclinic phenomena
 246 in the HR model focuses on codimension-one and codimension-two bifurcations, but, as expected
 247 in a three-parameter study, higher codimension configurations do exist. For instance, coalescence
 248 between IF and Belyakov bifurcations and transitions from C_1 to C_2 in Fig. 2 (right) are expected
 249 in the HR model. Nevertheless, although this codimension-three phenomenon has not been pre-
 250 viously considered in the literature, it is out of the scope of this paper. Despite this, any of the
 251 scenarios considered in Refs. 40 and 42 have been detected in model, but the bifurcation diagrams
 252 there proposed should inspire our future analysis of such configurations. These diagrams show
 253 pencils of codimension-one bifurcations connecting codimension-two bifurcation points. This is
 254 similar to what is shown in Figure 6 in Ref. 20.

255 B. Slow-fast dynamics and fold-hom bursters

256 Equilibrium points in the full system (1) are given, after substituting the parameter values, by
 257 the intersection of the plane

$$z = 4(x + 1.6), \quad (3)$$

258 and the curve

$$\begin{cases} 0 = 1 - 5x^2 - y, \\ 0 = y - x^3 + bx^2 - z + I. \end{cases} \quad (4)$$

259 They do not depend on ε , but there can be one, two or three equilibrium points depending
 260 on the values of parameters b and I . Projections of the plane (3) and the curve (4) on the plane
 261 (z, x) are illustrated in Figure (4) for $b = 2.7$ and $I = 2.2$, see the brown colored straight line and
 262 the green-red colored Z-shaped curve, respectively. For these parameter values there is a unique
 263 equilibrium point in the full system (1).

264 A detailed discussion about local bifurcations was given in Ref. 26. In particular, the descrip-
 265 tion provided in Ref. 26 (Figure 3) is similar to the information given at the bottom panels in our
 266 Figs. 5 and 6. As reference, we use the bottom panel in Fig. 6 for the value $\varepsilon = 0.08$. For param-
 267 eters in the purple region there are three equilibrium points. Outside this region (at least in the range
 268 of parameters under consideration) there is only one equilibrium point that is attracting for param-
 269 eter values on the green region until it undergoes a Hopf bifurcation (yellow line). The pale blue
 270 region correspond to saddle-focus (SF) equilibria with stability index 1, that is, equilibria where
 271 the linear part has eigenvalues λ_s and $\rho_u \pm \omega$, with $\lambda_s < 0 < \rho_u$ and $\omega \neq 0$. The transition from
 272 the pale blue to the red region means the change from SF to saddle-node (SN) equilibria (with
 273 stability index 1), that is, equilibria where the linear part has eigenvalues λ_s , λ_u and λ_{uu} such that
 274 $\lambda_s < 0 < \lambda_u < \lambda_{uu}$, with $\lambda_s < 0 < \lambda_u < \lambda_{uu}$. Note that $\lambda_u = \lambda_{uu}$ for parameters on the borderline
 275 between the pale blue and the red regions. This transition is related to the existence of Belyakov
 276 bifurcations, which were described in the previous subsection. The difference between red and
 277 white regions – labelled SN1 and SN2, respectively – has to do with conditions on the eigenvalues
 278 which are used to characterize specific cases of flip bifurcations (see Remark 2). In any case, both
 279 regions correspond to SN equilibria with stability index 1.

280 The Hindmarsh-Rose model is a prototypical example of a fast-slow system. The bifurcation

281 diagram of the fast subsystem

$$\begin{cases} \dot{x} = y - x^3 + bx^2 - z + I, \\ \dot{y} = 1 - 5x^2 - y, \end{cases} \quad (5)$$

282 obtained when $\varepsilon = 0$ is crucial to explain the dynamics when ε is small². It should be remarked
 283 that each time that we refer to the fast subsystem (5), z is considered as an additional parameter.
 284 Fixing b and I , the model analysis provides two invariant objects: a curve of equilibrium points,
 285 with equations given in (4), and a manifold of limit cycles. As illustration, in Fig. 3, we show
 286 a partial bifurcation diagram of (5) with $b = 2.7$ and $I = 2.2$. The Z-shaped curve corresponds
 287 to equilibrium points: solid green lines correspond to stable equilibria, whereas dashed red lines
 288 correspond to unstable points. Note that the displayed curve corresponds to the projection of
 289 the curve with equation (4) on the plane (z, x) . Stability along the lower branch is lost at a fold
 290 bifurcation point. There is also a second fold where the equilibria recover their stability to become
 291 again unstable when they undergo a Hopf bifurcation. The emerging limit cycles disappear in a
 292 homoclinic bifurcation to emerge again for lower values of z through an additional homoclinic
 293 bifurcation. This second family of limit cycles disappears at a Hopf bifurcation point which is not
 294 displayed in the figure. We also show the maximum and minimum values of the x variable along
 295 the periodic orbits with solid blue lines. So, in general, we identify two invariant manifolds. On
 296 the one hand, the fast manifold \mathcal{M}_{fast} , also named spiking manifold, given by the second family
 297 of attracting limit cycles of the fast subsystem (5) and, on the other side, the slow manifold \mathcal{M}_{slow} ,
 298 formed by the equilibrium points of the fast subsystem (5). It follows from the Fenichel theory that
 299 for values of z where these manifolds are normally hyperbolic, they perturb to invariant manifolds
 300 $\mathcal{M}_{fast}^\varepsilon$ and $\mathcal{M}_{slow}^\varepsilon$ which exist for ε small enough in the full system.

301 Bursting in the full system emerges because orbits repeatedly switch between $\mathcal{M}_{slow}^\varepsilon$ and $\mathcal{M}_{fast}^\varepsilon$.
 302 An example of a bursting orbit with 5 spikes for $\varepsilon = 0.01$ is shown in Fig. 3. Top panel shows
 303 the bursting orbit projected on the plane (z, x) and superimposed on the picture of the fast-slow
 304 decomposition. The time series of the x component of the solution is displayed in the bottom
 305 panel. Note that the active regime begins close to a fold bifurcation of equilibria and finishes
 306 at a homoclinic bifurcation of limit cycles in the limit case. Due to this reason, following the
 307 Izhikevich⁶ classification of bursting types, we say fold/hom bursting (also named square-wave
 308 bursting) to refer to the case illustrated in Fig. 3. The classification in Ref. 6 is based on the
 309 fast/slow decomposition (first developed in Ref. 32) of the model. Detailed explanations about the
 310 previous description of the bursting phenomena in the HR model can be found, for instance, in

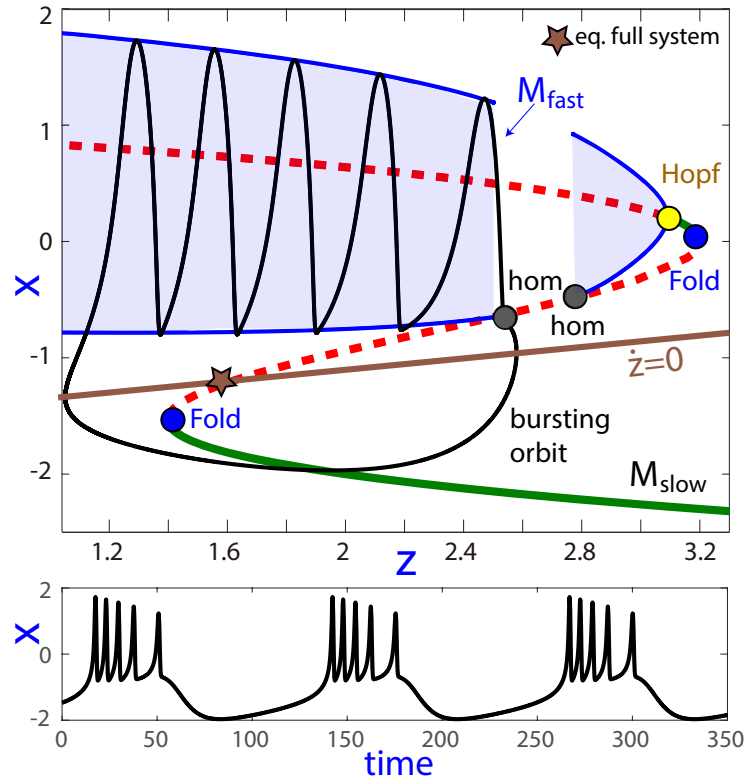


FIG. 3. Illustration of a slow-fast decomposition in the HR model with $b = 2.7$ and $I = 2.2$. Top panel shows a bifurcation diagram of the fast subsystem (5) when variable z is considered as a bifurcation parameter. Straight line $\dot{z} = 0$ is also depicted to visualize the equilibrium point that exists for the full system. A periodic orbit with 5 spikes is superimposed on the fast and slow manifolds. The time series of the x -component of the solution is shown in the bottom panel.

311 Refs. 15 and 33.

312 In the literature there is a large number of papers devoted to the study of the variation in the
 313 number of spikes that can be observed when one parameter is changed. Thus, plots similar to those
 314 of Fig. 4 are obtained (see also, for instance, Fig. 4 of Ref. 34), where the number of spikes in the
 315 neuronal response increases from two to six as a parameter is varied, and where each spike adding
 316 transition is characterized by a strong increase in the L_2 integral norm of the orbit. By spike-adding
 317 process we mean any mechanism leading to the formation of extra excursions around the tubular
 318 invariant manifold \mathcal{M}_{fast} (and therefore the addition of one spike to the bursting orbit).

319 In Fig. 4 we use the HR model to exemplify a process of spike-adding. We fix $\varepsilon = 0.01$
 320 and $I = 2.2$ and let b vary as the continuation parameter of a periodic orbit. It is clear from the
 321 picture that a sequence of fold bifurcations (blue dots in the figure) is involved, giving rise to

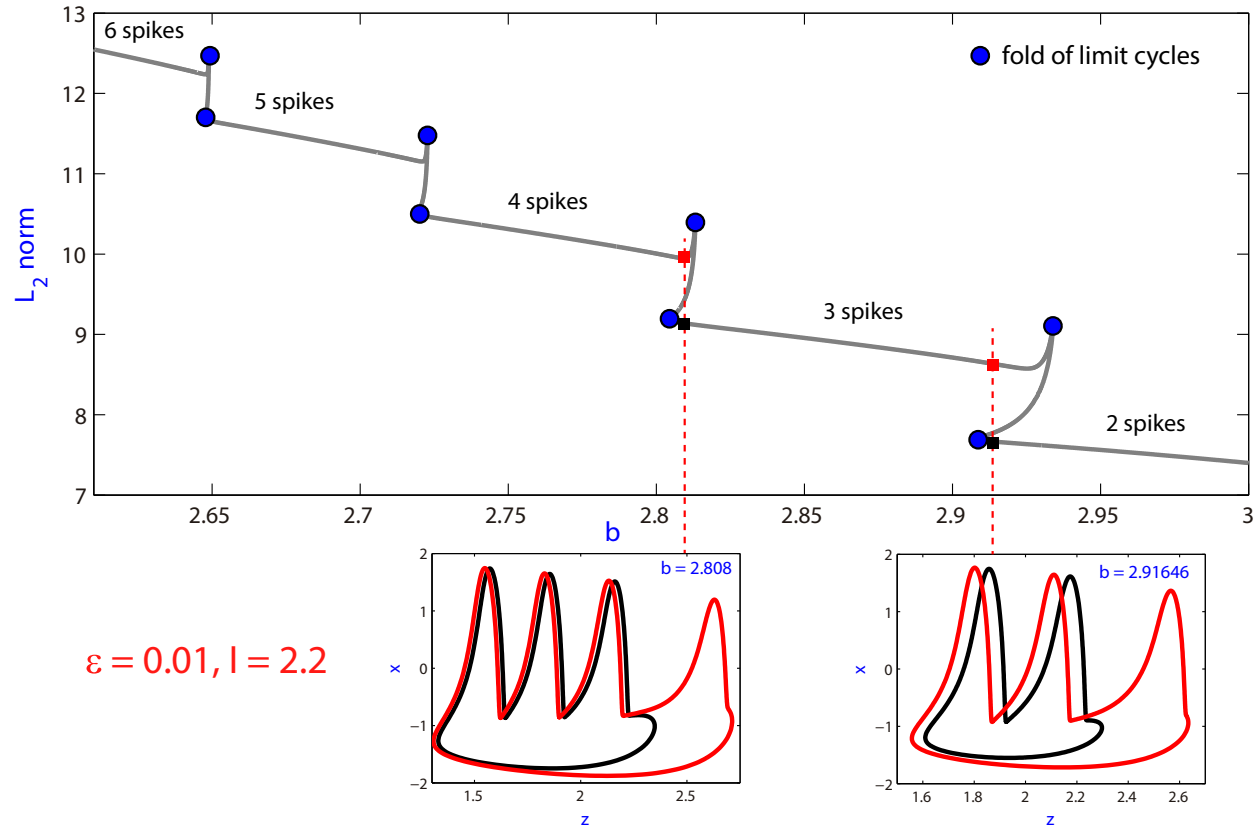


FIG. 4. Example of a spike-adding process in the HR model. A periodic orbit is continued with b varying when $\varepsilon = 0.01$ and $I = 2.2$. As b decreases, the change in the L_2 integral norm can be seen. The increase in the number of spikes is illustrated by showing a collection of orbits corresponding to specific positions along the bifurcation curve. We observe how this type of spike-adding process is associated to fold bifurcations of periodic orbits. Two coexisting stable periodic orbits are shown in the small plots for two values of b .

322 hysteresis phenomena and the appearance of bistability regions (in Fig. 4 we show two examples
 323 of coexisting stable periodic orbits). Although they are not shown, period doubling bifurcations
 324 may be also present. As shown in Refs. 15, 20, 26, and 27, at least in the case of the HR model,
 325 all these bifurcations of periodic orbits are related to homoclinic phenomena.

326 III. ANALYSIS WITH ε FIXED

327 In this section we begin our analysis by describing all the information provided by a selection of
 328 horizontal slices with the small parameter ε fixed. These selected slices will show us the different
 329 scenarios that we can find by changing ε , and it will help us later to develop a complete three-

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330 dimensional bifurcation diagram in the parameter space (b, I, ε) shown in next sections. Also,
331 these two-parameter plots will show the connection of the spike-adding process with the “far-
332 away” codimension-two homoclinic bifurcation points. Recall that the notation $hom^{(n,n+1)}$ was
333 already introduced in Section I to refer to codimension-one homoclinic bifurcation curves.

334 As a first analysis, Figs. 5 and 6 show the results we have obtained in the plane (b, I) for differ-
335 ent values of ε . In total, eight different values of ε are considered and for each value two panels are
336 exhibited. The selected values cover all the different possibilities found in the tests. Upper panel
337 combines a two-parameter sweep done with the SC technique (that counts the number of spikes
338 per burst of the stable periodic orbit) with a parameter continuation of bifurcation curves as in
339 Refs. 15 and 27. The lower panel provides information about the number and type of equilibrium
340 points in different regions of the parameter plane (see Subsection II B).

341 All the ingredients that we need in our description of dynamical and topological changes are
342 shown in Figs. 5 and 6. The displayed bifurcations are the following: *black lines* correspond to
343 $hom^{(1,2)}$ bifurcation curves; *red lines* represent period-doubling bifurcation curves; *yellow lines*
344 stand for Hopf bifurcation curves; *red points* are Belyakov bifurcation points and *green* and *grey*
345 *points* represent, respectively, IF and OF bifurcation points. When displayed all together, the ho-
346 moclinic bifurcation curves $hom^{(n,n+1)}$ are not distinguishable because for low values of ε they
347 are exponentially close and the largest is $hom^{(1,2)}$, the one shown. Therefore, the IF and Belyakov
348 bifurcation points corresponding to different homoclinic curves are superimposed (they are in dif-
349 ferent homoclinic curves but at a very small distance). The OF bifurcation points also correspond
350 to several homoclinic curves (to be studied later), but they are clearly distinguished. In Fig. 7 we
351 provide an alternative schematic view. Taking four representative values of ε , we show separately
352 the homoclinic curves $hom^{(1,2)}$, $hom^{(2,3)}$ and $hom^{(11,12)}$ and some connected bifurcations. These
353 figures illustrate the changes that can be expected in our global study and that we should explain.

354 In each lower panel of Figs. 5 and 6, the parameter plane is partitioned in different regions
355 corresponding to different types of equilibrium points. As already explained in Subsection II B
356 this classification does not depend on ε . There is either a unique equilibrium point (purple region
357 labeled 1EP and only displayed for $\varepsilon = 0.07$ and $\varepsilon = 0.08$) or three equilibrium points (3EP).
358 In fact, we only need to pay attention to regions where the unique equilibrium point is a saddle-
359 focus (region SF in the plots) or a saddle-node (regions SN1 and SN2 in the plots). Distinction
360 between regions SN1 and SN2 has to do with two different cases for **IF** bifurcations characterized
361 in Subsection II A. Namely, if a **Case C** of **IF** bifurcation is detected for parameter values on

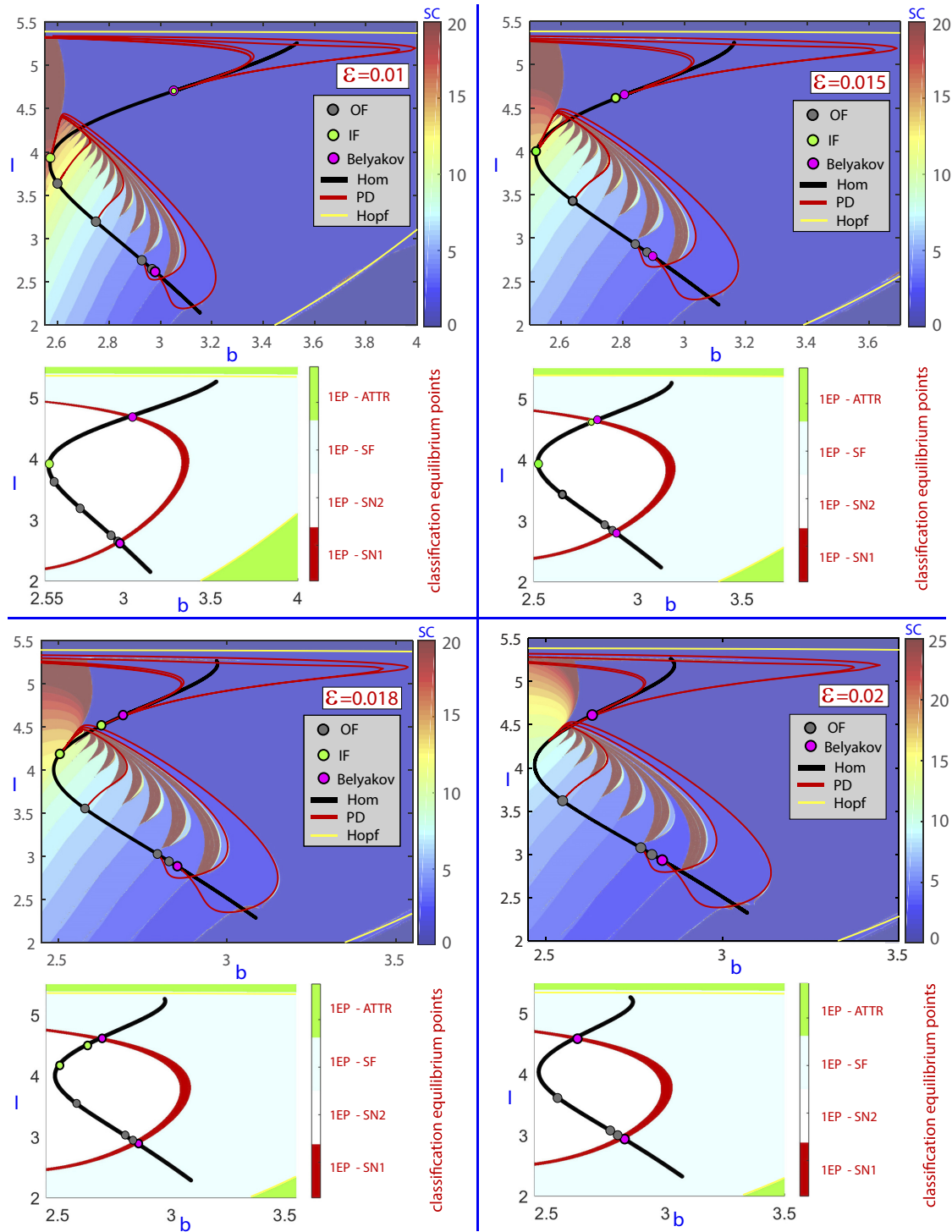


FIG. 5. Parametric plane (b, I) for $\varepsilon = 0.01, 0.015, 0.018, 0.02$. In the upper panel, and for each ε , a SC sweep is overlaid with several bifurcation curves and points. In the lower panel the parameter plane is partitioned in different regions corresponding to different types of equilibrium points. See the text for details about the curves and points displayed.

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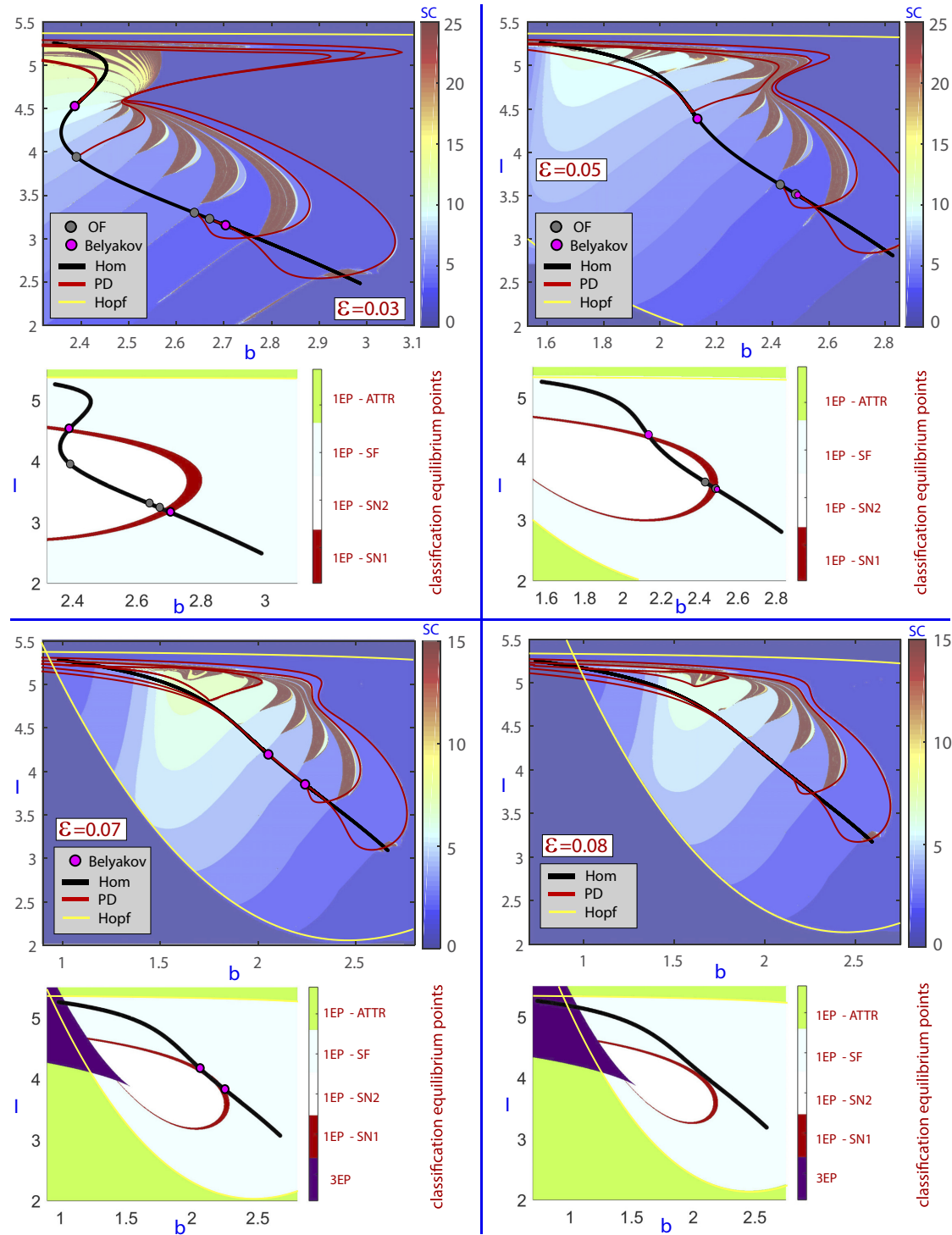


FIG. 6. Parametric plane (b, I) for $\varepsilon = 0.03, 0.05, 0.07, 0.08$. In the upper panel, and for each ε , a SC sweep is overlaid with several bifurcation curves and points. In the lower panel the parameter plane is partitioned in different regions corresponding to different types of equilibrium points. See the text for details about the curves and points displayed.

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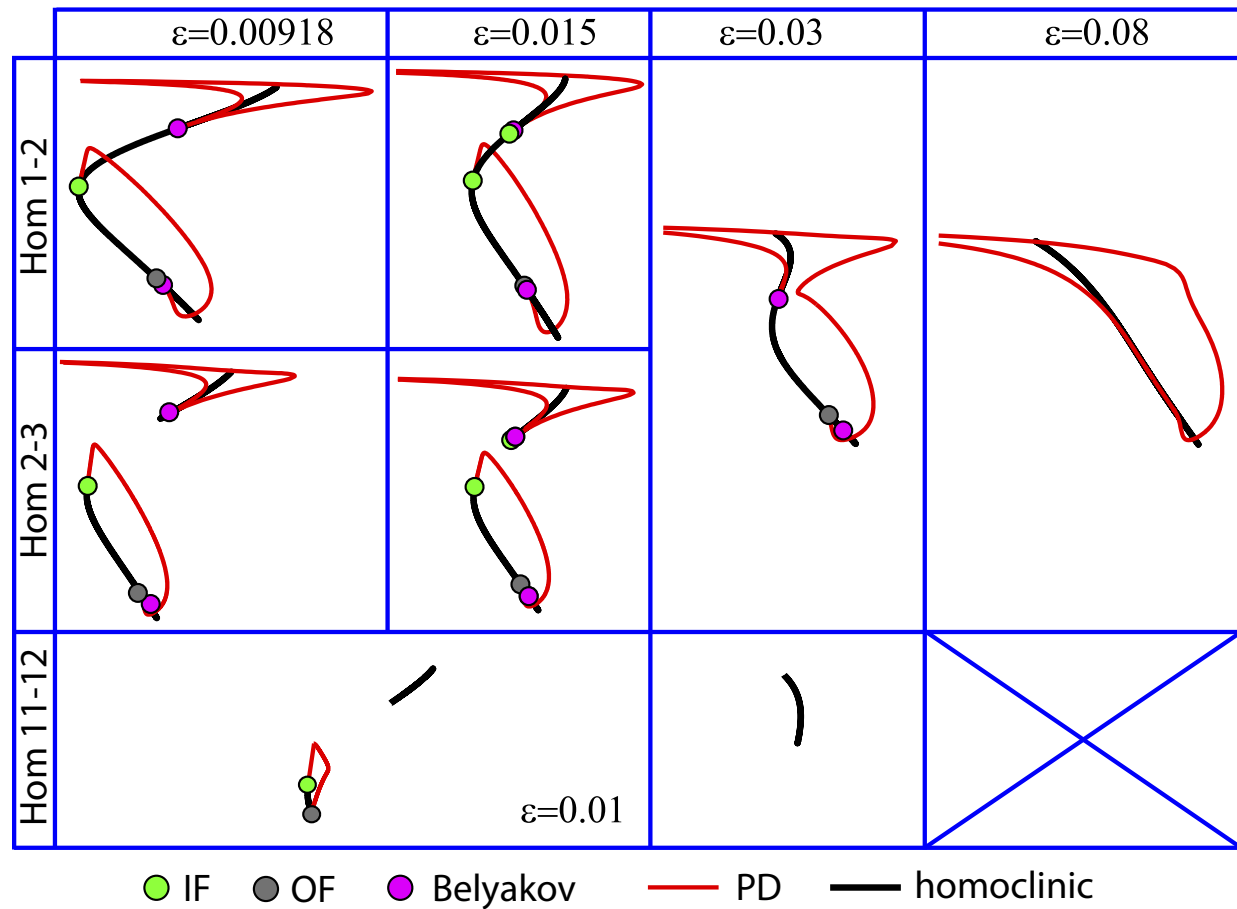


FIG. 7. Global schemes with the different possibilities on the plane (b, I) when the small parameter ε changes. The schemes shown correspond to the obtained results from AUTO for particular values of ε .

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362 SN1 (resp. SN2), hence eigenvalues correspond to the region C_1 (resp. C_2) shown in Fig. 2
 363 (left). Moreover, eigenvalues at the saddle-node point for parameter values in regions SN1 and
 364 SN2 correspond to region C in Fig. 2 (right), where the cases for the OF bifurcations are shown.
 365 In short, all IF and OF bifurcations are in **Case C**. Lower panels also display the curve $hom^{(1,2)}$
 366 to understand all the different types of homoclinic bifurcations: saddle-focus homoclinic orbits
 367 along sections contained in region SF and saddle-node homoclinic orbits along sections contained
 368 in regions SN1 and SN2.

369 Several changes can be observed as ε increases. First of all, as we have already noted in Ref. 46,
 370 there is an evolution in the shape of the homoclinic bifurcation curves. For lower values of ε , the
 371 homoclinic bifurcation curves have a C-shape, with just one visible fold (as we can see in the
 372 case $\varepsilon = 0.01$). For intermediate values of ε , the C-shape transforms into a Z-shape, with two
 373 visible folds (see $\varepsilon = 0.03$). Lastly, for higher values of ε , the homoclinic bifurcation curves have

374 no visible folds ($\varepsilon = 0.07$). As shown in Refs. 22, 23, 46, and 47, the C-shape is typical of the
 375 homoclinic bifurcation curves in the fast-slow regime.

376 Another apparent change is the disappearance of some codimension-two bifurcations. Regard-
 377 ing IF points, when ε is small enough (for instance $\varepsilon = 0.00918$) there is only one IF point. When
 378 ε increases a little ($\varepsilon \approx 0.01$) there are two IF points. When $\varepsilon = 0.01$ (see Fig. 5) the upper-
 379 most IF point is superimposed to the Belyakov point. For smaller values of ε , the role of the IF
 380 point is taken by the Belyakov bifurcation point. Besides, for large values of the small parameter
 381 ($\varepsilon \geq 0.02$) there are no IF points. Obviously, these facts need a more detailed analysis provided by
 382 the three-parameter study done in the next section as one may ask him/herself about codimension-
 383 three bifurcation points. Regarding OF bifurcation points, for $\varepsilon = 0.015$ (see Fig. 5) we show four
 384 OF, one for each homoclinic bifurcation curve $hom^{(1,2)}$, $hom^{(2,3)}$, $hom^{(6,7)}$ and $hom^{(11,12)}$ (there
 385 are more OF points on each curve but we just present one to show a scheme). For $\varepsilon = 0.03$ (see
 386 Fig. 6) only three OF remain, due to the disappearance of the one on $hom^{(11,12)}$. In fact, the com-
 387 plete homoclinic curve $hom^{(11,12)}$ disappears, together with the strip corresponding to 11 spikes
 388 per burst. For $\varepsilon = 0.05$ there are two OF points placed on $hom^{(1,2)}$ and $hom^{(2,3)}$ (more strips have
 389 disappeared). Finally, for $\varepsilon = 0.07$ no OF have been found (although there are some bands with
 390 bursting dynamics). Again, all these changes ask for a detailed three-parameter study. Recall that
 391 attending to the lower panels of Figs. 5 and 6 we can conclude that all OF and IF bifurcations are
 392 in **Case C**. This fact implies the birth of an infinite number of fold and period-doubling bifurcation
 393 curves emerging from these points, as well as infinitely many secondary homoclinic bifurcation
 394 curves with extra passages close to the equilibrium point (see Fig. 2).

395 The bifurcation diagrams on Figs. 5 and 6 also show the disappearance of the Belyakov bi-
 396 furcation points. As ε increases the distance between the two Belyakov points shrinks until they
 397 collapse; for $\varepsilon = 0.08$ there are no Belyakov bifurcation points. Lower panels help to understand
 398 how the Belyakov bifurcation points disappear. As ε increases, the homoclinic bifurcation curve
 399 has a smaller portion in regions SN1 and SN2. Note that the Belyakov bifurcation points appear
 400 when the homoclinic bifurcation curve intersects the borderline between regions SN1 and SF.

401 As it can be observed in the upper panels of $\varepsilon = 0.018, 0.02, 0.03$, qualitative changes in the
 402 period-doubling (PD) bifurcation curves occur for values of ε near to the value for which IF
 403 bifurcation points disappear ($\varepsilon \approx 0.0197$). For $\varepsilon = 0.015$ we have plotted just one of the PD
 404 bifurcation curves emerging from each IF bifurcation point and for each one of the homoclinic
 405 bifurcation curves (in fact the theory³⁷ regarding IF bifurcation points shows that infinitely many

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one-sided PD bifurcation curves emerge, see Fig. 2). A continuation of these curves in the plane
(b, ε) shows that pairs of PD bifurcation curves are transformed into a single curve that persists for
higher values of ε . This fact is a direct consequence of the disappearance of IF points where the
pencils of PD and fold bifurcation curves are born. Therefore, the curves do not have a mechanism
to finish and so they have to continue connecting both branches. Effects of this type have been
already reported in the literature in other contexts (e.g. Refs. 48 and 49).

In order to summarize all the previous results, we show in Fig. 7 the complete global schemes
with the different possibilities on the parameter plane (b, I) when the parameter ε changes. The
schemes correspond to the results obtained for particular values of ε , but each bifurcation diagram
is persistent, that is, it is qualitatively equivalent on any close enough horizontal slice. In the
figure, we show a table in which each row corresponds to a certain transition from n to $n + 1$
spikes, while each column corresponds to a given value of ε . For each n and for each value of
 ε , we show the corresponding homoclinic bifurcation curve(s), the codimension-two homoclinic
bifurcation points and some PD bifurcation curves. Colour codes are those used in Figs. 5 and
6. When two adjacent boxes share the same diagram we mean that the corresponding two cases
are qualitatively the same. When a certain box appears crossed out, it means that there is no
homoclinic structure for the corresponding transition in the number of spikes and for the given
value of ε . This organization allows the reader to have a clear sight of all the different situations
and to understand how the homoclinic structures vary as ε moves and different number of spikes
are considered.

The first row of the table, i.e., the cases associated with 1 spike, has been already discussed.
As it can be easily observed, the main difference between the case $n = 1$ (change from 1 to 2
spikes) and the other cases is that in the latter cases there is no longer a unique homoclinic curve
for all values of ε , but two homoclinic curves exist for low values (this is the first time this fact
is observed in the HR model). Secondly, it is also important to note that the number and the
type of codimension-two bifurcation points vary significantly with n . In the case $n = 2$, for all
the values of ε the codimension-two points present a similar situation to their analogues of 1 – 2
spikes. However, in the case $n = 11$ some of the codimension-two points that appear in the former
cases do not exist (see for example the Belyakov points for $\varepsilon = 0.00918$ and 0.015). Lastly, the
case $n = 11$ reveals that the persistence of the homoclinic structure as ε increases depends on the
number of spikes to which it is associated (see the fourth column, corresponding to $\varepsilon = 0.08$).
This fact suggests the existence of a mechanism of disappearance of the global structures for large

438 number of spikes when ε grows. All these numerical findings and hypothesis underlying these
439 differences will be discussed in the next sections.

440 Note that all the previous discussions make clear that when dealing with fast-slow systems the
441 understanding of the mechanisms of creation and destruction of spikes requires studies in spaces
442 of parameters which include the “small parameters”. It is essential to have a global view of the
443 bifurcations and next sections will stress the relevance of this goal.

444 IV. GLOBAL ANALYSIS CHANGING ε

445 As shown in the previous section, a higher dimensional analysis is needed in the parameter
446 space in order to explain the changes in the bifurcation diagrams observed in planes (b, I) . In
447 this section we will discuss the three-dimensional structures associated to the different homoclinic
448 bifurcation curves we have observed.

449 In Figs. 8, 9 and 10 we provide bifurcation diagrams in the three-parameter space (b, I, ε) .
450 Codimension-one homoclinic bifurcations are shown in black, Belyakov bifurcations in magenta,
451 IF bifurcations in green and OF bifurcations in grey, as in previous pictures of this article. We have
452 calculated curves of codimension-one homoclinic bifurcations with a step of 0.001 in the param-
453 eter ε using AUTO software, in order to visualize surfaces. For each case, the three-dimensional
454 diagram is shown, as well as projections in the planes (b, I) and (I, ε) . These representations allow
455 us to understand the mechanisms of appearance or disappearance of the different codimension-two
456 bifurcation curves. It must be remarked that we have found difficulties for the continuation of OF
457 bifurcation curves with AUTO in the HR model. For that reason, the continuation of OF curves
458 is only partial in Figs. 8 and 9. In the parametric zones where we have been able to obtain the
459 OF points we provide an interpolated curve in grey color. We conjecture, taking into account the
460 points already calculated and the rest of bifurcation curves, that the full OF bifurcation curve in
461 these two cases will be similar in shape to the IF curve. They will show a fold for large ε values,
462 and for $\varepsilon \searrow 0$ they can continue or they can end in either a codimension-three point (such as the
463 IF curve in Fig. 8) or at one turning point of the homoclinic codimension one curves when they
464 have two components (such as the IF curve in Figs. 9 and 10 and the OF curve in Fig. 10). In any
465 case, the numerical results show us a complete picture of the global dynamics of the system.

466 Looking at the first two cases in Fig. 5, we observe how a IF bifurcation point appears close to
467 the upper Belyakov point. If we observe now Fig. 8, we clearly see that it seems that the IF and

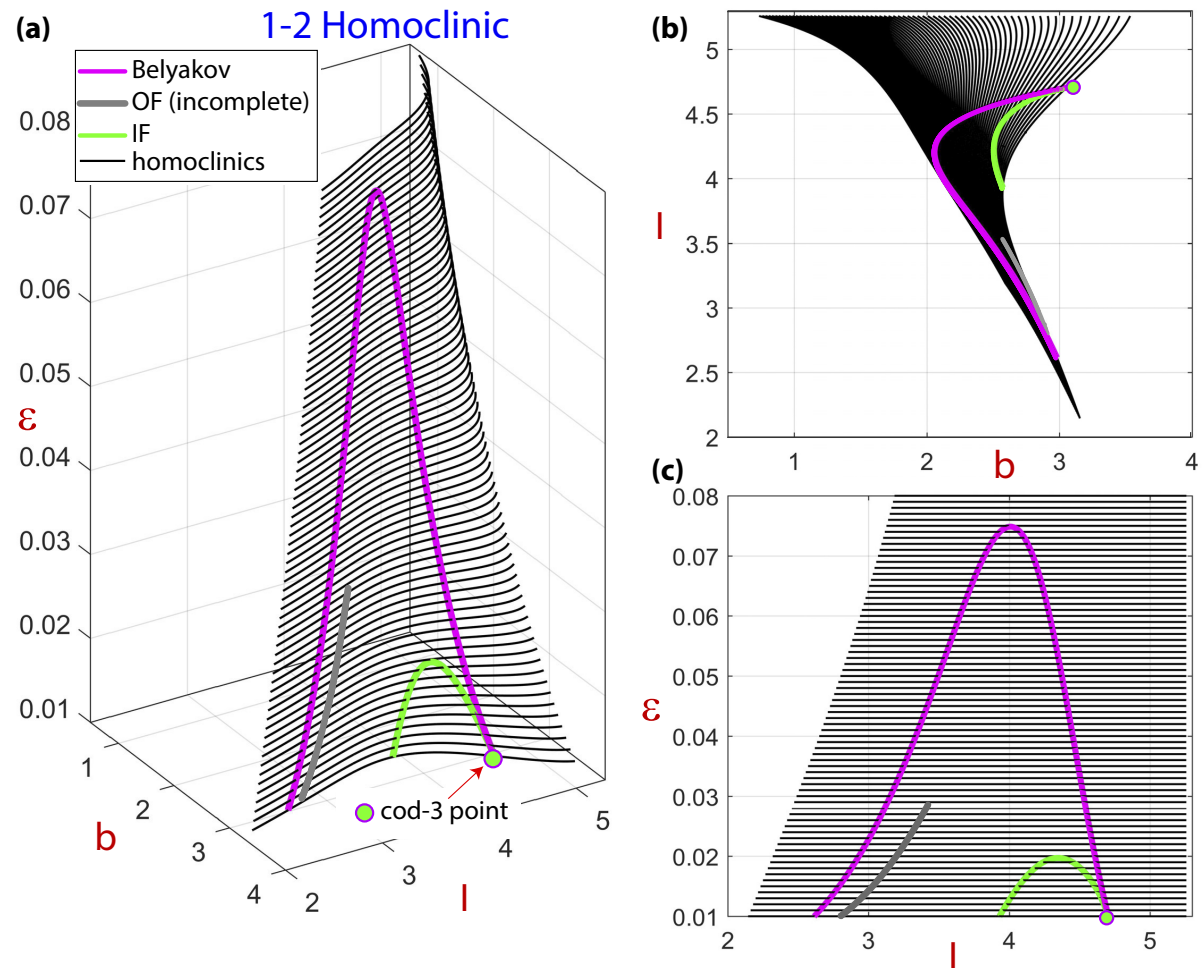


FIG. 8. (a) Three-parameter plot (b, I, ε) for the $hom^{(1,2)}$ homoclinic case; (b) and (c) plane projections. Homoclinic bifurcations of codimension-one and two are shown. The OF bifurcation curve in grey is only part of the complete curve.

468 Belyakov bifurcation curves collide at the numerically obtained parameter values:

$$\varepsilon \approx 0.009189, \quad b \approx 3.102, \quad I \approx 4.713.$$

469 This “collision” would give rise to a codimension-three point that it is not studied in literature,
 470 but it is out of the scope of this article. Besides, it is clear that, in the case $hom^{(1,2)}$ (Fig. 8), the
 471 Belyakov bifurcation points and also the IF bifurcation points disappear due to a folding of the
 472 bifurcation curve with respect to ε (the maxima we can observe in the 3D plots) of their corre-
 473 sponding bifurcation curves in the three-dimensional parameter space. Specifically, the Belyakov
 474 bifurcation curve has its folding point at $\varepsilon \approx 0.0748$ and the IF bifurcation curve at $\varepsilon \approx 0.0197$.

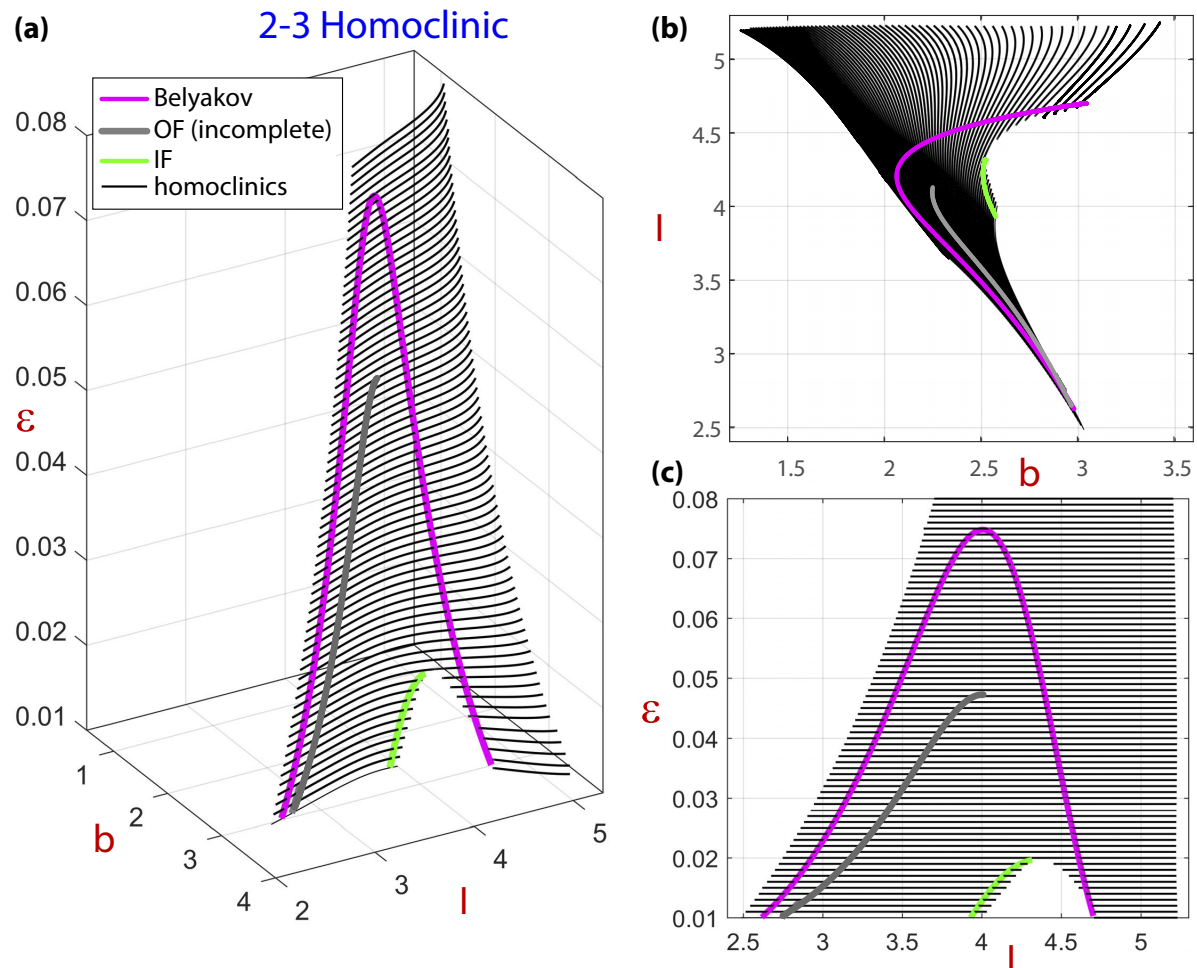


FIG. 9. (a) Three-parameter plot (b, I, ϵ) for the $hom^{(2,3)}$ homoclinic case; (b) and (c) plane projections. Homoclinic bifurcations of codimension-one and two are shown. The OF bifurcation curve in grey is only part of the complete curve.

475 In the case of $hom^{(2,3)}$ (Fig. 9), the Belyakov bifurcation curve presents a similar behaviour to the
 476 $hom^{(1,2)}$ case. However, there is a very important difference in the way the IF bifurcation curve
 477 disappears. Note that curves forming the surface $hom^{(2,3)}$ have two disconnected components for
 478 (fixed) low values of ϵ . In addition, the system ceases to exhibit homoclinic connections in one
 479 of the regions in the parameter space where the geometry of the flow is the appropriate for the
 480 formation of IF bifurcations. This situation appears again in all the codimension-two curves in the
 481 case of $hom^{(11,12)}$ (Fig. 10). Therefore, we can observe a clear difference between $hom^{(1,2)}$ and all
 482 the other cases. This change in the topology of the homoclinic surfaces will be explained in more
 483 detail in Section V.

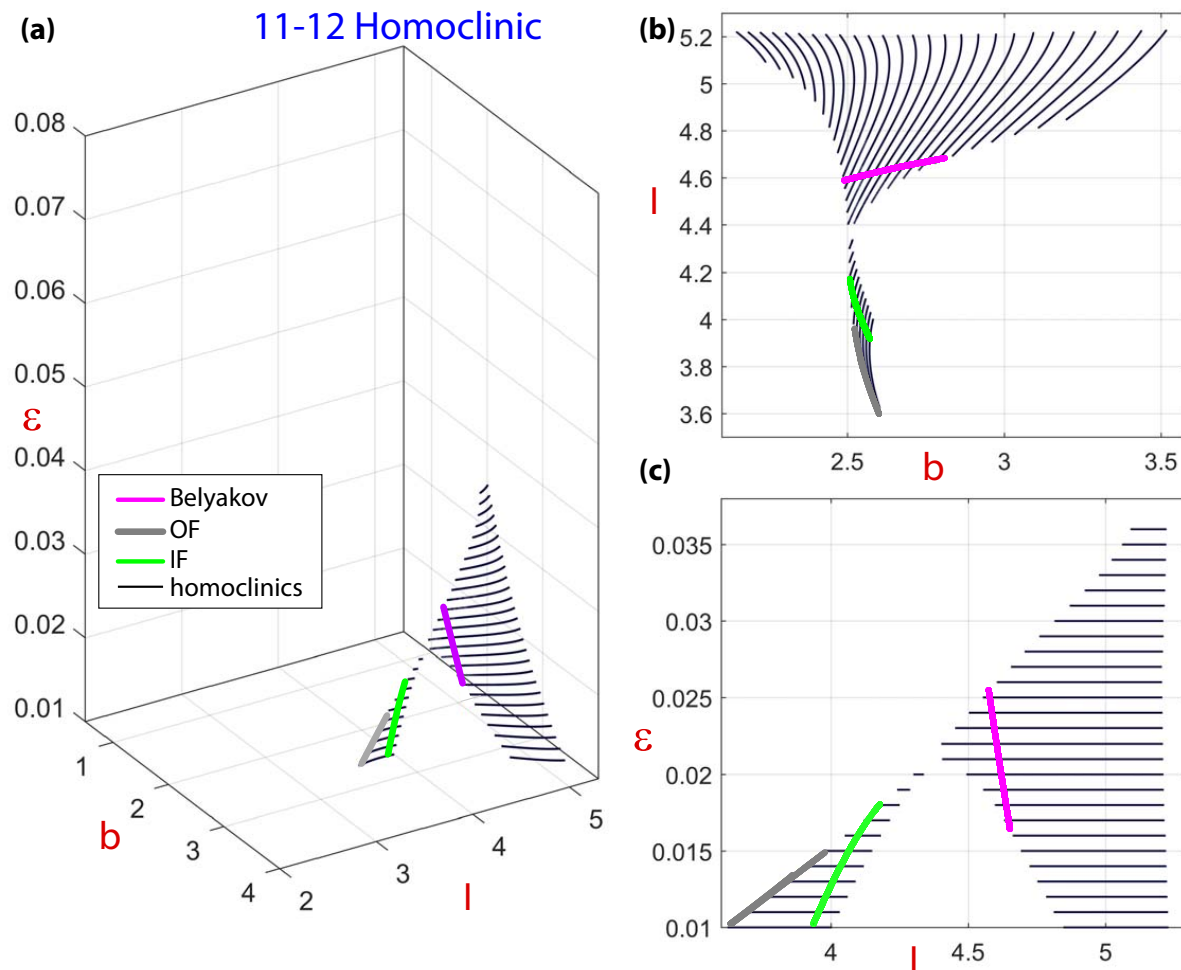


FIG. 10. (a) Three-parameter plot (b, I, ε) for the $hom^{(11,12)}$ homoclinic case; (b) and (c) plane projections. Homoclinic bifurcations of codimension-one and two are shown.

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484 There is also another remarkable difference regarding the values of the small parameter for
 485 which each homoclinic surface disappears. In the cases $hom^{(1,2)}$ and $hom^{(2,3)}$ it can be seen that
 486 the homoclinic curves clearly persist for all the values of ε we have studied, namely up to $\varepsilon = 0.08$.
 487 Note that for larger values we cannot consider the system as a fast-slow one. However, in the
 488 case $hom^{(11,12)}$ the homoclinic surface has disappeared at $\varepsilon \approx 0.038$. Using the SC technique we
 489 discover band structures in the parameter planes with ε fixed, as shown in Figs. 5 and 6. Each
 490 band is associated to a given number of spikes per burst. The spike-adding process in fold/hom
 491 bursters was connected recently^{25,50} with saddle-type canards^{51,52}. Besides, the necessary fold
 492 bifurcations of periodic orbits of the spike-adding process for fold/hom bursters were also recently
 493 connected with codimension-two homoclinic bifurcation points, and also the homoclinic orbits

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494 experiment a canard phenomena on one turning point of the homoclinic bifurcation curves^{15,27}.
495 Our numerical findings also support this idea, as they show clearly that the disappearance of a
496 band corresponding to n spikes is linked to the disappearance of the corresponding homoclinic
497 curves (surfaces) $hom^{(n,n+1)}$. This is a quite important consequence of the three-parameter plots,
498 as they explain the simplifications that are observed in the band structure of the fold/hom regime
499 as ε increases, giving rise to burst phenomena with a small number of spikes (see in Figs. 5 and 6
500 how the number of color stripes decreases when ε grows).

501 All the above mentioned features, together with the SC sweeps, suggest that the bigger the
502 number n of spikes is, the smaller is the value of ε for which the corresponding homoclinic curve
503 vanishes. Moreover, the numerical results show that the different homoclinic curves are stacked in
504 a certain direction, being $hom^{(1,2)}$ the first one, providing an upper bound for “length and shape”.
505 The other homoclinic surfaces are disposed, exponentially close each other, as slabs in increasing
506 order with respect to number of spikes per burst, but decreasing their size.

507 We have checked that Belyakov and IF bifurcation curves of different number of spikes overlap
508 with each other in all the points in the (b, I, ε) where they coexist (they are exponentially close each
509 other, like the homoclinic bifurcation surfaces). One can understand that the magenta (Belyakov)
510 and green (IF) curves are placed in fixed location in all the diagrams due to the requirements for
511 their existence, and the existence or not of bifurcation points for some of the ε values depends if the
512 corresponding homoclinic bifurcation curves (black curves) cut them. However, OF bifurcation
513 curves corresponding to different number of spikes do not coincide with each other, and in fact
514 they are quite far. This behaviour is consistent with the role of OF bifurcation points in the spike-
515 adding process as stated in Refs. 15, 20, and 27.

516 What remains in the numerical tests is to reveal what is the aspect of the homoclinic surface in
517 all cases, that is, if it is just a one leave surface or it has folds and it is a two (or more) leaves surface.
518 This is in fact a relevant question as it will give the global structure of the homoclinic leaves. We
519 are going to show the structure of isolas displayed by the different homoclinic bifurcation curves,
520 once the parameter ε is fixed. We do not pay much attention to explain the transitions from n to
521 $n + 1$ spikes on a given curve or surface (for details of this process see Refs. 27 and 31) on both
522 sharp folds of the isolas. Isololas are isolated closed curves of solution branches, hence the curve is
523 homotopic to a circle. In literature there are several examples of isolas of equilibria^{53,54} or limit
524 cycles^{55–57}. Computing many isolas is tedious and requires an adequate strategy. For instance, in
525 Ref. 53, the authors develop a strategy for locating families of isolas of equilibria. In this article

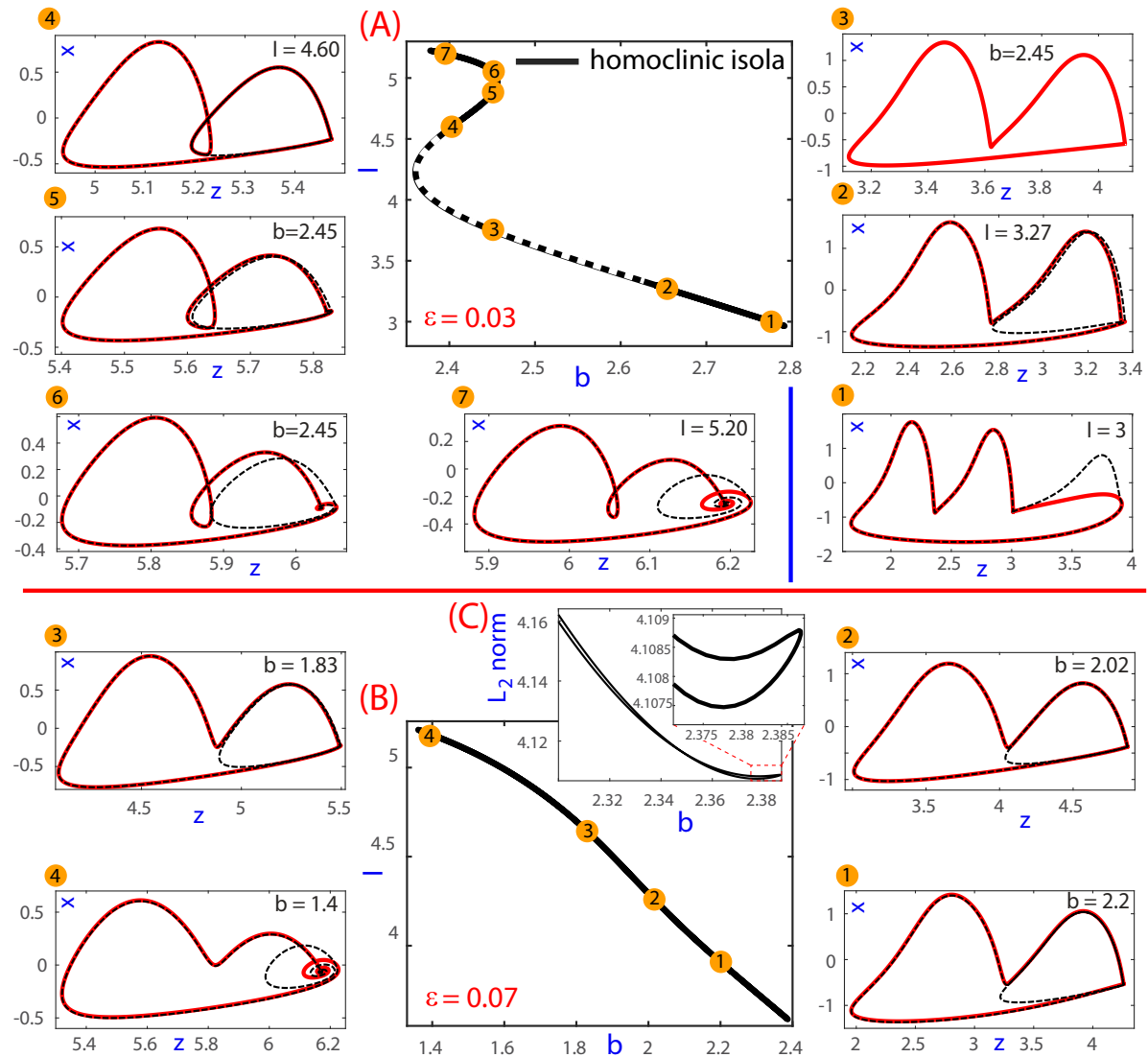


FIG. 11. Codimension-one homoclinic isolas in the parameter plane (b, I) for the surface $hom^{(2,3)}$. Sections $\epsilon = 0.03$ (A) and $\epsilon = 0.07$ (B) are shown. On both cases several xz projections of two homoclinic orbits on the curve for fixed values of either I or b parameter are displayed. In the case $\epsilon = 0.03$ the black-and-white portion denotes where the AUTO software is not able to connect one side of the isola. Displayed on panel C we observe magnifications of the sharp fold located on the left side of the isola, but on a plane $(b, \|\cdot\|_2)$.

526 we focus on the detection of isolas of homoclinic orbits (see also Ref. 58) in the parameter space.

527 By performing sections on the surface $hom^{(2,3)}$ and using AUTO, with a large number of points
 528 and steps to guarantee some numerical precision in the computations, we have obtained the results
 529 given in Fig. 11. The pictures show codimension-one homoclinic isolas in the parameter plane
 530 (b, I) for $\epsilon = 0.03$ (panel A) and $\epsilon = 0.07$ (panel B). In the case $\epsilon = 0.03$ the AUTO software is

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531 not able to connect one side of the isola and adjusting different parameters of the software just
 532 slight increments in the length of the bifurcation curve is obtained (the black-and-white portion of
 533 the homoclinic curve denotes where the AUTO software stops the computation in one side). On
 534 the other hand, for higher values ε , like $\varepsilon = 0.07$ shown on panel B, the software is able to connect
 535 both sides of the isola giving a close curve. On both cases several xz projections of two homoclinic
 536 orbits on the curve for fixed values of either I or b are displayed. The study of what happens at the
 537 right sharp fold of the homoclinic curve is explained in detail in Fig. 6 of Ref. 27 (this corresponds
 538 with the subplot –1– of the case $\varepsilon = 0.03$), but the complete evolution along the isola is not given
 539 in that article. For $\varepsilon = 0.03$, the passage through the milder visible folds (compared with the sharp
 540 U-turns of both extremes of the isolas) of the homoclinic curve exhibit no bifurcations as the plots
 541 xz along the isola show (–3– to –4–, and –5– to –6–). It is important to remark that taking the
 542 homoclinic orbits close to the values of the parameter where the continuation software stops for
 543 $\varepsilon = 0.03$, subplots –2– and –4–, the different orbits show exactly the same behaviour, with just
 544 small modifications (as it also shows the intermediate subplot –3– for one side). Therefore, it
 545 is perfectly logical to conjecture in this case that both sides of the curve are connected giving an
 546 isola, even more taking into account the results for $\varepsilon = 0.07$ where the isola is fully obtained. Note
 547 that in Ref. 27 the homoclinic isolas and the homoclinic organization were not detected as their
 548 main interest was the spike-adding and canard process of the homoclinic orbits on the lower-right
 549 sharp fold of the homoclinic bifurcation curve for ε fixed. In Panel C (Fig. 11) we show two
 550 magnifications of the lower sharp fold of the isola for $\varepsilon = 0.07$. In these zooms, instead of plotting
 551 on the parametric plane (b, I) , we use the plane with b and the AUTO norm L_2 to get a clearer
 552 image of the fold, showing two curves, and thus it illustrates one extreme of the isola.

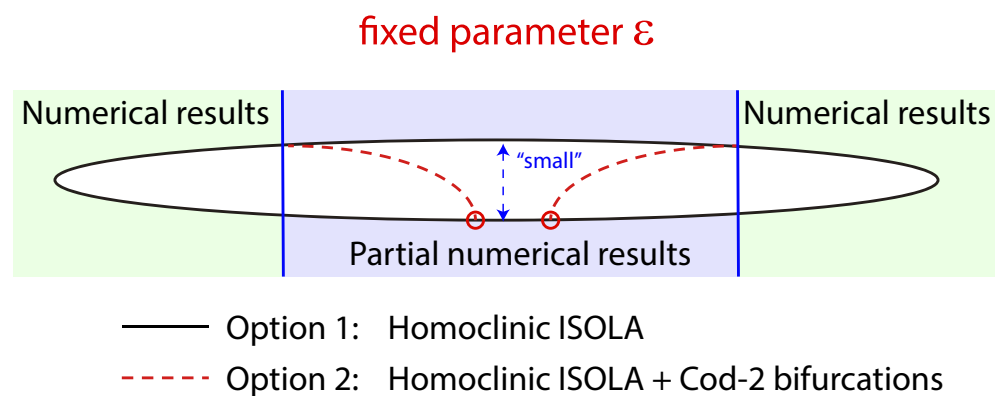


FIG. 12. Theoretical scheme of the codimension-one homoclinic isolas for ε fixed.

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553 In any case, the numerics only can give strong evidences of the existence of the isola. This
 554 fact is shown in the theoretical scheme shown in Fig. 12. The black curve is our conjectured isola
 555 (based in our numerical results), but, as the observed phenomena is on a small distance in the
 556 parameter space (the isola is very “thin”, with a width about 10^{-8}) other options can be possible,
 557 like the existence of foldings in both sides but also some extra homoclinic codimension-two points,
 558 that is, two connected isolas, that are able to give rise to the folds (one option can be the dotted
 559 curve in Fig. 12). In any case, all of our numerical results show that it seems that we really have
 560 isolas, that is, the topological structure of the black curve in Fig. 12.

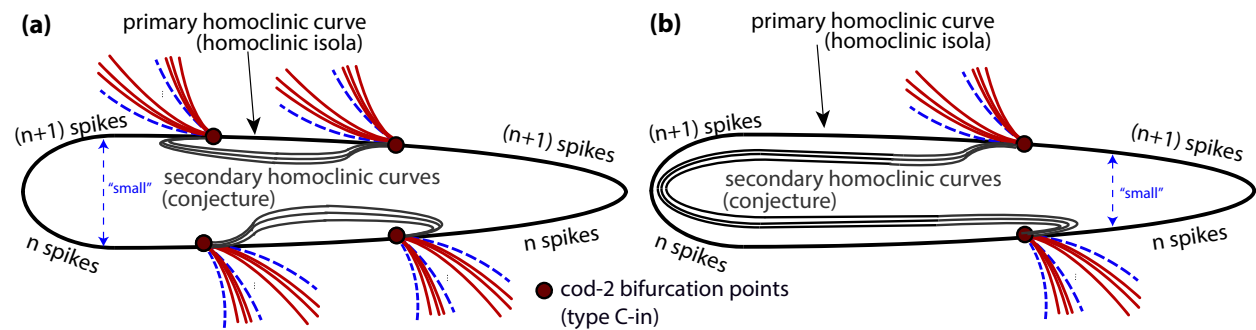


FIG. 13. Conjectured theoretical scheme of the codimension-one secondary homoclinic bifurcation curves for ε fixed for cases with an (a) even or (b) odd number of pairs of codimension-two points.

561 If one looks at the theoretical unfolding of the OF, IF codimension-two points shown in Fig. 2
 562 there is a infinite fan of secondary codimension-one homoclinic bifurcation curves. None of the
 563 numerical simulations on the system (our studies in this article and on Refs. 15, 20, and 46, and
 564 on the Refs. 26 and 27 of other authors) show any of these bifurcations and any dynamical effect
 565 that can be related to them. This fact allows us (as also done in Ref. 27) to conjecture that the
 566 secondary homoclinics are inside the very thin homoclinic isola, and therefore it is not computa-
 567 tionally possible to observe any of them. With these elements we propose in Fig. 13 a theoretical
 568 scheme of the secondary homoclinic bifurcation curves and their connections (in a similar way as
 569 in Ref. 40) in the cases of having an even or odd number of pairs of codimension-two points.

570 As already remarked, it is apparent that there is an overlap between the different $hom^{(n,n+1)}$
 571 bifurcation curves (in fact they are exponentially close to each other as commented above), except
 572 for the higher values of ε where a slight separation can be observed. This separation of the curves
 573 occurs progressively as ε increases, and it can be appreciated for $\varepsilon > 0.07$. In Fig. 14 we show
 574 superimposed the three homoclinic isolas $hom^{(1,2)}$, $hom^{(2,3)}$ and $hom^{(11,12)}$ for $\varepsilon = 0.036$ and

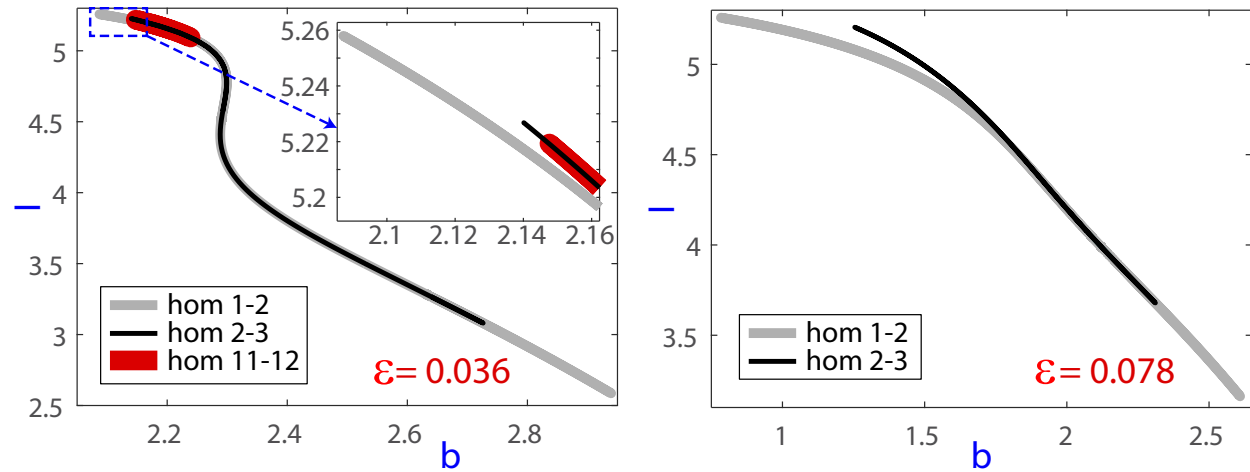


FIG. 14. Homoclinic isolas $hom^{(1,2)}$, $hom^{(2,3)}$ and $hom^{(11,12)}$ for $\varepsilon = 0.036$ and $\varepsilon = 0.07$ showing their relative position.

575 $\varepsilon = 0.07$ to show that the isolas are outside one each other but exponentially close.

576 V. THEORETICAL SCHEME: THE HOMOCLINIC “MILLE-FEUILLE”

577 In Section IV we have explored the three-dimensional parameter space of the HR model con-
 578 sidering in detail the homoclinic structure. What it remains is to provide a complete theoretical
 579 scheme that connects all the basic ingredients of the spike-adding process in fold/hom bursters.
 580 That is, on one hand we have that in the parameter-space the system experiments the spike-adding
 581 process far from the homoclinic bifurcations. On the other hand, the spike-adding process requires
 582 of two fold bifurcations to give rise a hysteresis phenomena and canards on one side to generate
 583 the extra spike (see Refs. 20, 25, and 50). But where are generated these fold bifurcation points?
 584 These points form bifurcation curves that are born at codimension-two bifurcation points located
 585 on the “far-away” homoclinic bifurcation lines. All the bifurcation lines, in fact pencils of fold and
 586 PD bifurcation lines, are born, like the “pages-of-a-book” at the OF and IF points of the $hom^{(n,n+1)}$
 587 curves as shown in Figs. 5 and 6 and in Refs. 15 and 27. But there is no reference on the literature
 588 (up to our knowledge) where it is explained globally in the parameter-space why we have more
 589 spike-adding phenomena as $\varepsilon \rightarrow 0$.

590 The numerical findings shown in previous sections permit us to establish a global theoretical
 591 scheme to describe the whole picture (see Figs. 15, 16 and 17). First, in Fig. 15 we show the
 592 different homoclinic surfaces. All of them are composed of one or two tubular structures. As the

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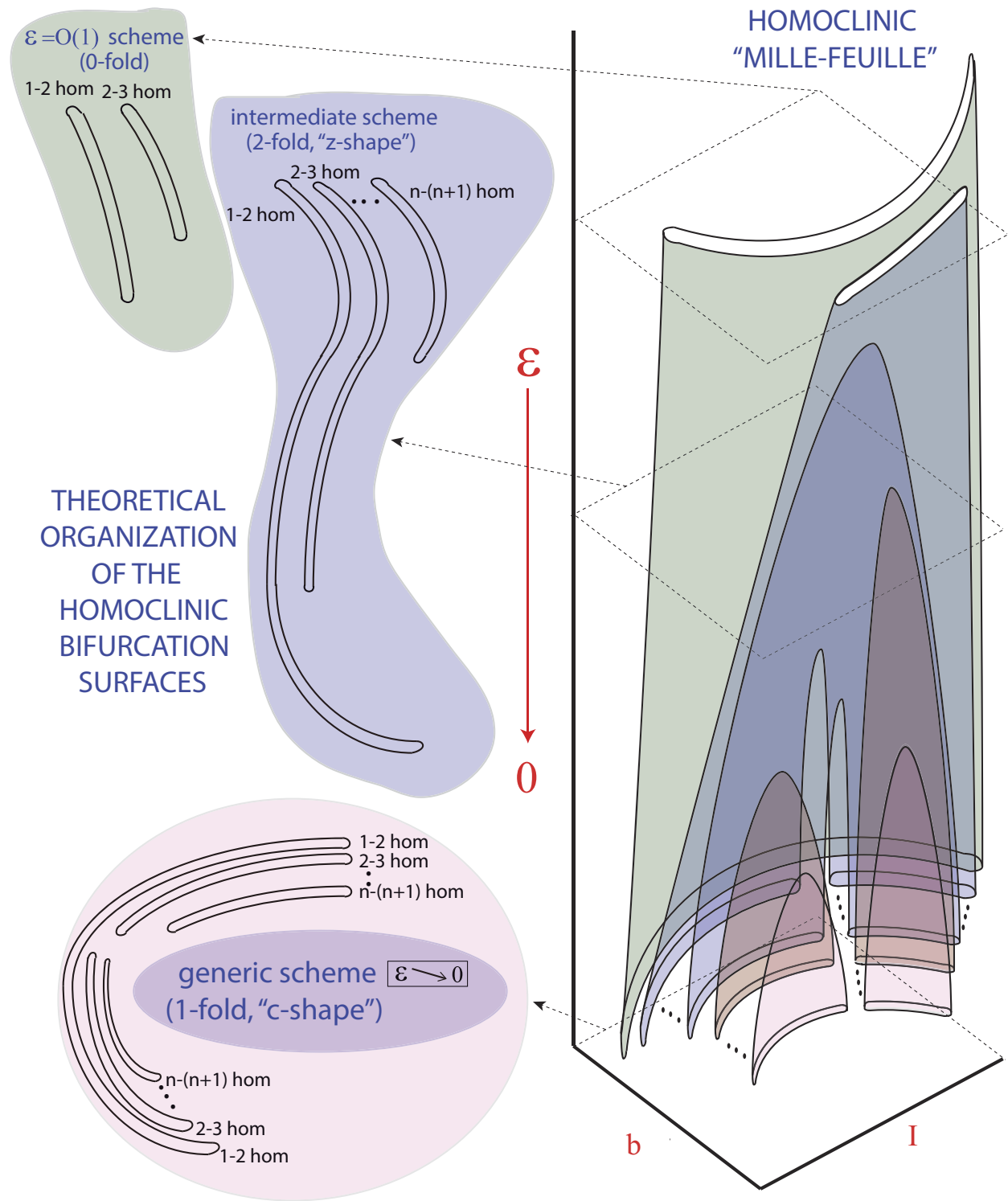


FIG. 15. Homoclinic "mille-feuille" organization in fold/hom bursters.

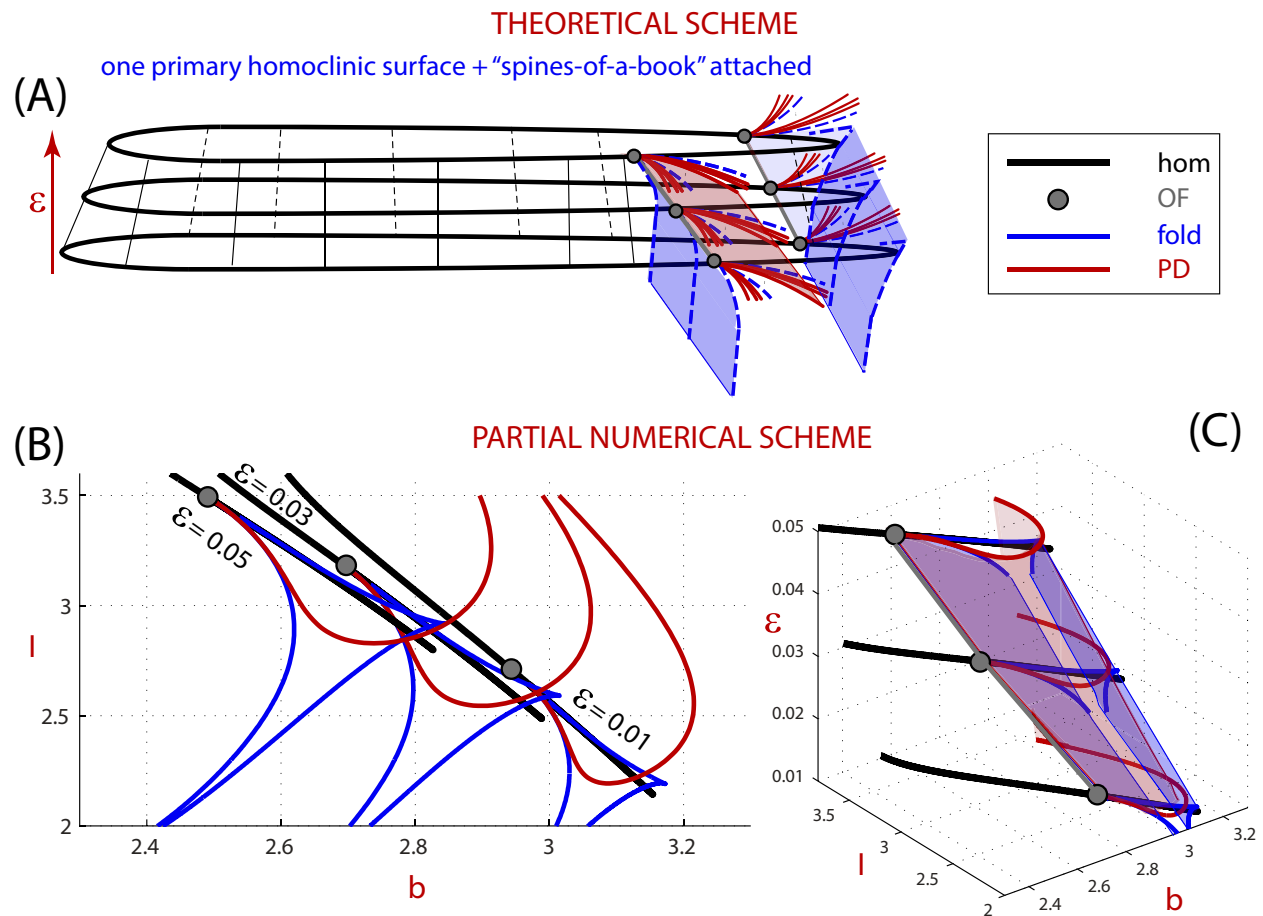


FIG. 16. Theoretical and numerical illustration of the “spines-of-a-book” structure on the $hom^{(1,2)}$ homoclinic surface. Each of the curves of codimension-two homoclinic bifurcations is identified with the “spine-of-a-book” gathering “pages” of fold bifurcations, period-doubling (PD) bifurcations and also (not showed) secondary homoclinic bifurcations. Panel A shows this theoretical model in the case of a “spine” of orbit flip (OF) points. Panels B and C show numerical results illustrating typical “pages” of one of these “books”. Namely, panel B shows numerical slices of a “book” projected on the (b, I) plane. A three dimensional view is given in Panel C. Attached to each “spine” we see two “pages” of fold bifurcation and one “page” of period-doubling.

593 number of spikes of the homoclinic orbit grows we distinguish three types, either a tubular surface
 594 ($hom^{(1,2)}$), or two tubular surfaces connected ($hom^{(2,3)}, \dots, hom^{(k,k+1)}$) or, finally, surfaces that
 595 disappear when ε grows ($hom^{(k+1,k+2)}, \dots$). Note that Figs. 8, 9 and 10 also illustrate numerically
 596 each one of these three types of surfaces. In the scheme, the different homoclinic surfaces are
 597 clearly separated one from each other, but in the real parameter space they are extremely close

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598 when ε is small, being organized in shape and size by the $hom^{(1,2)}$ surface. When ε is large the
599 separation becomes evident, showing that, indeed, these homoclinic surfaces have no contact point
600 when $\varepsilon > 0$ (see Fig. 14).

601 If we take a section fixing the value of ε we find three different situations, already partially
602 described in Ref. 46, depending on the value of ε . When ε is large ($\mathcal{O}(1)$), the slices just show a
603 few homoclinic isolas corresponding to a small number of spikes and without *visible* folds. For
604 intermediate values of ε , the isola corresponding to $hom^{(1,2)}$ have Z-shape with two *visible* folds.
605 The other isolas complete a Z-shape, or not, depending on their length. Finally, for small ε ,
606 that is, in the generic situation when we are concerned with fast-slow systems, the principal isola
607 for $hom^{(1,2)}$ has a C-shape with one *visible* fold. The curves corresponding to $hom^{(n,n+1)}$, with
608 $n \geq 2$, split into two isolas also disposed in such a way that they are adapted to the C-shape of the
609 principal isola. In this case all the homoclinic curves have two components (isolas) but the first
610 one $hom^{(1,2)}$, and all of them have folds with branches exponentially close each other.

611 Due to the fact that, from a certain point of view, homoclinic surfaces are piled up one upon
612 another, we refer to this *conjectured* global theoretical structure as the *fold/hom homoclinic “mille-
613 feuille” organization*. Note that for ε fixed we have a finite number of homoclinic curves, but the
614 number of them grows as ε decreases^{25,33}.

615 Codimension-one homoclinic bifurcations that form each surface $hom^{(n,n+1)}$ must be under-
616 stood as primary bifurcations. These surfaces contain curves of codimension-two homoclinic
617 bifurcation: IF, OF and Belyakov points. Emerging from these curves there exist surfaces of bi-
618 furcation of periodic orbits: PD or folds, some of them involved in the spike-adding process. Also
619 attached to these curves there are surfaces of secondary homoclinic bifurcations arising in the in-
620 ner side of the surface, that is, separated from the surfaces of bifurcation of periodic orbits by the
621 surface of primary homoclinic bifurcations (see case $C(in)$ in Fig. 2). Note that this scenario is
622 covered by the classical unfolding theory of codimension-two homoclinic bifurcations^{37,38}. We re-
623 mark that these unfoldings have to be “glued” to the homoclinic surfaces given by the “homoclinic
624 mille-feuille”. Fig. 16 illustrates the described scenario. Each of these curves of codimension-
625 two bifurcations behaves as the “*spine-of-a-book*” located on the homoclinic surfaces (like the
626 “bookselves” of a “bookcase”) whose “*pages*” consist of surfaces of bifurcations of periodic or-
627 bits and secondary homoclinic bifurcations. The plot 16.A provides the theoretical scheme of a
628 homoclinic surface with the curve of codimension-two bifurcation points that form the “*spine-
629 of-a-book*” structure creating the pencils of surfaces of fold and PD bifurcations. On plots 16.B

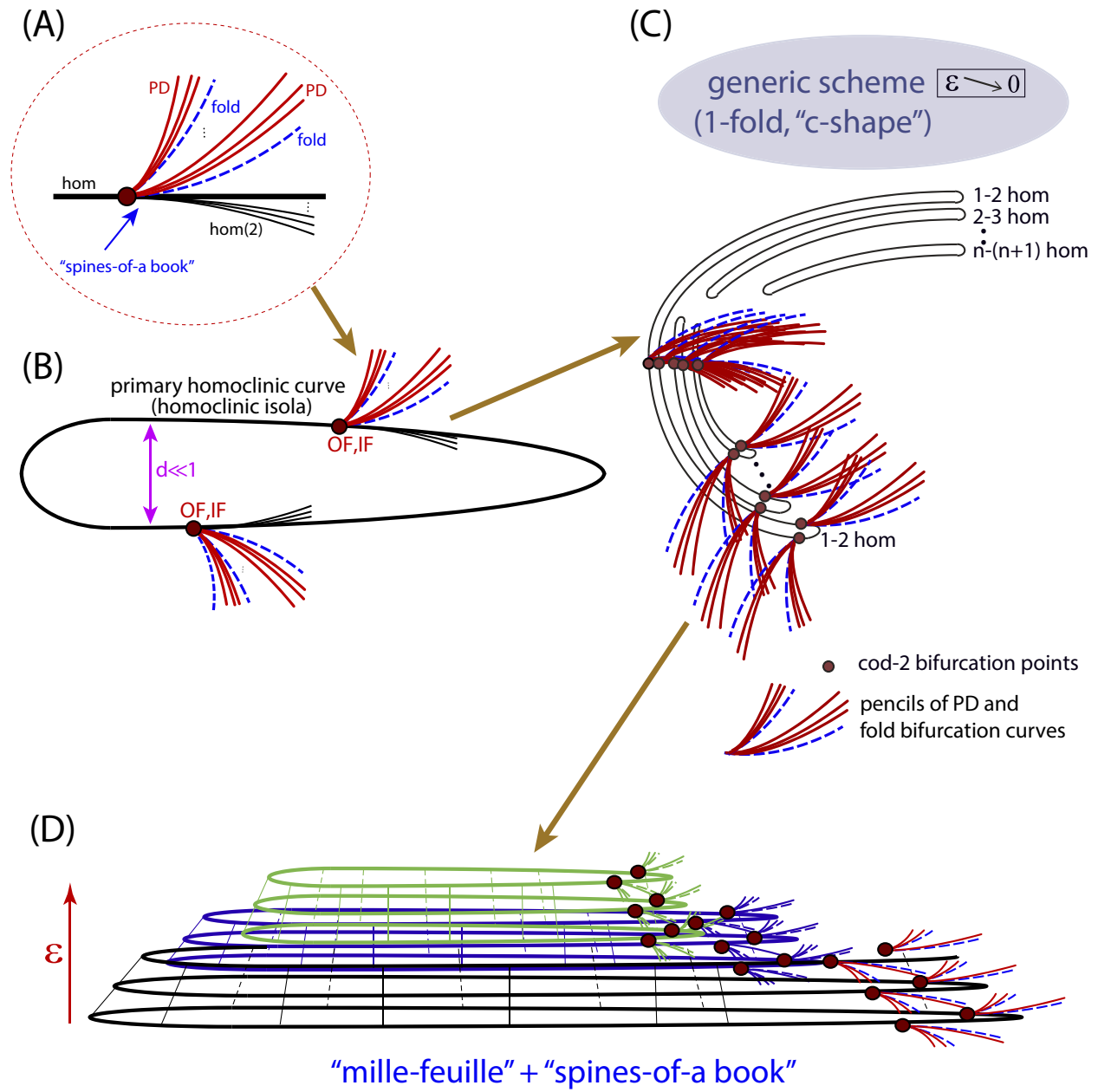


FIG. 17. Complete "mille-feuille" and "spines-of-a-book" theoretical structure. In Panel A we recall the unfolding of the bifurcation diagram associated to a OF bifurcation: there are pencils of PD and fold bifurcation of periodic orbits and also a pencil of secondary homoclinic bifurcations. In Panel B we see how these pencils are attached along a primary homoclinic curve. The isola has an exponentially small width d . Panel C illustrates a collection of isolas for a small value of ϵ . Finally, a three dimensional scheme is provided in Panel D. We see three "bookshelves" (homoclinic surfaces) and with some "books" (codimension-two points and the bifurcations generated) on them.

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630 and 16.C we show some numerical results illustrating such a theoretical scheme. The plot 16.B
631 presents a projection of the homoclinic structure for three values of ε . And on the plot 16.C we
632 see the global three-parametric view illustrating the theoretical scheme proposed in 16.A.

633 Finally, Fig. 17 illustrates the complete “mille-feuille” organization together with the “books”
634 of bifurcation of periodic orbits. Now we can identify each layer of the “mille-feuille” with a
635 “bookshelf” keeping as many “books” as “spines” of codimension-two homoclinic bifurcations it
636 contains. So, we have a complete “bookcase” of bifurcations of periodic orbits. Moreover, we
637 must notice that each surface in the “mille-feuille” has their own collection of “spines”, that is,
638 their own collection of “books”. This figure gives an idea of how much entangled the bifurcations
639 involved in the spike-adding process is. As illustrated in Fig. 17 (Panel B), there are “pages” of
640 the “books” involved in the spike-adding process. We remark that the Fig. 17 provides a complete
641 theoretical explanation of all the numerical findings obtained in this article (and in the literature).
642 Our conjectured theoretical structure permits to link the global three-parametric structure (the
643 homoclinic surfaces) with the spike-adding phenomena that can be observed on parameter regions
644 that are quite far from the homoclinic curves. In addition, if we use another set of parameters,
645 we can also observe the fold/hom spike-adding processes, even without homoclinic bifurcations in
646 the entire parametric plane. This is easily explained from the Fig. 15, as if our parameters do not
647 cut the homoclinic surface we cannot observe the homoclinic orbits themselves. But what remains
648 are the fold and PD surfaces generated on the codimension-two points attached to the homoclinic
649 surfaces, as shown in Figs. 16 and 17. Following with the “bookcase” analogy, this will be the case
650 if we have “books” wider than the “bookshelves”, and we observe it without seeing the bookcase.

651 Obviously, our theoretical scheme is necessary a partial one, as other bifurcations and phenom-
652 ena may be present on the complete global picture, but it englobes all the current numerical and
653 theoretical analysis in literature. This article provides new insights on the spike-adding process
654 and the global parametric study of the Hindmarsh-Rose model. We hope that it may be applied to
655 other fold/hom bursters, and this is part of our future work.

656 VI. CONCLUSIONS

657 In this article we have presented a three-parameter study of homoclinic bifurcations in the
658 canonical Hindmarsh-Rose neuron model when it evolves in the fold/hom bursting regime. We
659 have introduced a new structure, the homoclinic “mille-feuille” connected with the fold/hom spike-

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660 adding process. Fold/hom bursting is found in numerous fast-slow models, and we expect that
661 most of the findings of this article will be present in many similar problems. Exploration of other
662 fold/hom bursters is a goal for our future work, but a preliminary study, as well as the theoretical
663 scheme of the spike-adding process was introduced in Ref. 20.

664 Our numerical analysis using different techniques allows us to conjecture the global theoret-
665 ical homoclinic organization. There exists a “mille-feuille” structure of tubular-like homoclinic
666 surfaces. Each of them corresponds to a transition where the homoclinic orbit increases the num-
667 ber of spikes by one, that is, taking the appropriate paths of parameters, one could observe in the
668 phase-space how the orbits pass from n to $n + 1$ spikes for certain n . Moreover, as ε increases, the
669 disappearance of a homoclinic surface associated to the transitions from n to $n + 1$ spikes means
670 the “de facto” disappearance in the surroundings of the band of periodic orbits with $n + 1$ spikes.
671 This structure provides a theoretical explanation of why there is not a regular fold/hom bursting
672 regime with a large number of spikes when the small parameter grows. Moreover, due to the tubu-
673 lar structures, an analysis for fixed values of the small parameter gives rise to the appearance of
674 isolas of homoclinic bifurcation points.

675 Note that previous relevant studies in literature^{15,26,27} focus their attention on the spike-adding
676 and canard process of the homoclinic orbits on the lower-right sharp fold of the homoclinic bifur-
677 cation curve for ε fixed. The other sharp fold, the isolas and also the complete bifurcation scheme
678 where not identified and studied.

679 Located on each homoclinic surface we find curves of codimension-two homoclinic bifurca-
680 tion. These curves act as the organizing centers for the framework of fold and period doubling
681 bifurcations of periodic orbits which is behind one of the main spike-adding mechanisms. The
682 discovering of the global structure of orbit-flip, inclination-flip and Belyakov bifurcations is one
683 of our main motivations. Homoclinic surfaces can be compared with “bookshelves” where the
684 “books” of bifurcation of periodic orbits are kept. Hence, curves of codimension-two homoclinic
685 bifurcations can be compared with the “spines-of-a-book”.

686 The global structure (homoclinic “mille-feuille” + “spines-of-a-book”) which is revealed in the
687 three parameter space is a motivation for further study of higher codimension bifurcation points
688 which appear on the homoclinic bifurcation surfaces. In fact, the global structure we have uncov-
689 ered gives clues about part of the bifurcations which should be expected when dealing with such
690 bifurcation points (and their connections, in a similar way as some codimension-three phenomena
691 provides a global theoretical picture in Ref. 40). These relevant open problems are out of the scope

692 of this article but they are part of our current research.

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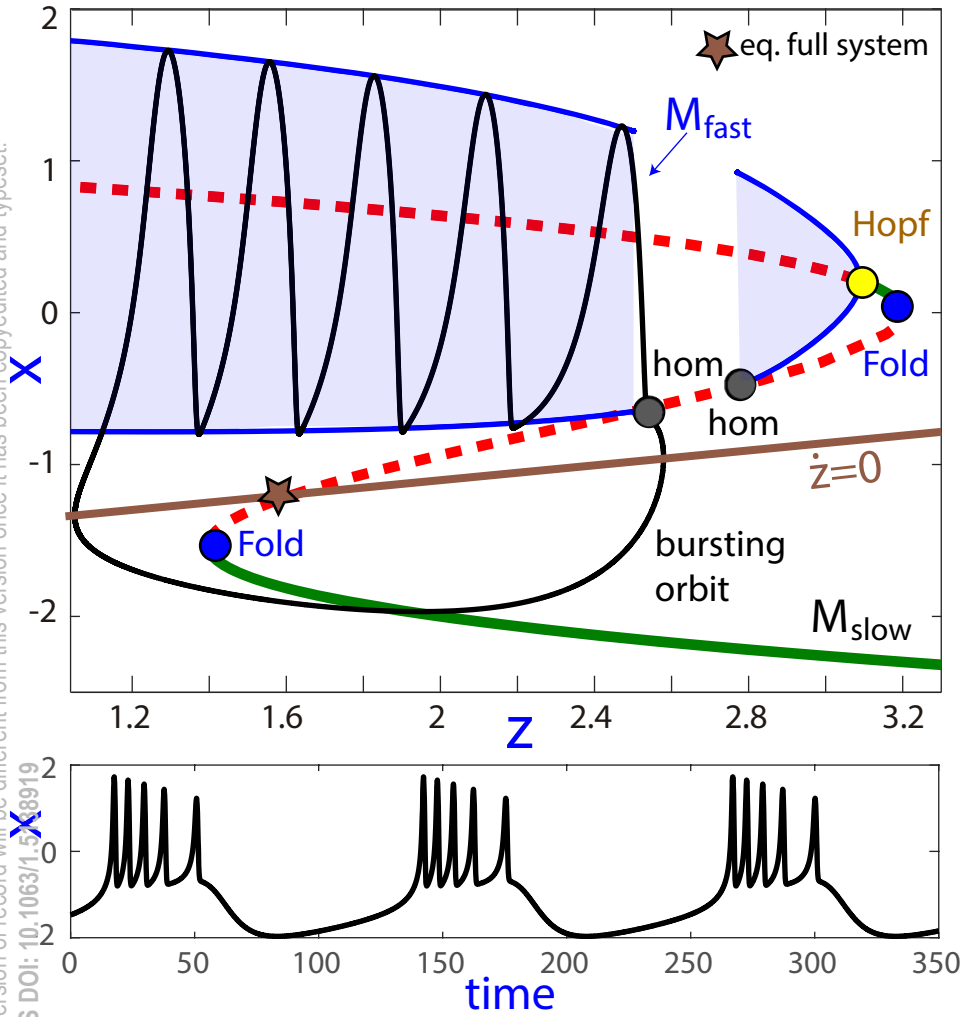
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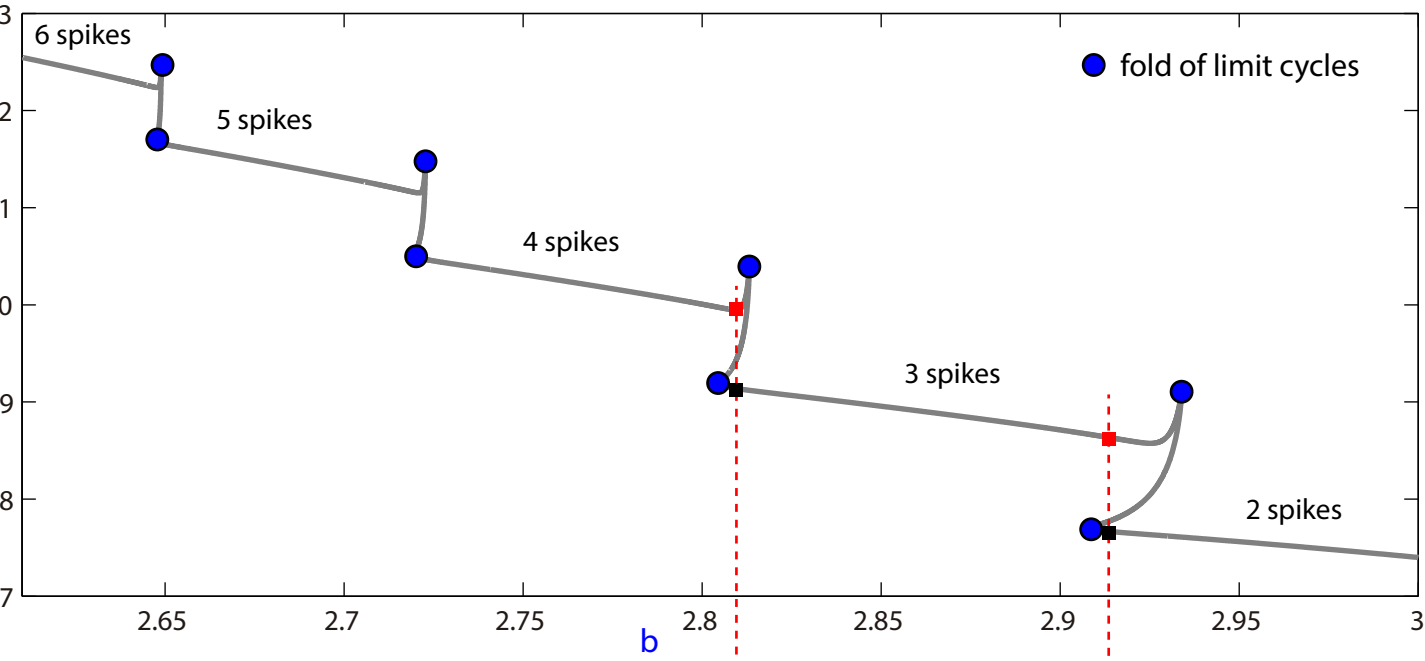
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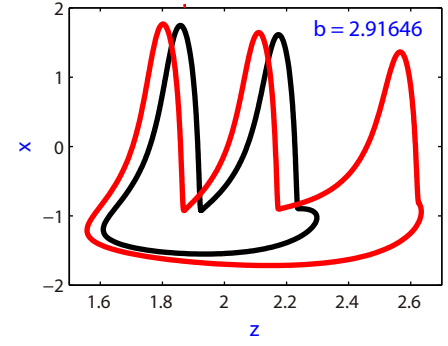
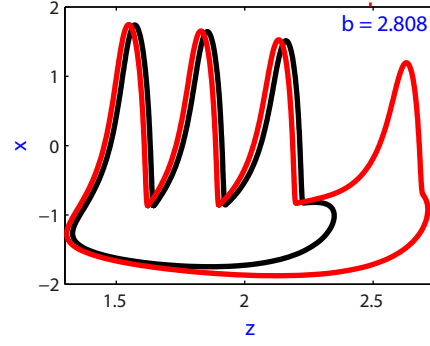
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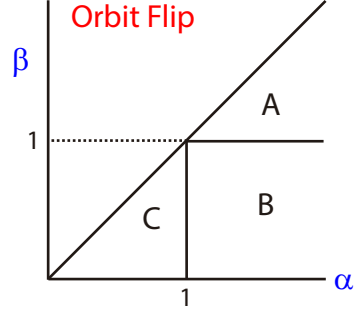
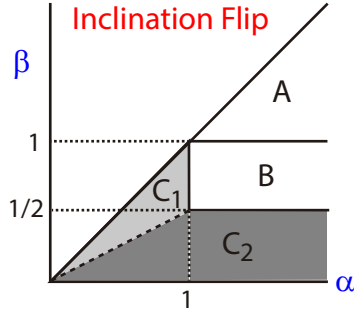
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$$\varepsilon = 0.01, l = 2.2$$

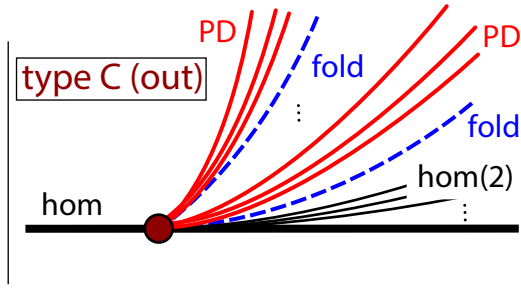
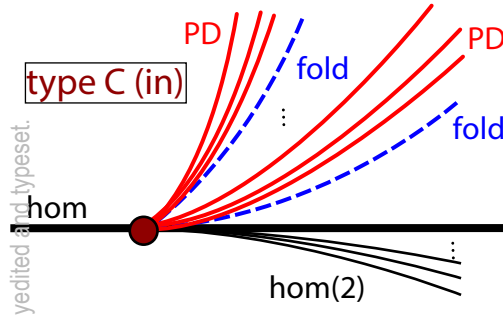


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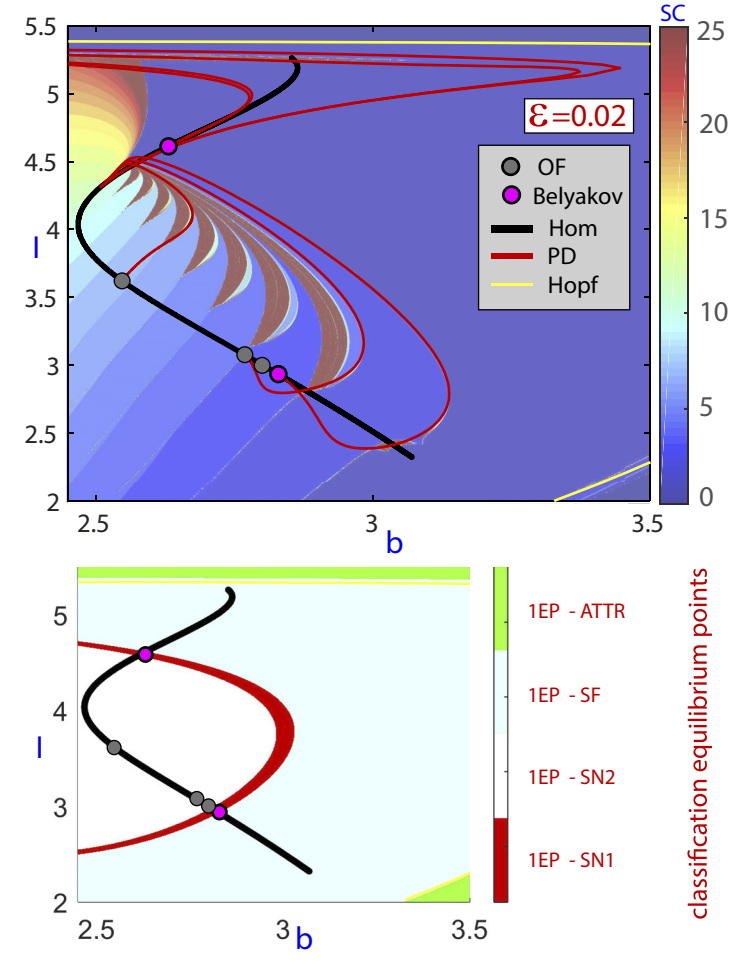
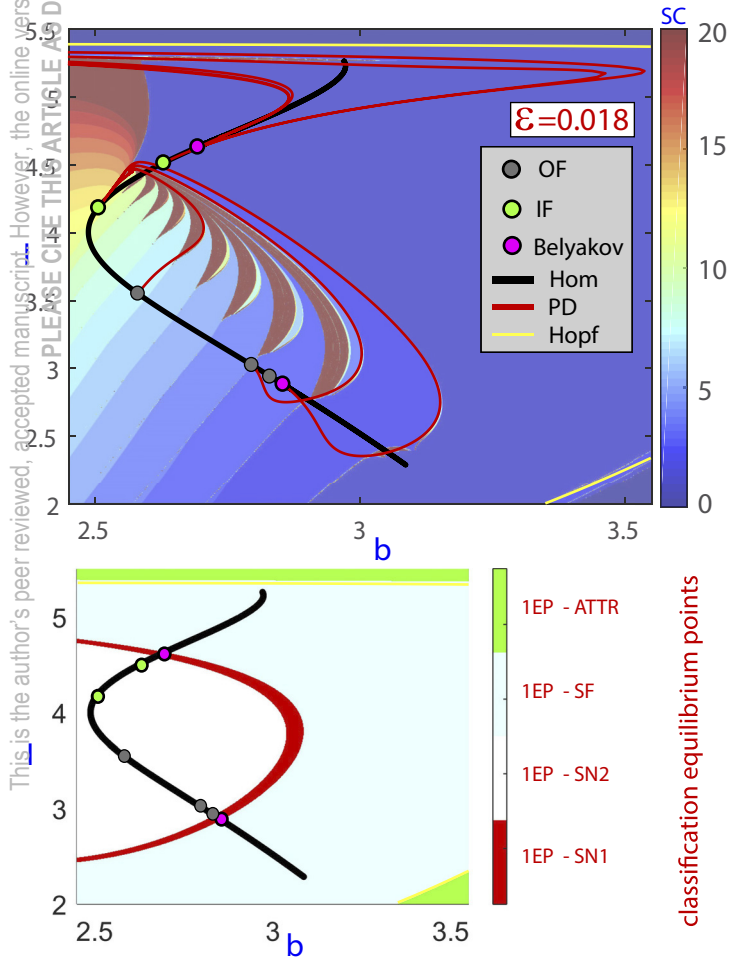
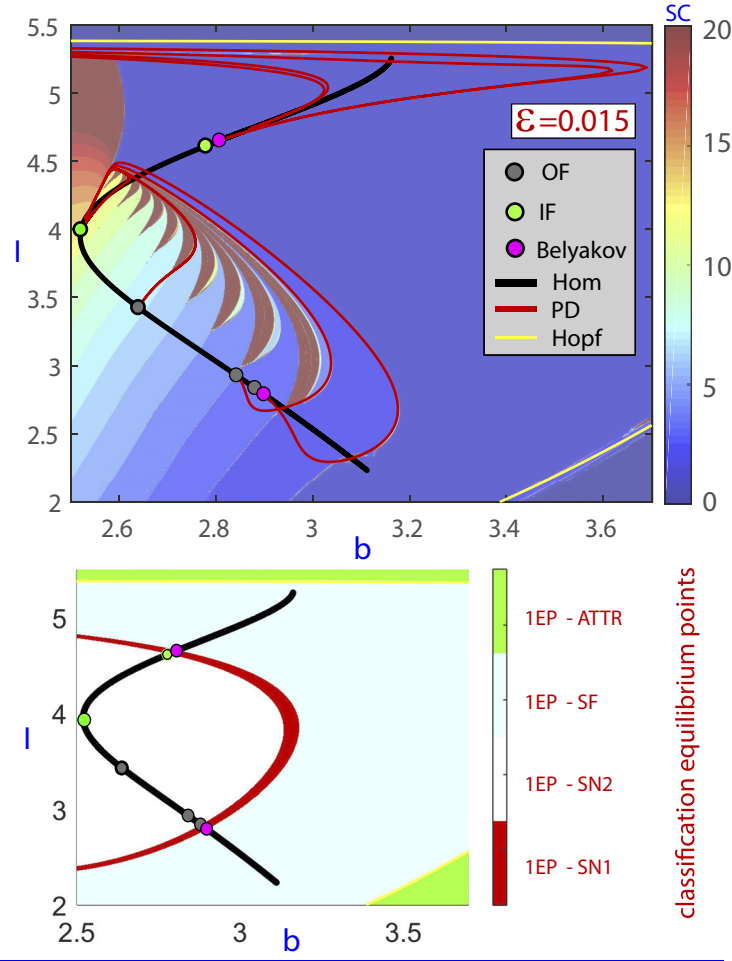
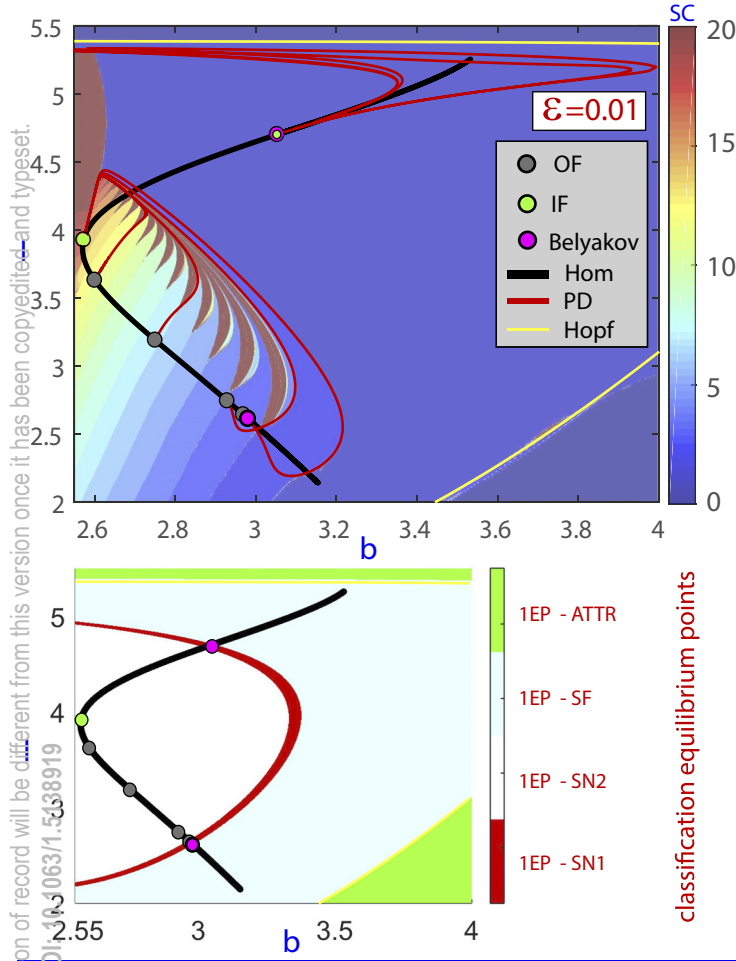


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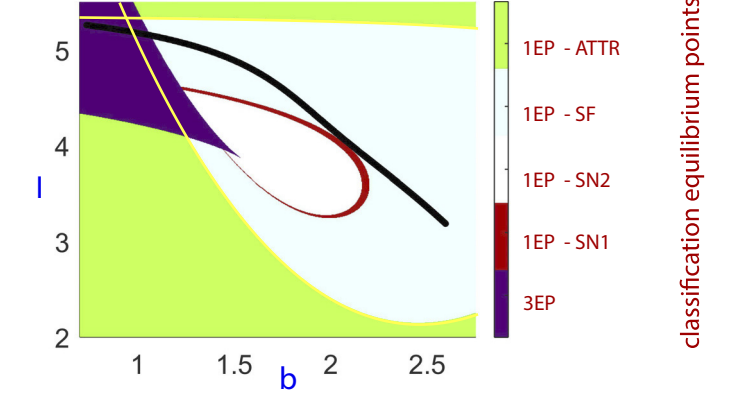
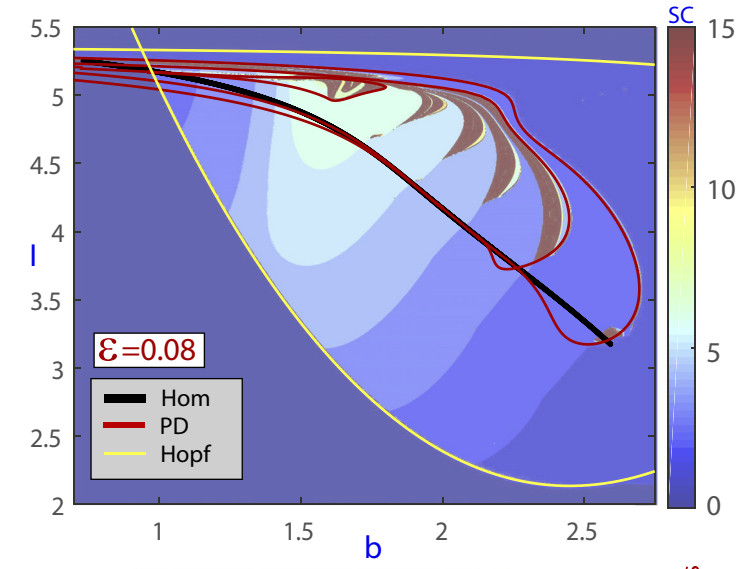
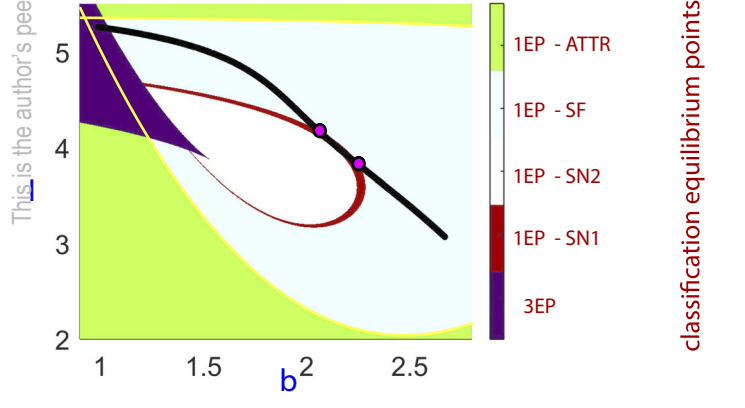
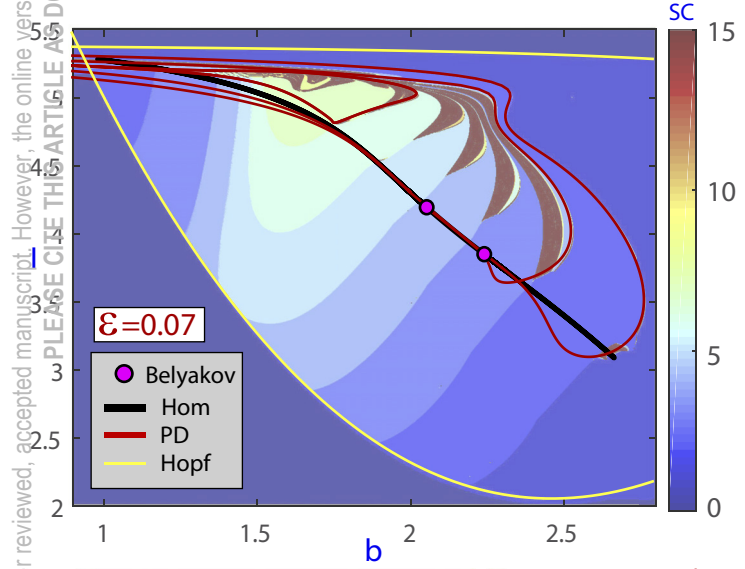
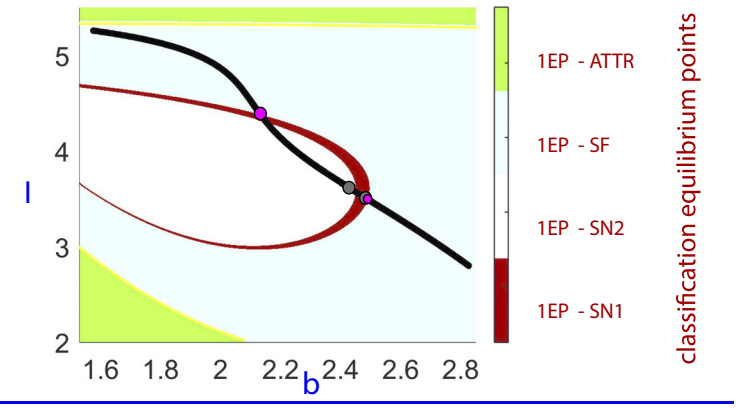
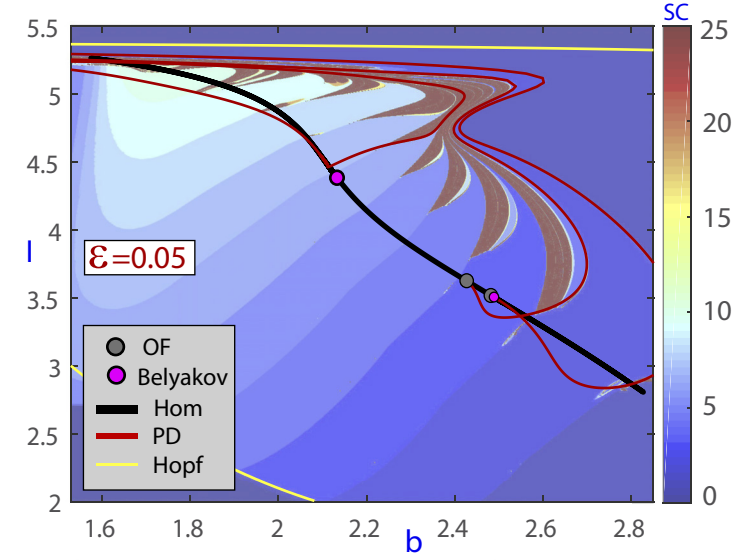
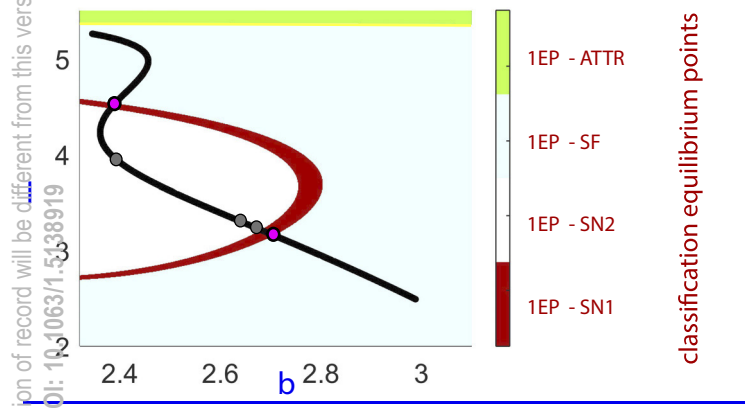
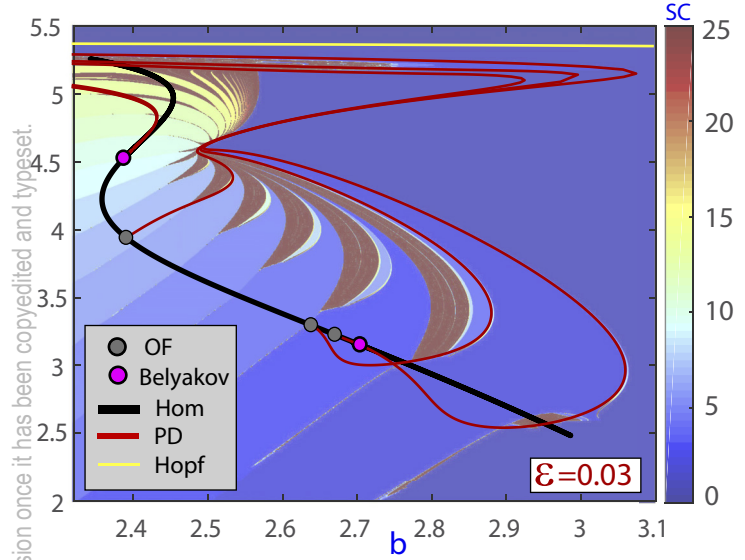
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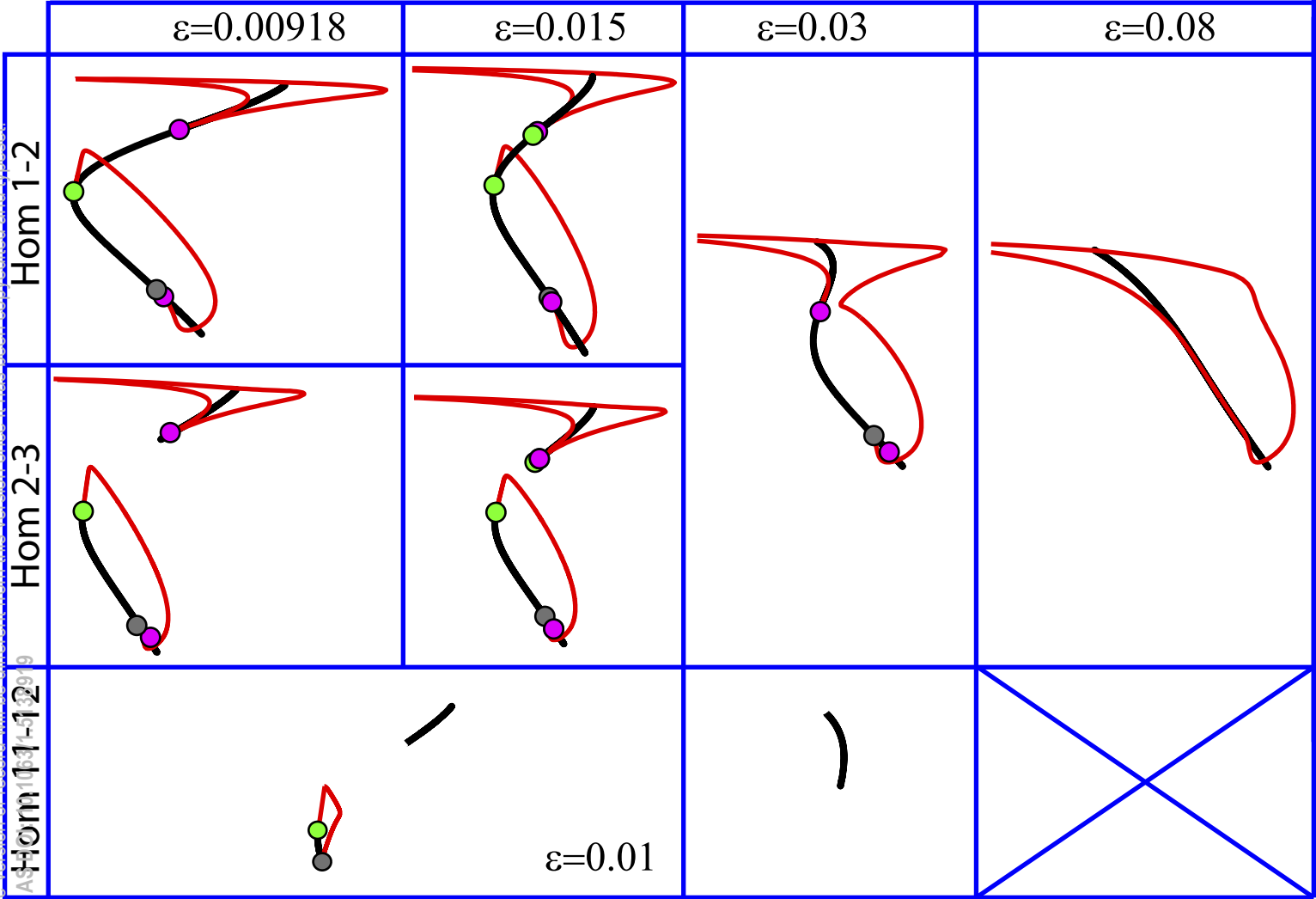
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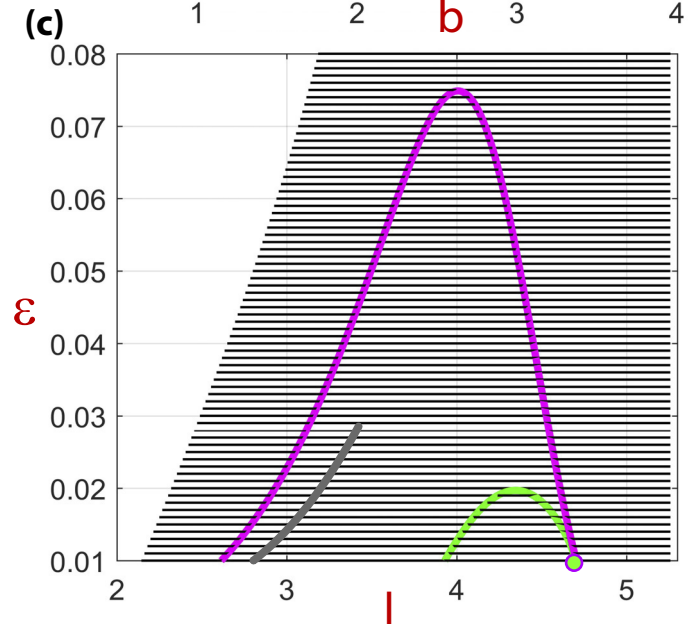
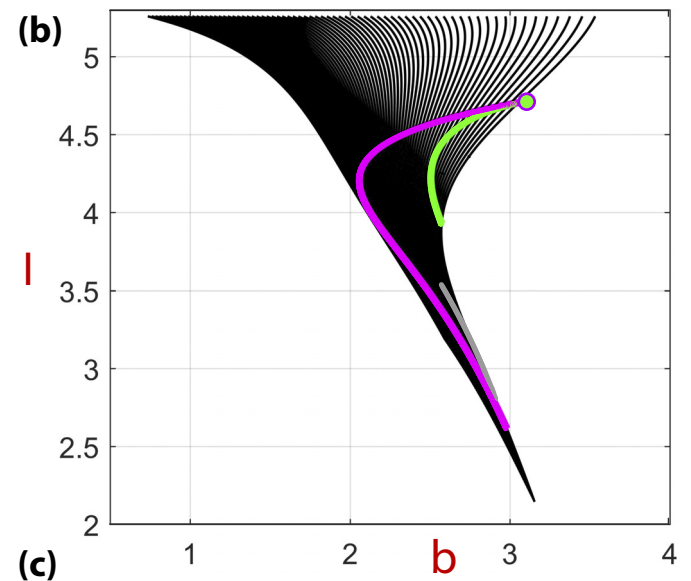
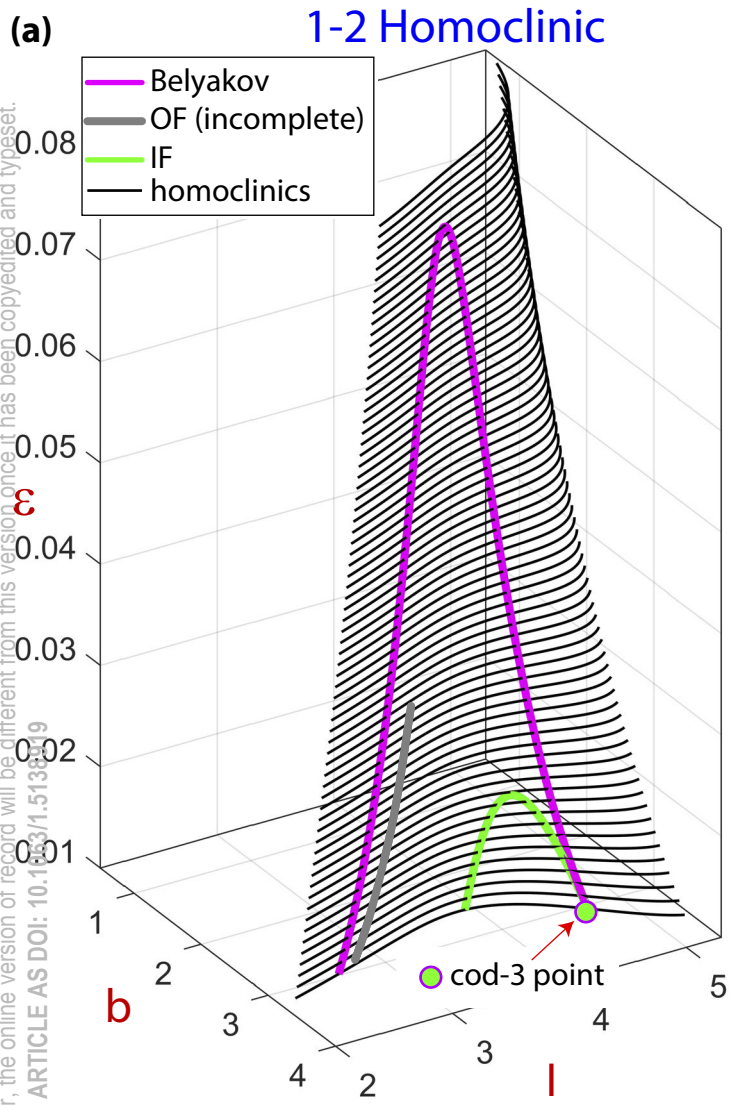
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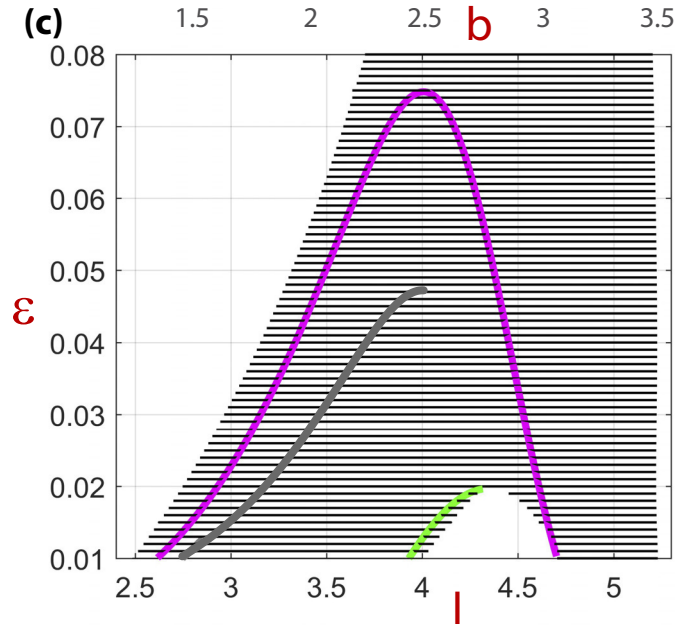
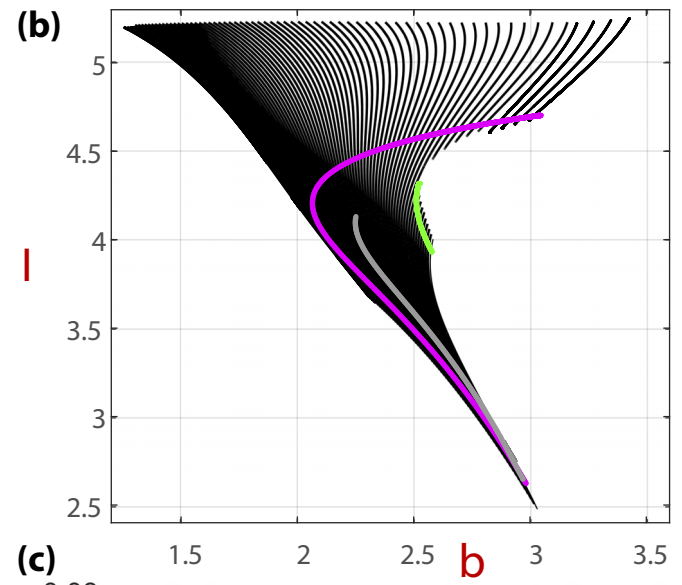
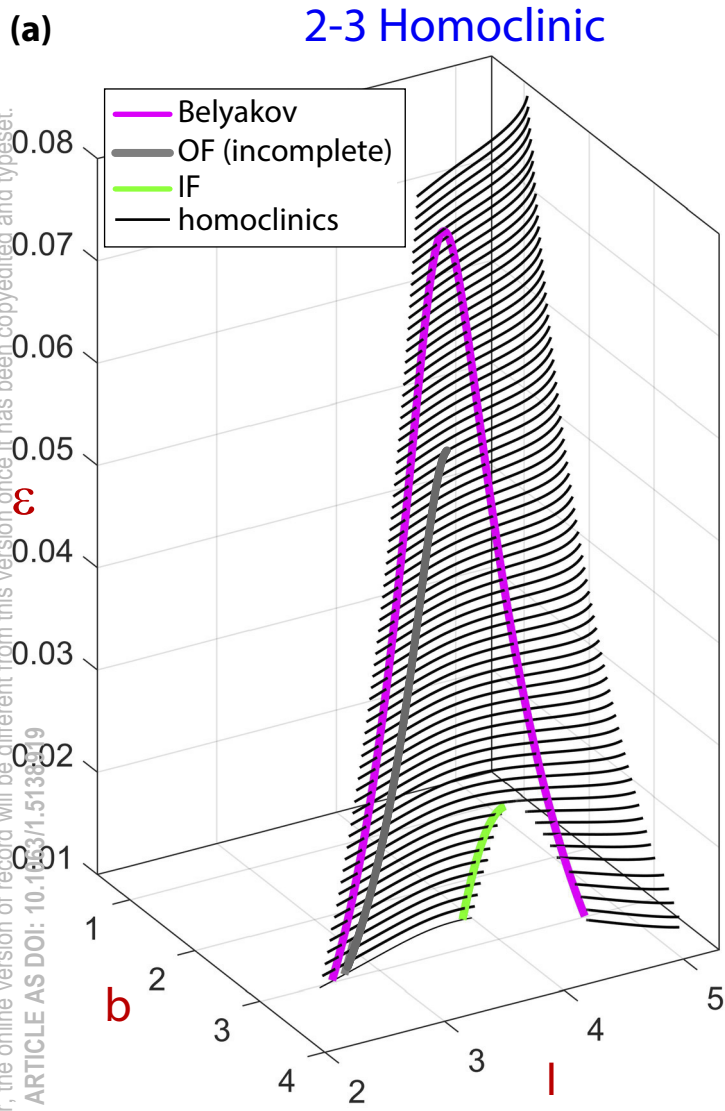
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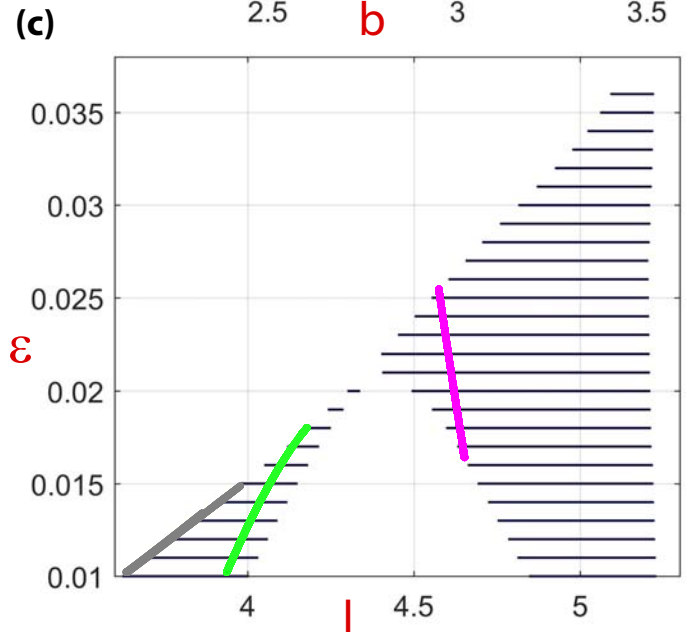
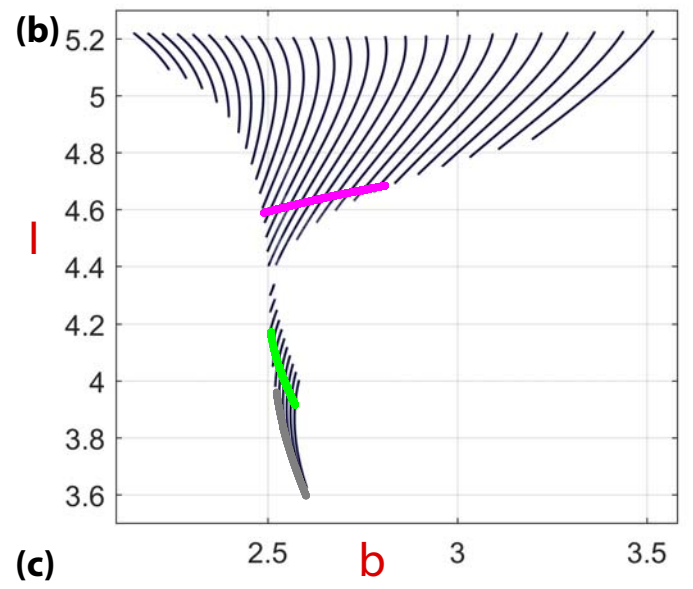
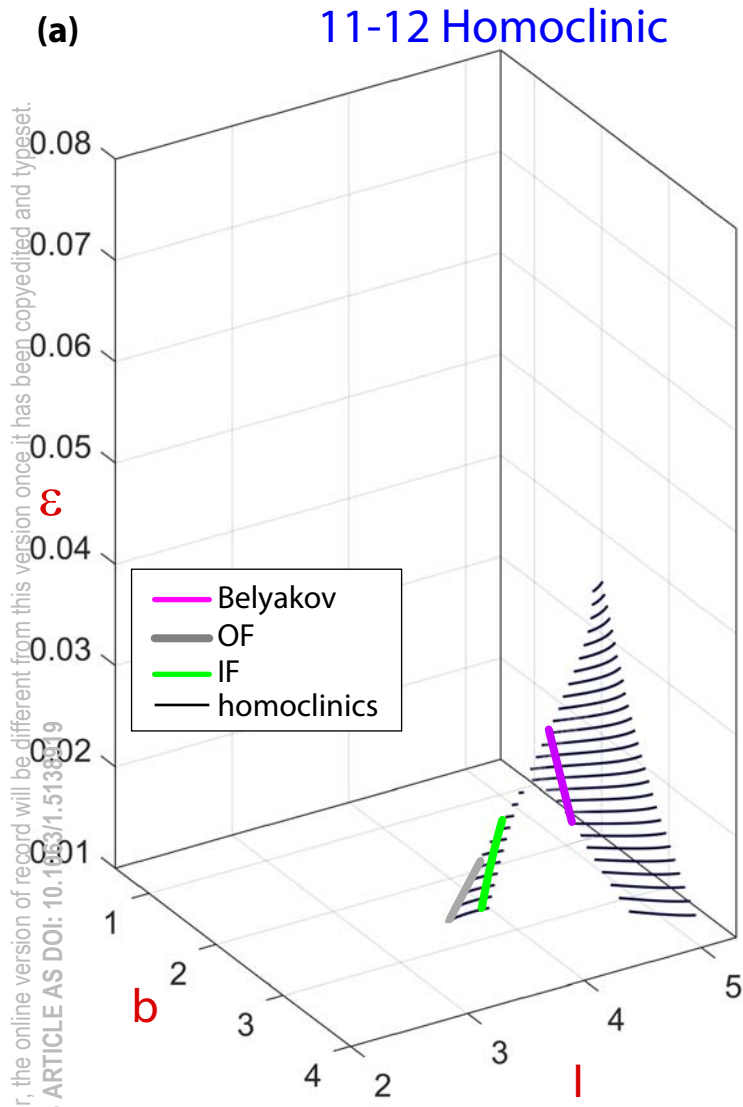
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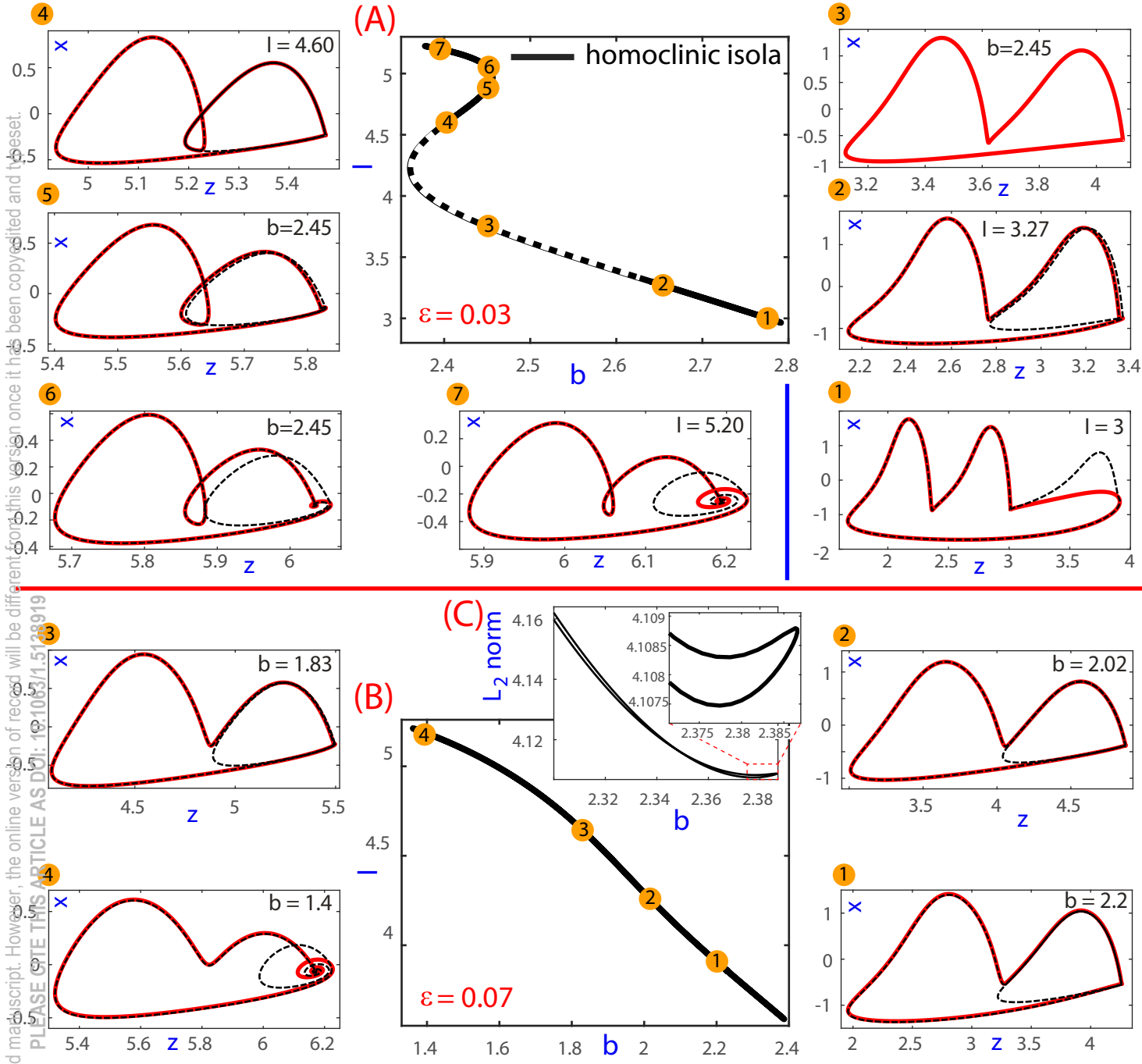




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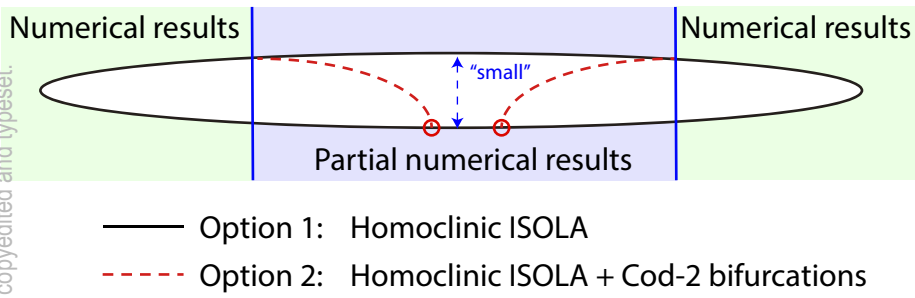
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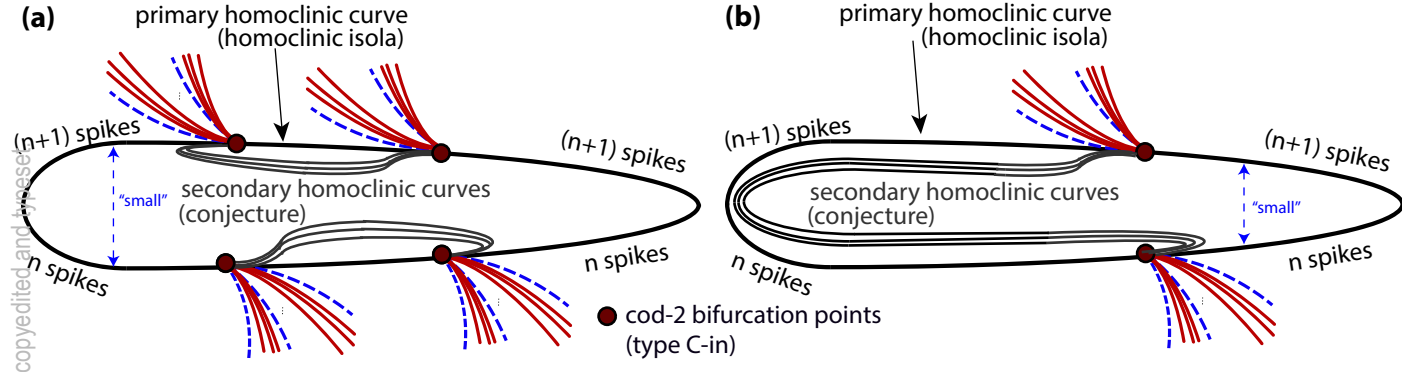


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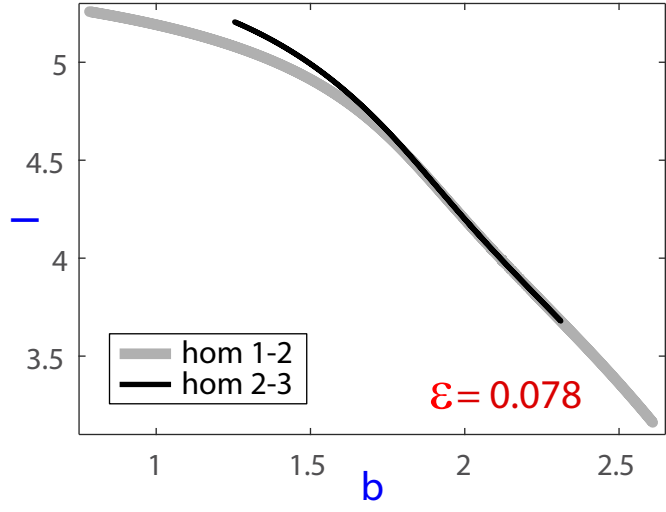
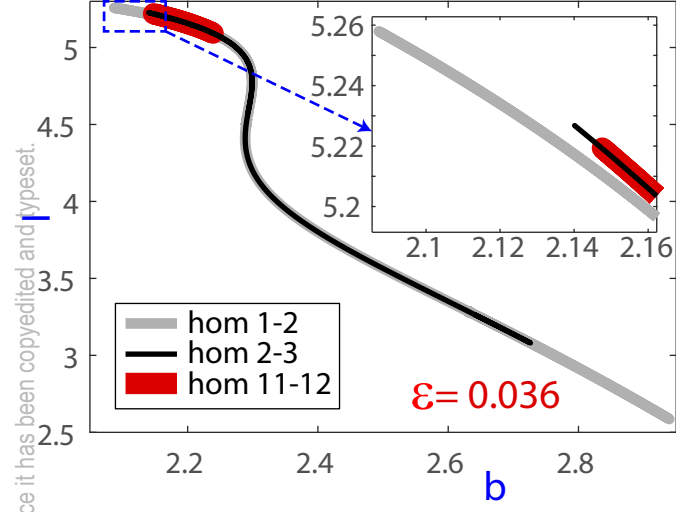
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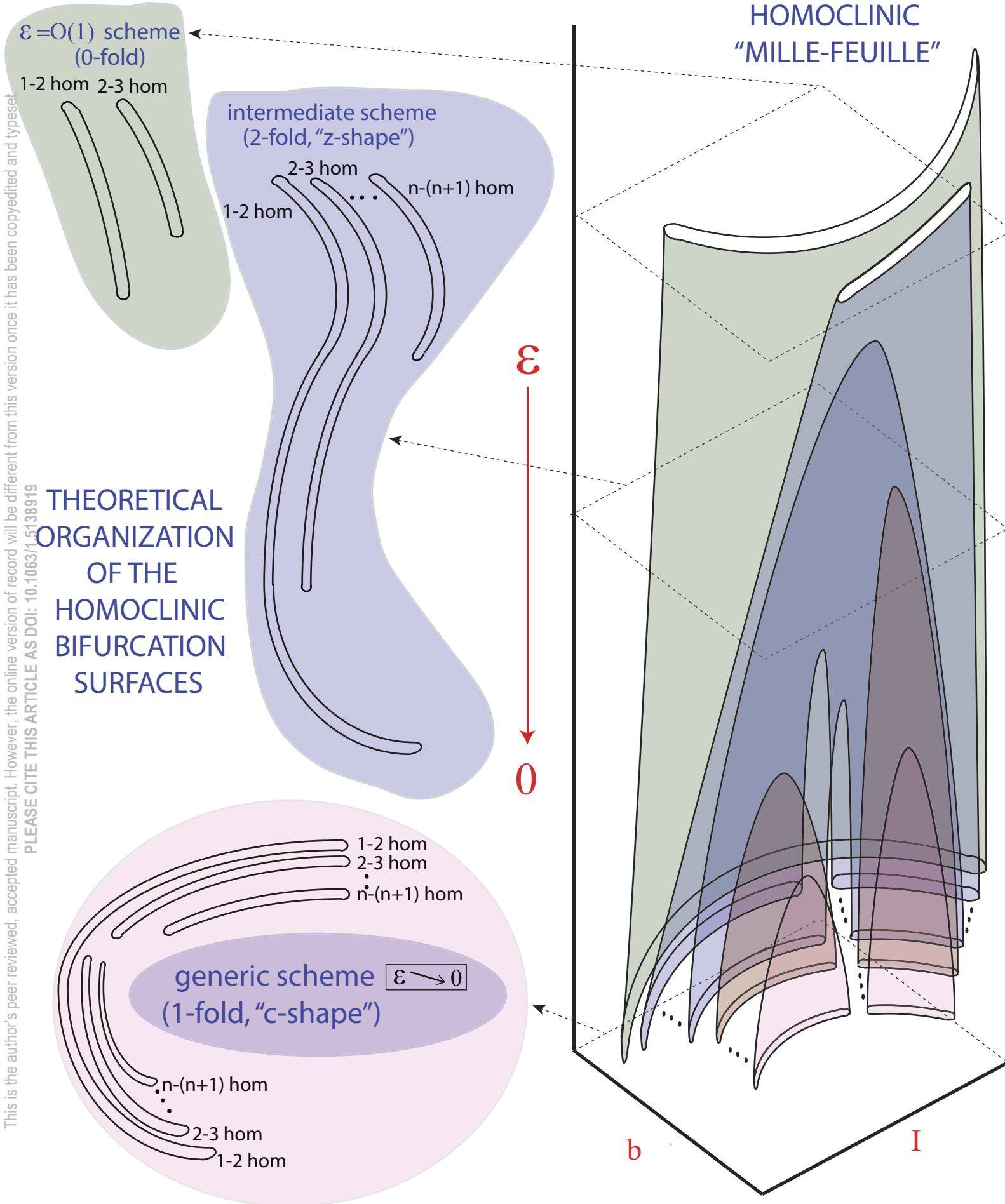


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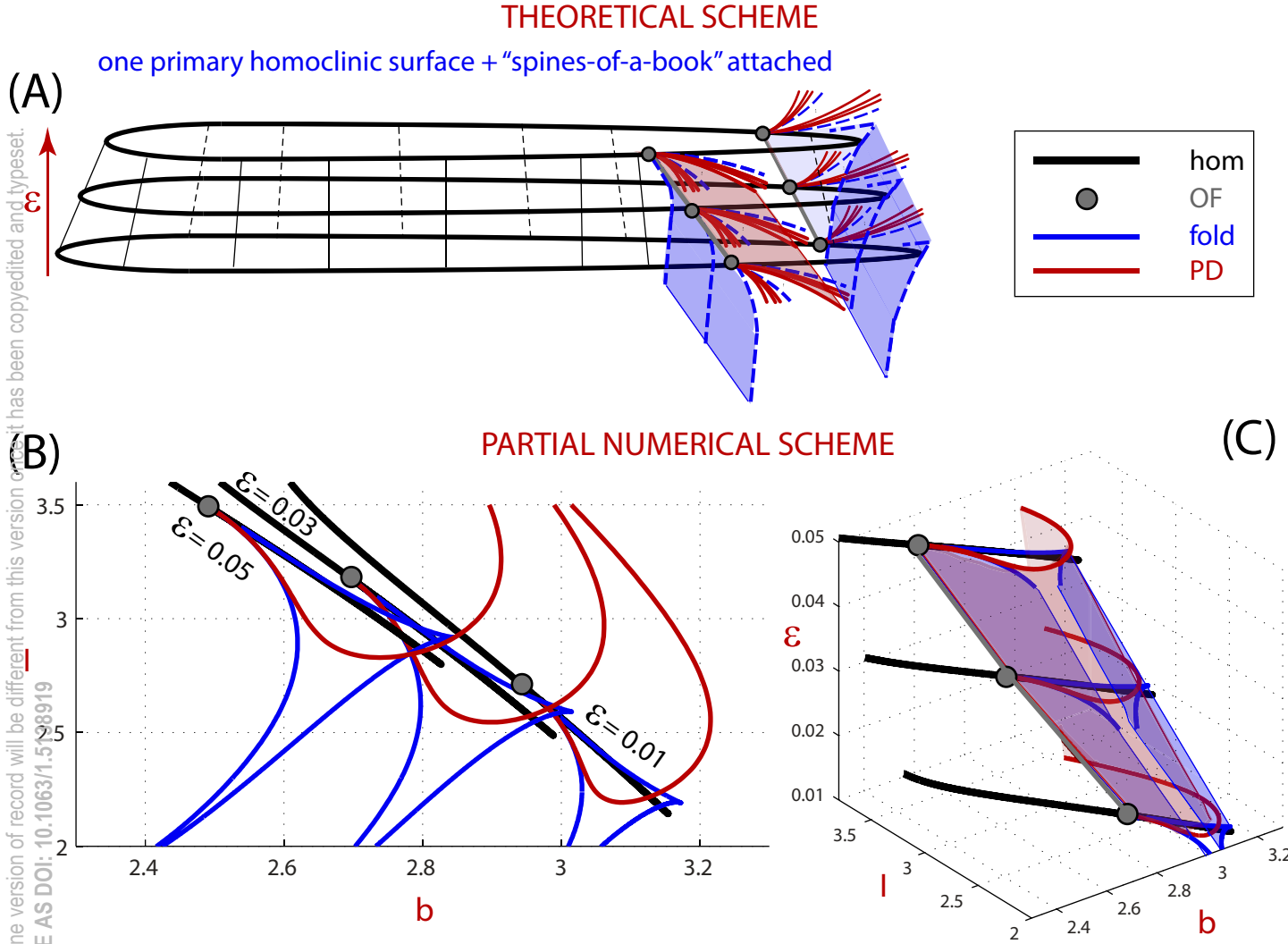


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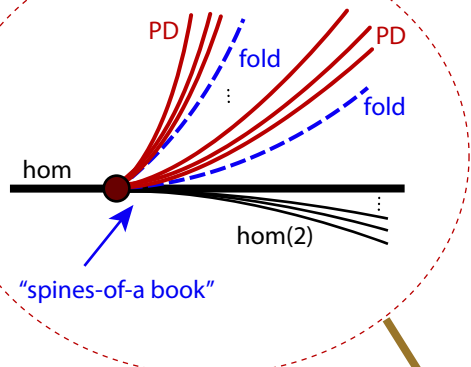


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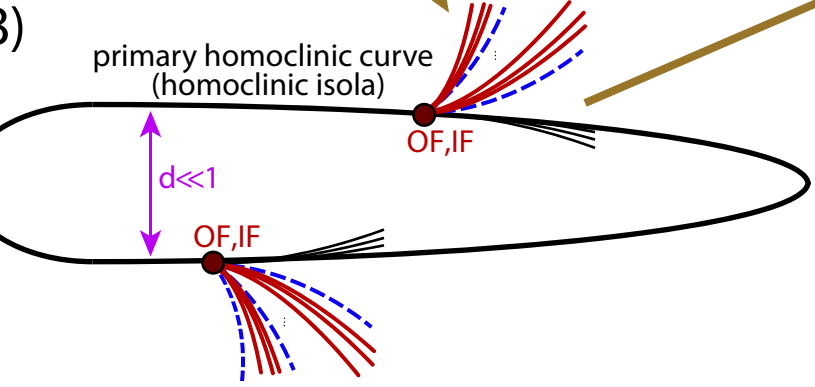


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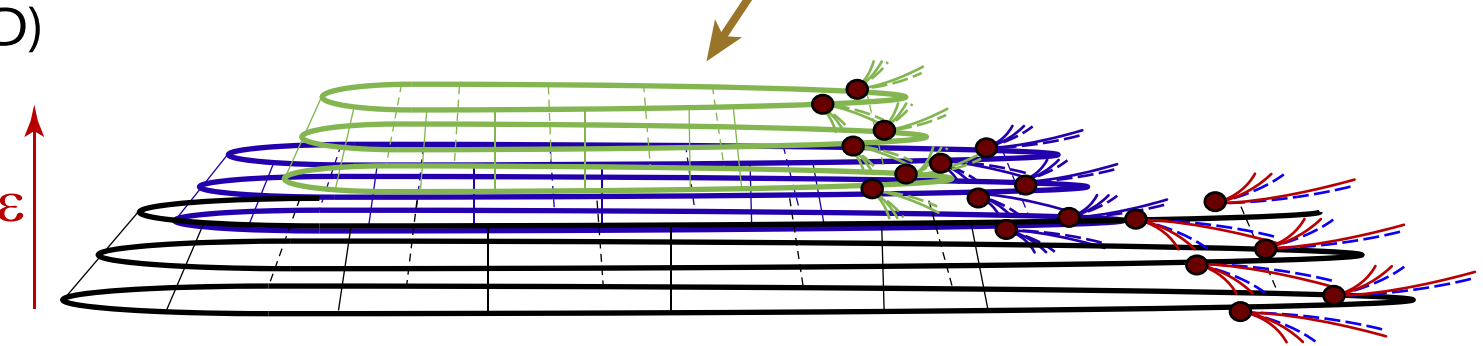
(A)



(B)



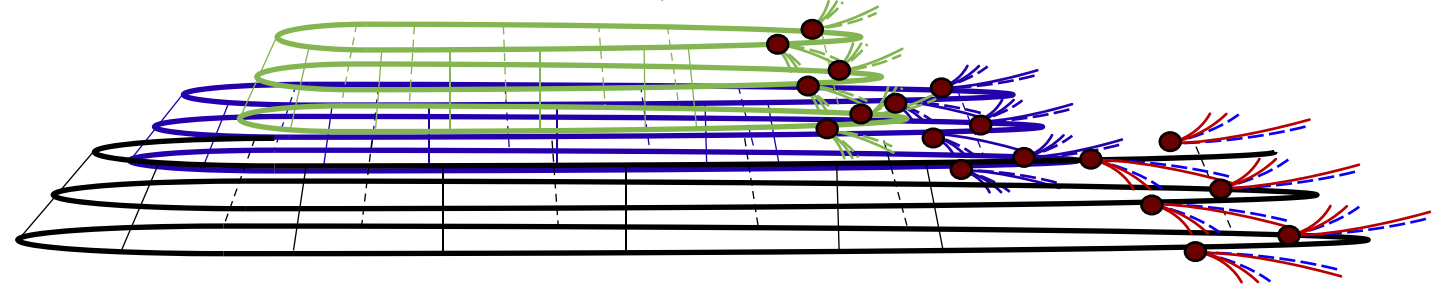
(C)



(D)

generic scheme $\varepsilon \rightarrow 0$
 (1-fold, "c-shape")

ε ↑



"mille-feuille" + "spines-of-a book"