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# Optimal Control of the Lotka-Volterra Equations with Applications

Bernard Bonnard<sup>1</sup> and Jérémy Rouot<sup>2</sup>

**Abstract**—In this article, the Lotka-Volterra model is analyzed to reduce the infection of a complex microbiote. The problem is set as an optimal control problem, where controls are associated to antibiotic or probiotic agents, or transplantations and bactericides. Candidates as minimizers are selected using the Maximum Principle and the closed loop optimal solution is discussed. In particular a 2d- model is constructed with 4 parameters to compute the optimal synthesis using homotopies on the parameters.

**Index Terms**—Lotka-Volterra equations, Optimal control, Maximum Principle, Regular synthesis, Population dynamics

The Lotka-Volterra equations is a model to study biological species interactions and comes from a generalization of the prey predator model, see [12]. In this memoir the problem is already set in the control frame since the model aims to explain the evolution of two fishing species in relation with diminution of the fishing activity during the first World War.

The system is written as the 2d-dynamics:

$$\frac{dN_1}{dt} = N_1(\lambda_1 + \mu_1 N_2), \quad \frac{dN_2}{dt} = N_2(\lambda_2 + \mu_2 N_1) \quad (1)$$

where  $N_1, N_2$  are the two species,  $N_1, N_2 \geq 0$  and  $\lambda_1, \lambda_2, \mu_1, \mu_2$  are real parameters. In the prey predator model  $\lambda_1 > 0, \lambda_2 < 0, \mu_1 < 0, \mu_2 > 0$ .

The system is conservative and can be integrated using the first integral:

$$\mu_2 N_1 + \lambda_2 \ln N_1 - (\mu_1 N_2 + \lambda_1 \ln N_2) = \text{constant}.$$

In the prey predator model, the evolution of each species in the quadrant  $N_1, N_2 > 0$  is periodic and there exist a single persistent equilibrium:  $\Omega = (K_1, K_2)$ . Moreover  $K_1, K_2$  represents the averaged population of each species on a period  $T$

$$\langle N_i \rangle = \frac{1}{T} \int_0^T N_i(t) dt = K_i, \quad i = 1, 2.$$

The effect of the fishing activity is to replace:

$$\lambda_1 \rightarrow \lambda_1 - \alpha \lambda, \quad \lambda_2 \rightarrow \lambda_2 - \beta \lambda,$$

where  $\alpha, \beta$  are the modes of destruction of each species and  $\lambda(t)$  is the control intensity.

Constant controls lead to shift the permanent equilibrium and hence to shift the averaged populations.

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More generally the model leads to consider two vector fields  $(X, Y)$  defined by (1) with different parameters and to introduce the control system:

$$\frac{dx(t)}{dt} = u(t)X(x(t)) + (1 - u(t))Y(x(t)),$$

$x = (N_1, N_2)$  and  $u \in [0, 1]$ .

The Lotka-Volterra equations can more generally described the interaction of  $n$ -species  $x = (x_1, \dots, x_n)^\top$ ,  $x_i \geq 0$ , and is given by the dynamics:

$$\frac{dx}{dt} = (\text{diag} x)(Ax + r), \quad (2)$$

where  $\text{diag} x$  is the diagonal matrix with entries  $(x_1, \dots, x_n)$ ,  $A = (a_{ij})$  is the matrix of interaction coefficients and  $r = (r_1, \dots, r_n)^\top$  is the vector of individual growth of the species. Recently based on the model of [11] of the intestinal microbiote with  $n = 11$  species, Jones et al. [6] analyzed the problem of reducing *C.difficile* infection (a pathogenic agent) using either antibiotic or fecal transplantation.

Denoting by  $X(x) = (\text{diag} x)(Ax + r)$  the  $n$ -dimensional dynamics ( $n = 11$ ) with parameters given in [11], the control system writes as:

$$\frac{dx(t)}{dt} = X(x(t)) + u(t)Y(x(t)) + \sum_{i=1}^k \lambda_i \delta(t - t_i) Y'(x), \quad (3)$$

where  $Y(x) = (\text{diag} x)\epsilon$ ,  $\epsilon = (\epsilon_1, \dots, \epsilon_n)^\top$  is the sensitivity vector to the antibiotic of the species and  $u(t)$  is a piecewise constant mapping. The second control actions is associated to jumps  $x(t_i) \rightarrow x(t_i) + \lambda v$  in the state, and  $Y'(x) = v$ , corresponding to ratio of each species in the transplantation.

Denoting by  $x_1$  the *C. Difficile* population, the optimal control problem can be set as a Mayer problem:  $\min x_1(t_f)$  where  $t_f$  is the number of days of the treatment or in a dual form: reach in minimum time  $t_f$  a specific level  $d$  of infection that is:  $x_1(t_f) = d$ .

The optimal control problem can be posed in the general frame of mixing permanent controls associated to antibiotic treatment or sampled-data controls associated to transplantations.

In both case the optimal control problem can be analyzed with an indirect scheme based on the Maximum Principle [9] in the permanent case or an adaptation in the sampled-data control case, or by a direct numerical optimization scheme.

In this article, due to space restriction we shall only analyze the effect of an antibiotic or probiotic treatment restricting to a control system of the form:

$$\frac{dx(t)}{dt} = X(x(t)) + u(t)Y(x(t)),$$

with  $x(t) \in \mathbb{R}^n$ , the set of admissible controls  $\mathcal{U}$  being the set of measurable mappings valued in  $]-1, +1[$  (for convenience we assume  $u = -1$  being associated to no treatment,  $u = +1$  to maximum dosing regimen). We consider the problem of steering  $x(0) = x_0$  to a terminal manifold  $N$  of codimension one, e.g.:  $x_1 = d$ , in minimum time.

Our analysis is based on a series of recent articles [2], [8], [3] to classify the closed loop optimal solutions in a neighborhood of the terminal manifold, using semi-normal forms for the triple  $(X, Y, N)$ , under generic assumptions. They can be globalized in the frame of polynomial systems using homotopies on the parameters.

Due to space restrictions the techniques will be presented mainly restricting to the 2d-case.

## I. THE MAXIMUM PRINCIPLE IN THE PERMANENT CASE AND THE CLASSIFICATION OF THE EXTREMALS

### A. Maximum Principle

Denote  $F(x, u) = p \cdot (X(x) + uY(x))$  and  $H = p \cdot F(x, u)$  the Hamiltonian lift defining the pseudo-Hamiltonian,  $p \in \mathbb{R}^n \setminus \{0\}$  being the adjoint vector. If  $(x(\cdot), u(\cdot))$  is optimal on  $[0, t_f]$  then there exist  $(z(\cdot), u(\cdot))$ ,  $z = (x, p)$  such that a.e.:

$$\begin{aligned} \frac{dx}{dt}(t) &= \frac{\partial H}{\partial x}(x(t), p(t), u(t)), \\ \frac{dp}{dt}(t) &= -\frac{\partial H}{\partial p}(x(t), p(t), u(t)). \end{aligned} \quad (4)$$

Moreover the optimal control satisfies a.e. the maximization condition

$$H(z(t), u(t)) = \max_{|v| \leq 1} H((z(t)), v) = M(z(t)), \quad (5)$$

where  $M((z(t)) \geq 0$  is constant.

At the final time the transversality condition is satisfies:

$$p(t_f) \perp T_{x(t_f)}^* N. \quad (6)$$

*Definition 1:* An extremal  $(z, u)$  is a solution of (4)-(5) on  $[0, t_f]$ . It is called a BC-extremal if the transversality condition (6) is satisfied. An extremal is called regular if a.e.  $u(t) = \text{sign} H_Y(z(t))$  and singular if  $H_Y(z(t)) = 0$  identically. A regular extremal is called bang-bang (BB) if the the number of switches is finite. An extremal  $(x, p, u)$  is called strict if  $p(\cdot)$  is unique up to a factor.

*2.2 Small time classification of regular extremals near the switching surface.:* One needs the following see [7] for the details.

Let  $t \rightarrow z(t)$  be a regular extremal on  $[0, t_f]$  and we denote by  $t \rightarrow \Phi(z(t)) = H_Y(z(t))$  the switching function and let  $\Phi_\varepsilon$  the switching function along a bang arc extremal with  $u = \varepsilon = \pm 1$  constant. We denote respectively by  $\sigma_+, \sigma_-$ , bang arcs with  $u = \pm 1$  and  $\sigma_s$  a singular arc, while  $\sigma_1 \sigma_2$  denotes a  $\sigma_1$  arc followed by an  $\sigma_2$  (where each arc of the sequence can be empty). We denote by  $\Sigma$  the switching surface  $H_Y(z) = 0$  and  $\Sigma'$  the subset  $H_Y(z) = \{H_Y, H_X\}(z) = 0$ . The Lie bracket of two vector fields  $Z_1, Z_2$  being computed with the convention  $[Z_1, Z_2](x) = \frac{\partial Z_1}{\partial x}(x)Z_2(x) - \frac{\partial Z_2}{\partial x}(x)Z_1(x)$ . If  $H_i(z) = p \cdot Z_i(x)$  the Poisson bracket is  $\{H_1, H_2\} =$

$dH_1(H_2) = p \cdot [Z_1, Z_2](x)$ , where  $H_2 := (\nabla_p H_2, -\nabla_p H_2)$  is the Hamiltonian vector field.

Deriving twice the switching function  $\Phi(t)$  one gets:

$$\begin{aligned} \frac{d\Phi}{dt}(t) &= \{H_Y, H_X\}(z(t)), \\ \frac{d^2\Phi}{dt^2}(t) &= \{\{H_Y, H_X\}, H_X\}(z(t)) \\ &\quad + u(t)\{\{H_Y, H_X\}, H_Y\}(z(t)). \end{aligned} \quad (7)$$

Let  $t$  be a switching time so that  $\Phi(t) = 0$  and assume that at  $z(t)$  the surface  $\Sigma'$  is regular.

*Proposition 2:* Assume that the switching time  $t$  is ordinary that is:  $\Phi(t) = 0$  and  $\frac{d\Phi}{dt}(t)$  is non zero. Then near  $z(t)$  every extremal projects onto  $\sigma_+ \sigma_-$  if  $\frac{d\Phi}{dt}(t) > 0$  or  $\sigma_- \sigma_+$  if  $\frac{d\Phi}{dt}(t) < 0$ .

*Proposition 3:* Assume that at the switching time  $t$ , the switching function  $\Phi_\varepsilon(t)$  for  $u = \varepsilon = \pm 1$  is such that  $\frac{d\Phi_\varepsilon}{dt}(t) = 0$  and both  $\frac{d^2\Phi_\pm}{dt^2}(t) \neq 0$  where the second order derivative is given by (7). Then  $z(t)$  is called a fold point and we have:

- In the parabolic case:  $\frac{d^2\Phi_+}{dt^2}(t) \cdot \frac{d^2\Phi_-}{dt^2}(t) > 0$ , each extremal near  $z(t)$  projects onto  $\sigma_\pm \sigma_\pm \sigma_\pm$ .
- In the hyperbolic case:  $\frac{d^2\Phi_+}{dt^2}(t) > 0$ ,  $\frac{d^2\Phi_-}{dt^2}(t) < 0$  it projects onto  $\sigma_\pm \sigma_s \sigma_\pm$ .
- In the elliptic case  $\frac{d^2\Phi_+}{dt^2}(t) < 0$ ,  $\frac{d^2\Phi_-}{dt^2}(t) > 0$ , every extremal is bang-bang but the number of switches is not uniformly bounded.

*Computations of the singular extremals with minimal order:* The computations is standard, see [1]. Deriving twice with respect to times  $H_Y(z(t)) = 0$  one gets

$$\begin{aligned} H_Y(z(t)) &= \{H_Y, H_X\}(z(t)) = 0, \\ \{\{H_Y, H_X\}, H_X\}(z(t)) &= 0, \\ &\quad + u_s(t)\{\{H_Y, H_X\}, H_Y\}(z(t)) = 0. \end{aligned} \quad (8)$$

Assume the generalized Legendre-Clebsch condition  $\{\{H_Y, H_X\}, H_Y\}(z(t)) \neq 0$  holds for every  $t$  then from equation (8),  $u_s(t) = u_s(z(t))$  is the dynamic feedback:

$$u_s(z) = -\frac{\{\{H_Y, H_X\}, H_X\}(z)}{\{\{H_Y, H_X\}, H_Y\}(z)}$$

and plugging such  $u_s$  in the pseudo-Hamiltonian defines the true Hamiltonian:

$$H_s(z) = H_X(z) + u_s(z)H_Y(z).$$

Hence we deduce:

*Proposition 4:* Singular extremals with minimal order  $\{\{H_Y, H_X\}, H_Y\}(z) \neq 0$  are solutions of the Hamiltonian dynamics  $H_s(z)$  restricted to the invariant surface  $\Sigma'$ :  $H_Y(z) = \{H_Y, H_X\}(z) = 0$ .

*Definition 5:* Assume that we are in the strict case. Since the true Hamiltonian is constant then the singular trajectories projections of singular extremals of minimal order are stratified according to the following:

- Hyperbolic case:  $H_X(z) \cdot \{\{H_Y, H_X\}, H_Y\}(z) > 0$ ,
- Elliptic case:  $H_X(z) \cdot \{\{H_Y, H_X\}, H_Y\}(z) < 0$ ,
- Abnormal or exceptional case:  $H_X(z) = 0$ .

1) *Construction of the optimal synthesis in a neighborhood of  $N$* : Take a point  $x_0$  which can be identified to 0. Assume that at such point the surface  $N$  is regular. We denote by  $N^\perp$  the Hamiltonian lift:  $\{z = (x, p); x \in N, p = n(x)\}$  where  $n$  is the normal to  $N$  at  $x$ . We shall assume that the cone of limit directions  $\{X \pm Y\}$  is strict and one can suppose it is contained in an half-space, so that  $n$  can be chosen assuming  $n(x) \cdot X(x) > 0$ .

If  $n(x) \cdot Y(x) \neq 0$ , then every extremal near  $N$  is determined by the transversality condition:  $u = +1$  if  $n \cdot Y > 0$  and  $u = -1$  otherwise. Switches can occur only near points such that  $Y$  is tangent to  $N$ , that is  $n \cdot Y(x) = 0$ .

The regular synthesis [5] amounts to compute in a neighborhood  $U$  of  $x_0$ , in the domain  $n \cdot X(x) < 0$  the following strata:

- The switching locus  $W$  restricting to ordinary switches with strata  $W_+, W_-$  corresponding respectively to  $\sigma_- \sigma_+$  or  $\sigma_+ \sigma_-$ , and associated to optimal policies only.
- The set  $\Sigma_s$  filled by optimal  $BC$ -singular arcs.
- The cut locus  $C$  defined as follows. Every optimal arc  $\sigma(t)$  is integrated backwards in time, that is  $\sigma(t)$  is defined on  $[t_f, 0]$  so that  $t_f < 0$  and  $\sigma(0) \in N$ . The cut locus is the closure of the set of points  $z(t_c)$ ,  $t_f < t_c < 0$  so that  $z(t)$  is not optimal beyond the time  $t_c$ . It contains the separating locus formed by the set of points where there exist two distinct minimizers reaching  $N$ .

The contribution of the series of papers [2], [8], [3] describes the time minimal syntheses for all cases of codimension  $\leq 2$  in the jet spaces of the triples  $(X, Y, N)$  at  $x_0 = 0$ . We shall describe the main application, restricting to the 2d-case for the controlled Lotka-Volterra model, to describe geometrically the main features of the time minimal syntheses.

2) *The geometric determination of the time minimal syntheses for the Lotka-Volterra model*:

3) *Determination of the collinearity locus in relation with forced permanent equilibria*: Plugging  $u = \pm 1$  leads to forced equilibria with constant dosing regimen associated to no treatment with  $u = -1$  and maximal dosing regimen with  $u = +1$ .

Hence in the  $n$ -dimensional case we introduce the collinearity locus as the one-dimensional variety defines as projection on the state space of the set:

$$\{(x_e, \lambda) \in \mathbb{R}^{n+1}; \lambda = -u_e, X(x_e) = \lambda Y(x_e)\}.$$

The constant control  $u_e$  is such that  $(x_e, u_e)$  is a forced equilibrium and it has to be feasible that is  $|u_e| \leq 1$ .

Following Volterra [12] one can choose for each dynamics  $(\text{diag}x)(Ax + r)$  dimensionless coordinates so that up to translation the dynamics takes the form  $-\text{diag}(x+1)A^*x$ , where the persistent equilibrium is identified to 0 and the spectrum of the linearized dynamics is given by  $-\sigma(A^*)$  with  $\sigma(A^*) = \{\lambda_1, \dots, \lambda_n\}$  where each  $\lambda_i$  denotes an eigenvalue, with generalized eigenspace  $E_{\lambda_i}$ .

In the 2d-case the computation of the collinearity locus is simple and is the determinantal set

$$C = \det(X(x), Y(x)) = 0.$$

Straightforward computations defines a segment  $L_1$  when restricting to the persistent quadrant:  $x_1, x_2 > 0$ . Furthermore a subsegment  $L'_1$  is defined due to the control restriction  $|u_e| \leq 1$ .

Each point of this segment determines a forced equilibrium with a corresponding spectra.

*Example 6*: Consider the conservative case described by (1) with parameters  $(\lambda_1, \lambda_2, \mu_1, \mu_2)$  and  $\Omega = (K_1, K_2)$  the persistent equilibrium. The dynamics can be set in normalized coordinates introducing  $n_i = \frac{N_i}{K_i}$  and  $n_i \rightarrow n_i - 1$  so that it takes the form:  $-\text{diag}(x+1)A^*x$ .

Choosing  $\Omega$  in the quadrant  $N_i > 0$  imposes constraints:  $\lambda_1 \mu_1 > 0$  and  $\lambda_2 \mu_2 < 0$ . One can choose the ratio  $\lambda = \lambda_2 / \mu_2$  as an homotopy parameter and consider the one-dimensional dynamics  $\lambda \rightarrow (\text{diag}x)(A(\lambda)x + r(\lambda))$  where  $\lambda$  can be restricted to a segment.

a) *Determination of the singular locus*: In the  $2d$ -case, using  $H_Y(z) = \{H_X, H_Y\}(z) = 0$ , the singular locus is the determinantal set  $\mathcal{S}$  defined by:

$$\det(Y(x), [Y, X](x)) = 0.$$

In the persistent space they formed a line passing through the origin.

For some parameters value, the collinear and singular loci intersects at a single point denoted O. The main point of this section will be to discuss the construction of the time minimal synthesis in a neighborhood of O, illustrating the applications of the concepts and techniques from [2], [8], [3]. This will lead to identify four parameters to construct the global syntheses by homotopy. The geometric schematic picture is represented on fig.1 where we have reported symbolically on the extremities of the collinear locus the two cases studied by Volterra [12], illustrating clearly the global issues.

In the  $2d$ -case, much information about the global synthesis can be deduced using the clock form one-form  $\omega$  defined outside the collinearity locus by the relations:

$$\omega(X) = p \cdot X(x) = 1, \omega(Y) = p \cdot Y(x) = 0.$$

Green's theorem allows to deduces optimality status of  $\sigma_+ \sigma_-$  vs  $\sigma_- \sigma_+$ , in different domains, observing that  $d\omega$  vanishes precisely on the singular locus.

Since Lie brackets have complicated values, the use of a semi-normal form for the actions of local changes of coordinates and feedbacks  $u \rightarrow -u$  aims to simplify the computations.

In particular, such a construction will be useful to deduce the time minimal synthesis in a neighborhood of 0 and identify the homotopy parameters to construct the global synthesis.

b) *Construction of the semi-normal form*: First of all, one can choose coordinates such that  $O = (0, 0)$  and  $Y$  is identified to the vector field  $Y = \frac{\partial}{\partial x_2}$  (this amounts mainly to choose ln-coordinates), furthermore the singular direction can be identified to the axis  $(Ox_1)$ .

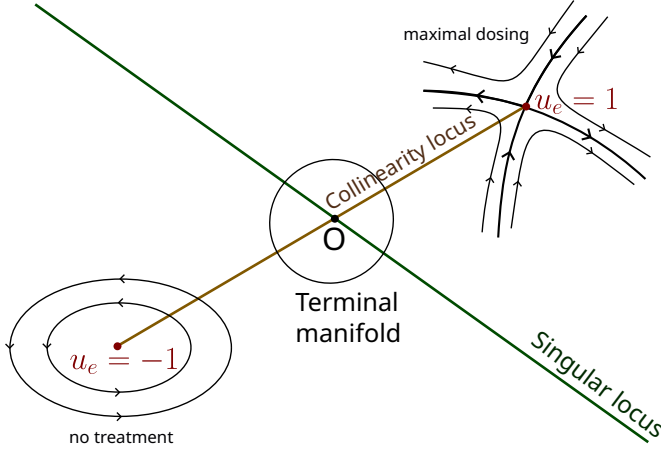


Fig. 1. Schematic representation of a case study: end-points of the collinear locus and intersection of the singular and collinear locus.

Expanding  $X$  in the jet space at  $O = (0, 0)$ , this leads to analyze the control system:

$$\frac{dx_1}{dt} = -\lambda x_1 + \alpha x_2^2, \quad \frac{dx_2}{dt} = (u - u_e),$$

with  $u_e \in ]-1, +1[$ ,  $|u| \leq 1$  and  $\alpha > 0$ .

c) *Properties of the system:* Computing Lie brackets in those coordinates shows relevant simplifications:

- $X(x) = (-\lambda x_1 + \alpha x_2^2) \frac{\partial}{\partial x_1} - u_e \frac{\partial}{\partial x_2}$ ,
- $Y(x) = \frac{\partial}{\partial x_2}$ ,
- $[Y, X](x) = -2\alpha x_2 \frac{\partial}{\partial x_1}$ ,
- $[[Y, X], Y](x) = -2\alpha \frac{\partial}{\partial x_1}$ .

Hence the singular line is given by:  $x_2 = 0$  and restricting to this line one has:

$$X(x_1) = -\lambda x_1 \frac{\partial}{\partial x_1}, \quad [[Y, X], Y](x_1) = -2\alpha \frac{\partial}{\partial x_1}.$$

Therefore for the restriction one has:

$$[[Y, X], Y](x_1) = \frac{2\alpha}{\lambda} X(x_1).$$

Then we have:

- The origin is an abnormal singular arc reduced to a point and the subarc of the line  $x_2 = 0$  is hyperbolic in  $x_1 > 0$  and the subarc is elliptic if  $x_1 < 0$ .
- The singular control along the line  $x_2 = 0$  is given by:  $u = u_e$  and is constant and strictly admissible if  $u_e \in ]-1, +1[$ .
- The collinear set is given by the parabola:  $x_1 = \frac{\alpha x_2^2}{\lambda}$ .
- The clock form is:  $\omega = \frac{dx_1}{(-\lambda x_1 + \alpha x_2^2)}$ .

Moreover for every constant control  $u = \varepsilon$ ,  $\varepsilon = \pm 1$ , the extremal system can be integrated.

One can construct a case study taking as terminal manifold  $N$  a circle centered at  $O=(0, 0)$ , with radius  $d$  intersecting the singular line at  $(\pm d, 0)$ . The time minimal synthesis outside the disk and near the two points  $(\pm d, 0)$  can be directly deduced from the classification of [3], thanks to the curvature of the terminal manifold in the chosen normal coordinates. It is represented on fig.2 and we have:

- *Top:*  $(-d, 0)$  lifts into a fold elliptic point. The singular line is time maximizing. The optimal policy is  $\sigma_+ \sigma_-$  or  $\sigma_- \sigma_+$  using the clock form and we have represented the two strata of the switching locus:  $W = W_- \cup W_+$  and there exists a cut locus  $C$ . The three curves of the stratification are ramifying at  $(-d, 0)$ .
- *Bottom:*  $(d, 0)$  lifts into an hyperbolic fold point and the time minimal synthesis is of the form:  $\sigma_- \sigma_s$  or  $\sigma_+ \sigma_s$ .

To construct the complete synthesis one must glue the two cases along the exterior of the circle and fill the interior of the disk.

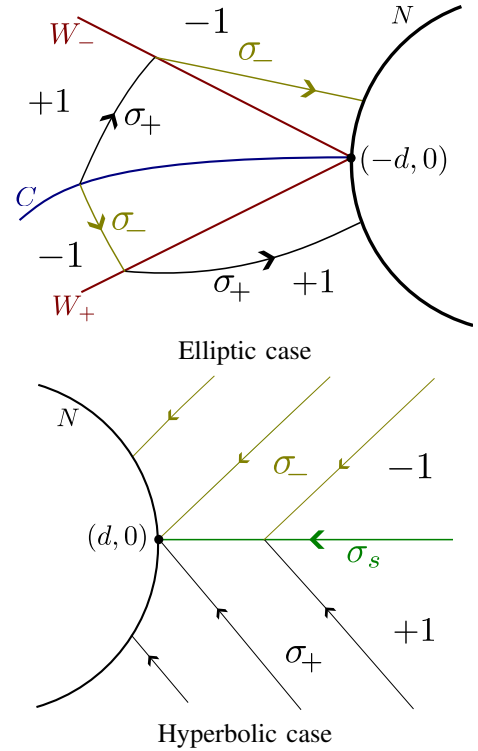


Fig. 2. 2d-syntheses near  $(\pm d, 0)$  outside the disk.

To simplify the computations, we have assume that  $u_e = 0$ . The synthesis is represented on fig.3.

Note that the singular line prolonged onto a cut locus terminating at  $(d, 0)$ . In the non symmetric case  $u_e \neq 0$ , the cut locus persists but is not coinciding with this segment.

In this synthesis we assume that the two points  $(\pm d, 0)$  lifts into fold points. But clearly we can obtain more general cases using unfolding the syntheses with parameter  $w$  by taking the system

$$\frac{dx_1}{dt} = -\lambda x_1 + w x_2 + \alpha x_2^2, \quad \frac{dx_2}{dt} = (u - u_e),$$

where  $w$  is a constant.

This leads to unfold the synthesis as represented on figs. 4-5. Note that the sign of  $w$  is not relevant in the pictures since one can change  $u$  into  $-u$  in the computations.

The switching locus  $W$  can be evaluated expanding the switching function, where the expansions are described in [3] and are in any case of order at most 2.

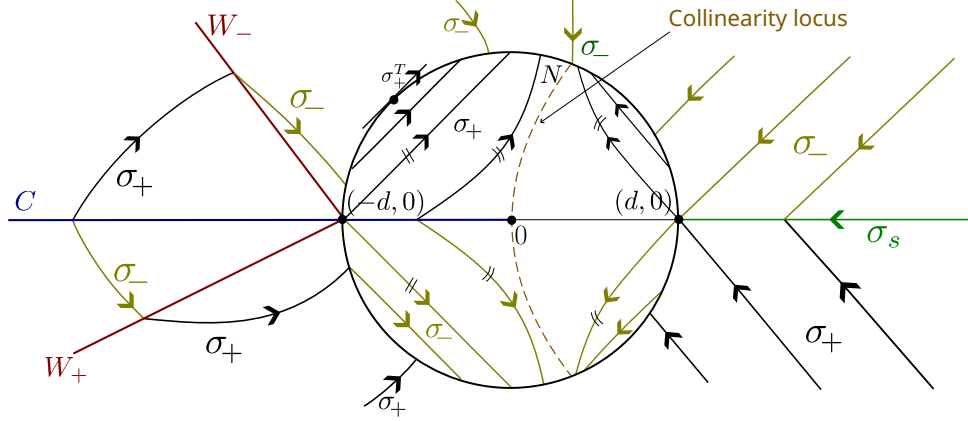


Fig. 3. Gluing hyperbolic and elliptic case with  $N$  being a circle; the symmetric case  $u_e = 0$ .

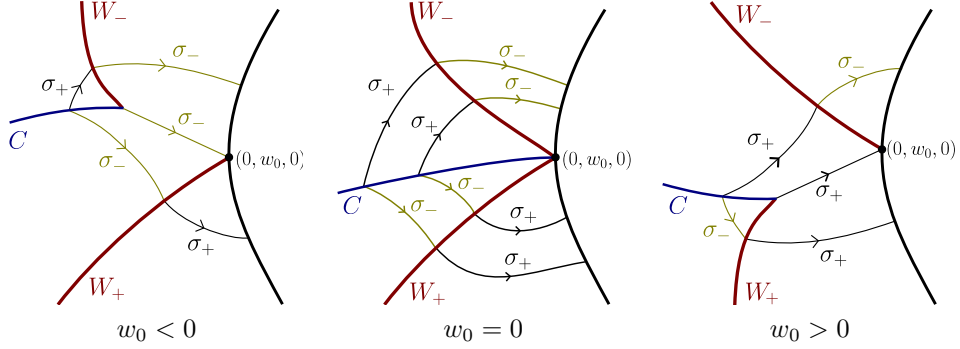


Fig. 4. Unfolding with parameter  $w_0$  in the elliptic case..

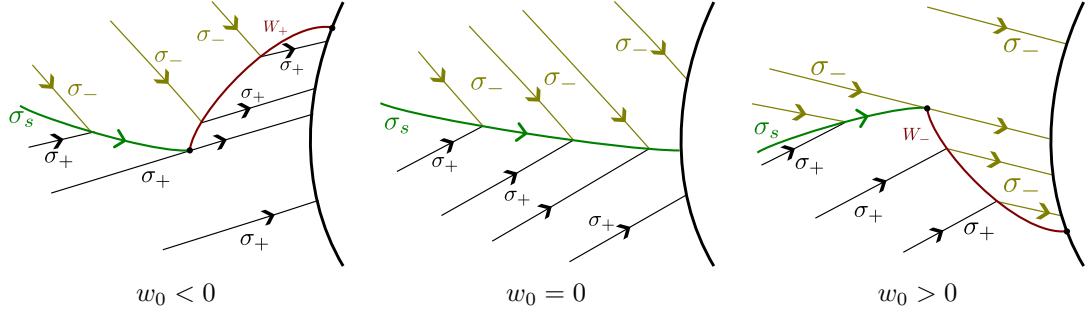


Fig. 5. Unfolding with parameter  $w_0$  in the hyperbolic case.

*Conclusion:* Our study shows the main features to compute time minimal syntheses in different neighborhood of  $O$  and with different terminal manifolds. The main singularity is the interaction between the collinearity and the singular loci. Different cases can be analyzed gluing different syntheses. In particular the detailed computations show the role of the singular locus to extend the synthesis for large times. We have introduced four homotopy parameters describing the main features of the geometric construction.

#### APPENDIX

In this appendix we present direct computations on the  $2d$ -model vs the use of the semi-normal form. To simplify the notations we note  $(x, y)$  the  $2d$ -coordinates so that one

has:

$$X = (x(r_1 + a_{11}x + a_{12}y), y(r_2 + a_{21}x + a_{22}y))^T,$$

$$Y = (x\varepsilon_1, y\varepsilon_2)^T.$$

Using  $\ln$ -coordinates it takes the form:

$$X = ((r_1 + a_{11}e^x + a_{12}e^y), (r_2 + a_{21}e^x + a_{22}e^y))^T,$$

$$Y = (\varepsilon_1, \varepsilon_2)^T.$$

Lie brackets are invariant and can be computed in such coordinates which simplify the calculations since the vector field  $Y$  becomes constant.

Moreover one can impose in the class two geometric normalizations to clarify the analysis.

Normalizations:

- One can suppose that the persistent equilibrium is  $\Omega = (1, 1)$ .
- One can assume that the persistent singular locus is the line:  $y = x$ .

This leads respectively to:

$$r_1 = -(a_{11} + a_{12}), r_2 = -(a_{21} + a_{22}), \quad (9)$$

and

$$\varepsilon_1(\varepsilon_2 a_{11} - \varepsilon_1 a_{21}) = \varepsilon_2(\varepsilon_1 a_{22} - \varepsilon_2 a_{12}). \quad (10)$$

Lie brackets are given by:

$$\begin{aligned} [X, Y] &= (x(\varepsilon_1 a_{11} x + \varepsilon_2 a_{12} y), y(\varepsilon_1 a_{21} x + \varepsilon_2 a_{22} y))^T, \\ [[Y, X], Y] &= (-x(\varepsilon_1^2 a_{11} x + \varepsilon_2^2 a_{12} y), -y(\varepsilon_1^2 a_{21} x + \varepsilon_2^2 a_{22} y))^T, \end{aligned}$$

the Lie bracket  $[[X, Y], X]$  is more complex and takes in ln-coordinates the form:

$$\begin{aligned} [[Y, X], X] &= ((\varepsilon_1 a_{11} e^x (r_1 + a_{12} e^y) + \varepsilon_2 a_{12} e^y (r_2 + a_{21} e^x) - a_{11} e^x \varepsilon_2 a_{12} e^y - a_{12} e^y \varepsilon_1 a_{21} e^x), (\varepsilon_1 a_{21} e^x (r_1 + a_{12} e^y) + \varepsilon_2 a_{22} e^y (r_2 + a_{21} e^x) - a_{21} e^x \varepsilon_2 a_{12} e^y - a_{22} e^y \varepsilon_1 a_{21} e^x))^T. \end{aligned}$$

One introduces the following determinants:

$$\begin{aligned} D &= \det(Y, [[Y, X], Y]), \\ D' &= \det(Y, [[Y, X], X]), \quad D'' = \det(Y, X). \end{aligned}$$

The generalized Legendre-Clebsch condition holds if along the singular line  $y = x$ ,

$$D = xy[\varepsilon_1^2 x(\varepsilon_2 a_{11} - \varepsilon_1 a_{21}) + \varepsilon_2^2 y(\varepsilon_2 a_{12} - \varepsilon_1 a_{22})]$$

is non zero.

This gives restricting to  $y = x$ ,

$$\begin{aligned} \frac{D}{xy} &= xC, \\ C &= \varepsilon_1^2(\varepsilon_2 a_{11} - \varepsilon_1 a_{21}) + \varepsilon_2^2(\varepsilon_2 a_{12} - \varepsilon_1 a_{22}) \neq 0. \end{aligned}$$

Using the normalization condition (10) we get the condition

$$(\varepsilon_1 \varepsilon_2 - \varepsilon_2^2)(\varepsilon_1 a_{22} - \varepsilon_2 a_{12}) \neq 0.$$

The singular control along the singular line  $y = x$  is given by:

$$u_s = -\frac{D'_{|y=x}}{D_{|y=x}}.$$

Computing  $D'$  restricted to  $y = x$  leads to introduce the coefficients:

$$\begin{aligned} A &= \varepsilon_1 \varepsilon_2 a_{11} r_1 + \varepsilon_2^2 a_{12} r_2 - \varepsilon_1^2 a_{21} r_1 - \varepsilon_1 \varepsilon_2 a_{22} r_2, \\ B &= \varepsilon_1 \varepsilon_2 a_{11} a_{12} + \varepsilon_2^2 a_{12} a_{21} - \varepsilon_2^2 a_{11} a_{12} - \varepsilon_1 \varepsilon_2 a_{12} a_{21} - \varepsilon_1^2 a_{21} a_{22} - \varepsilon_1 \varepsilon_2 a_{21} a_{22} + \varepsilon_1 \varepsilon_2 a_{21} a_{12} + \varepsilon_1^2 a_{22} a_{21}. \end{aligned}$$

Hence the first component (projecting on the  $x$ -axis) of  $-u_s Y$  restricting to the singular line  $y = x$  takes the form

$$-\frac{(A + Bx)}{C} \varepsilon_1 x.$$

It has to vanishes at  $x = 1$ , so that  $B = -A$ . The derivative at  $x = 1$  is  $\frac{-\varepsilon_1(A+2B)}{C} = \frac{\varepsilon_1 A}{C}$ .

Similarly at  $\Omega = (1, 1)$ ,  $X$  has to vanishes, which corresponds to (9) and the derivative at  $x = 1$  is  $-r_1$ .

Hence the dynamics along the singular line at  $x = 1$  is regular if

$$-r_1 + \varepsilon_1 \frac{A}{C} \neq 0. \quad (11)$$

Note that we can reverse the orientation on the singular line changing in the same category  $X$  into  $-X$ .

In particular one deduces the following:

*Theorem 7:* Under regularity conditions previously described, the singular flow along the singular line belongs to the one dimensional Lotka–Volterra form:  $\frac{dx}{dt} = x(r + ax)$  and at the persistent equilibrium point the eigenvalue of the linearized dynamics is given by  $-r_1 + \varepsilon_1 \frac{A}{C}$ .

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